FACTORS AFFECTING ALPINE GRASS SEED GERMINATION IN RELATION TO THEIR POTENTIAL USE IN RECLAMATION[1]

by

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Abstract. Poa alpina L. seeds germinated best under darkness and 16/8 h cycles of 22/15°C temperature while Agropyron latiglume L. seeds needed a 29/22°C regime and darkness for best germination. Rapid germination in both species occurred within a narrow range of temperature conditions. Light and suboptimal temperature conditions appeared to have an inhibitory effect on seed germination during the initial period of imbibition. Germination inhibition through external factors (secondary dormancy) and the presence of primary dormancy in the nursery-grown seeds may be their adaptation to extremely stressful alpine environments. This and the differences among populations for seed germination in both species are encouraging for the breeding program aiming at selecting genotypes with rapid germination while maintaining adaptation to stressful environments.

Additional Key Words: effect of temperature, light, population, seed germination, alpine grasses.

Introduction

The objectives of the native grass breeding program at the Alberta Environmental Centre are to develop cultivars suitable for reclamation of alpine disturbances and rangeland improvement in the eastern slopes of the Rocky Mountains. Achievement of both objectives depends on proper germination and stand establishment.

Germination and dormancy responses of plants have been the subject of extensive research. However, alpine species have received little attention worldwide, perhaps because of their relative unavailability and minor economic importance. Bliss (1958, 1962), Amen (1964, 1966), Bonde and Foreman (1964), Sayers and Ward (1966) and Clebsch and Billings (1976) studied seed germination of alpine plants

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mainly for academic interest. In most of these studies, germination of different alpine species was compared using seeds collected from different geographical areas at various times. Therefore, the results of the germination experiments may have been confounded by the effect of the environment under which the seeds were produced (McCullough and Shorpshire 1970; Urbanska and Schutz 1986). The experiments also ignored the presence of genotypic differences in seed germinability among populations within a species.

Germination capacity of commercially available rangeland grass seed is strongly influenced by temperature (McGinnes 1960; Tadmor et al. 1969; Hsu et al. 1985). Germination of several grasses was better at alternating temperatures than at constant temperatures (Stubbendieck and McCully 1972; McElgunn 1974; Harty and Butler 1975). However, some range grasses demonstrated similar germination under the two conditions (Ellern and Tadmor 1967; Young et al. 1981).

Light is known to have positive, negative or no influence on seed germination in different species and it may interact with temperature, making seed germination sensitive to light at certain temperatures but not at others (Koller et al. 1962; Mayer and Paljakoff-Mayber 1963). For example, Clebsch and Billings (1976) observed dark stimulated germination in Trisetum spicatum populations originating in the Rocky Mountains.

Some alpine and subalpine populations of alpine bluegrass collected from the Alberta Rocky Mountains exhibited variability in and adaptation to low temperature regimes for seed production (Hermesh and Acharya 1987). Clebsch and Billings (1976) reported that T. spicatum seeds from lower latitudes reached maximum germination at higher temperatures than those from higher latitudes. However, the data presented for Alberta material only show differences among seeds which originated in different parts of the Rocky Mountains.

In many alpine and subalpine habitats moisture conditions favorable for seed germination may only be present for periods of a few weeks (Sayers and Ward 1966). Therefore, genotypes capable of rapid seed germination might establish better than genotypes with slower rates.

The objectives of the present experiments on alpine and subalpine Poa alpina (alpine bluegrass) and Agropyron latiglume (broad glumed wheatgrass) populations were to determine (1) the effect of temperature and light, and their interaction, on seed germination while seeking the optimal conditions for this process, (2) the presence of variation among populations within a species for germinability, and (3) the presence of seed dormancy.

Materials and Methods

In the summers of 1984 and 1985, collections of P. alpina and A. latiglume were made from 318 sites scattered over the Rocky Mountains of Alberta. Ten tussocks of each grass were collected at random from each site (5 m in radius). For the present experiments, tussocks from five sites were used (Table 1). Sites 18 and 19 were in the alpine ecoregion, characterized as the zone above tree line, elevation 2200 m. The major ecological factors limiting plant survival and growth in this region are strong winds, summer coolness and frequent freezing temperatures during the warmest months (Strong and Leggat 1981). Sites 22, 23 and 42 were in the subalpine ecoregion, which is an altitudinal vegetation zone bounded above by the alpine, and below by the montane and aspen parkland ecoregions. It has a cordilleran climate, less severe than the alpine ecoregion, with cold, snowy winters and cool, showery summers (Strong and Leggat 1981). Collected tussocks were transported and nurtured as described earlier (Hermesh and Acharya 1987). The tussocks were then acclimatized outside for two weeks in pots before being transplanted to the Alberta Environmental Centre collection nursery at Vegreville, 100 km east of Edmonton. The nursery grown seeds of four morphologically homogeneous tussocks from each site were bulked to represent the population from that site for the germination experiments.

Mature seeds of P. alpina populations Poal 18, Poal 22 and Poal 23 and A. latiglume Agla 18, Agla 19 and Agla 42 (Table 1) were harvested during the last two weeks of June 1986. Seed set and development were mostly irregular (wild type), necessitating selection of well developed and undamaged seeds for experimentation.

Twenty five surface sterilized seeds from each population, constituting a replication, were placed into 9 cm petri dishes on two sheets of Whatman No. 40 filter paper. Starting on October 7, 1986, distilled water was added as necessary during incubation at 36/36, 36/29, 29/22, 22/22, 22/15, 15/8, 8/8 and 8/1°C day/night temperature regimes in germination chambers. Within each temperature regime the light treatment was provided by a 16 h photoperiod with an intensity of about $15\mu EM^{-2}S^{-1}$. The dark treatment was provided by covering the petri dishes with disposable aluminum-foil casserole pans. Within a germination chamber, temperature conditions varied considerably. To reduce the effect of such variability the light and dark treated

Table 1. Origin, summer[†] temperature conditions and population designations of the tested tussocks.

Site	Location	Elev. (m)	Mean daily summer Max. temp.	Min. temp.	% Chance of frost	Extreme low temp.	GDD[‡] above 0°C	Population designation Poal[§]	Agla
18	Sugar Loaf Mtn.	2510	13.4	3.2	80	-13.3	805	-	Agla 18
19	Sugar Loaf Mtn.	2500	13.4	3.2	80	-13.3	805	Poal 19	Agla 18
42	Hail Stone Butte	2150	14.9	4.2	33	- 9.4	904	-	Agla 42
22	Sugar Loaf Mtn.	2040	15.2	5.5	33	- 6.7	973	Poal 22	-
23	Sugar Loaf Mtn.	1550	17.2	6.4	33	- 6.0	1092	Poal 23	-

[†] June-August data based on climatic normals (Canada, Atmospheric Environment Service, 1982);

[‡] GDD = Growing degree days.

[§] Poal = Poa alpina; Agla = Agropyron latiglume.

dishes of every population were randomized in a tray and the trays representing four replications were randomized within a chamber constituting a temperature regime. Relative humidity was maintained at about 90%. The dishes were examined under green light, to avoid light exposure of dark treated seeds, every Monday-Wednesday-Friday till the end of the sixth week. Seedlings with distinct radicles were considered germinated and were removed from the petri dishes. At the end of six weeks the nongerminated seeds were treated with 100 ppm gibberelic acid and incubated under darkness and 16/8 h cycles of 22/15°C for twelve more weeks to test the viability. Using the same method and seed material, another germination test was conducted in the fall of 1987. Cumulative germination percentages at the end of every week were arcsin transformed, before analysis of variance (ANOVA) was carried out using the model in Table 2. Germination index (GI) indicating relative rate of germination for different treatments was calculated by using the formula

$$\mathrm{GI} = \frac{\Sigma\ (\text{No. of seeds germinated x No. of days})}{\text{total number of seeds germinated}}$$

A protected 5% least significant difference (LSD) was used for comparison of cumulative germination and germination index after 7, 14, 21, 28 and 42 days of imbibition.

Results

P. alpina and A. latiglume seeds did not germinate at the 36/36 temperature regime during 42 days of imbibition. However, removal of these seeds to a dark 22/15 regime

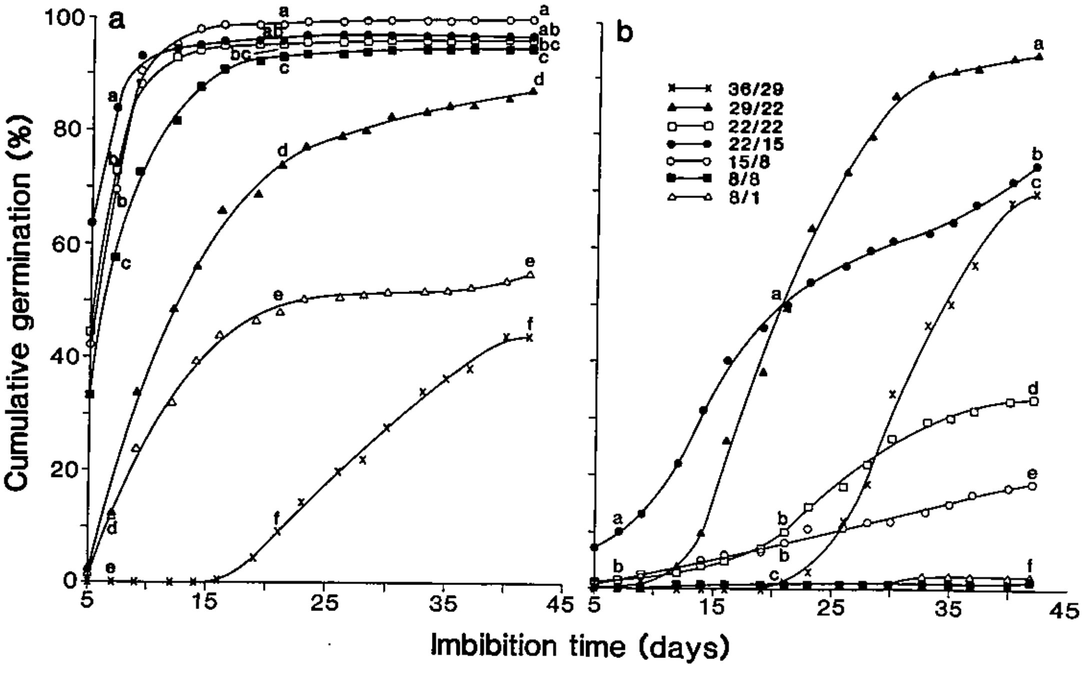

Figure 1. Influence of temperature on cumulative germination of (a) P. alpina, (b) A. latiglume. Points indicated by different letters at 7, 21 and 42 days of imbibition are significantly different (LSD, 5%).

resulted in 25% germination within 90 days. For *P. alpina* maximum germination occurred within 30 days of imbibition in all but 36/29, 29/22, and 8/1 temperature regimes (Figure 1a). At these regimes germination was occurring even at the end of the 6th week. At the 36/29 regime, germination started after two weeks of imbibition and increased steadily to reach 45% by the 40th day. The 22/15 temperature regime produced significantly higher total germination than the other regimes during the first week of imbibition. After that germination was similar for the 22/15 and 15/8 temperature regimes where 90% germination occurred within the initial 10 days of imbibition. Maximum total germination (95%) in *A. latiglume* was observed at the 29/22 temperature regime after 42 days of imbibition (Figure 1b). However, for the initial 19 days the 22/15 regime produced significantly greater total germination than the 29/22 regime. The only other regime where germination for this species crossed 60% at the end of six weeks was 36/29. In the 36/29 regime there was no germination till the 19th day. GI calculated over the six-week period indicated a highly significant temperature effect on both the grass species (Table 2).

Significantly higher cumulative germination occurred under darkness than under the 16 h photoperiod during the first 21 and 14 days of imbibition in *P. alpina* and *A. latiglume*, respectively (Figure 2). In the latter case the effect of light reversed after the 30th day of imbibition. Light had significant effect on GI during the initial two weeks for *P. alpina* and during the first two weeks and the 6th week of imbibition for *A. latiglume* (Table 2).

Table 2. Sources of variation, degrees of freedom and probability of obtaining as large an F value for germination index calculated after 14, 28, and 42 days of imbibition for each species.

Source	df	Poal			Agla		
		GI14	GI28	GI42	GI14	GI28	GI42
Replications (years)	1	NS	NS	NS	NS	NS	NS
Temperature	7	*	***	**	*	**	**
Error (a)	7						
Light	1	*	NS	NS	*	NS	*
Temperature x light	7	*	NS	NS	NS	NS	NS
Error (b)	8						
Population	2	*	*	**	NS	**	**
Temperature x population	14	NS	***	***	*	***	***
Light x population	2	NS	NS	NS	NS	NS	NS
Temperature x light x population	14	*	NS	NS	NS	NS	**
Error (c)	32						
Sampling Error	288						
Total	383						

***P=0.001; *P=0.05; NS=Not significant.

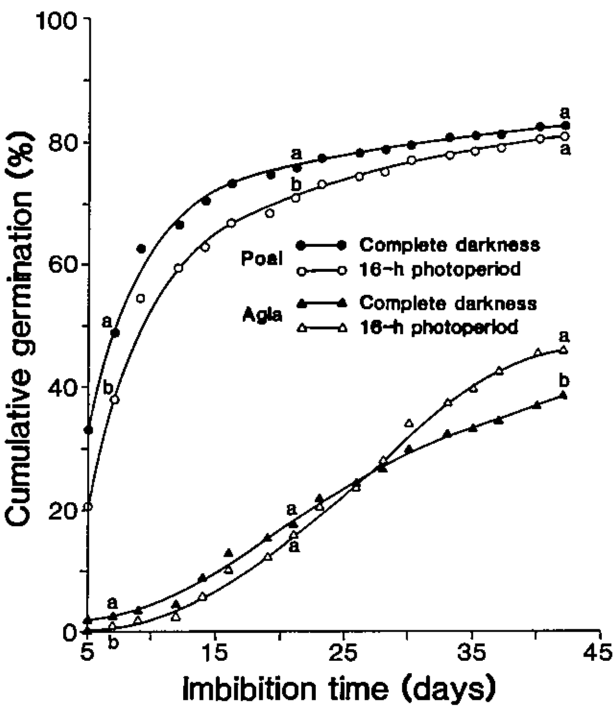

Figure 2. Influence of light on cumulative germination of P. alpina and A. latiglume. Points indicated by different letters at 7, 21 and 42 days of imbibition are significantly different (ANOVA, P = 0.05).

Cumulative germination of Poal 22 was significantly greater than the other two P. alpina populations (Poal 18 and Poal 23) initially (Figure 3). After three weeks of imbibition the three populations had similar germination. By day 42 the total germination of Poal 23 was significantly greater than Poal 18. Seeds of Agla 18 germinated significantly better than the Agla 19 and Agla 42 after 21 days of imbibition (Fig. 3). By day 30 the three populations differed significantly from each other. A significant effect of population on GI occurred during all six weeks in P. alpina and last four weeks in A. latiglume (Table 2). Significant population x temperature, population x temperature x light interactions occurred in both grass species GI (Table 2).

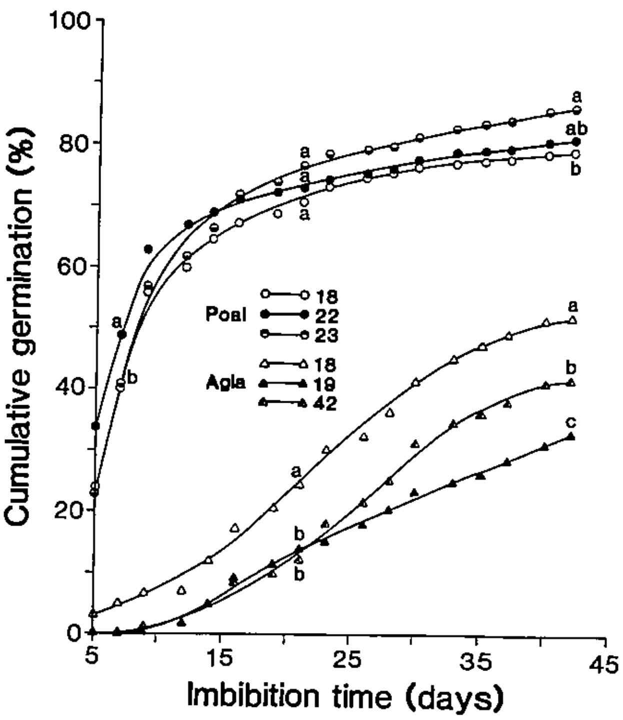

Figure 3. Influence of population on cumulative germination of P. alpina and A. latiglume. Points indicated by different letters at 7, 21 and 42 days of imbibition are significantly different (LSD, 5%).

Discussion

Poa alpina and Agropyron latiglume seed germination was strongly influenced by temperature and the optimum temperatures were 22/15 and 29/22°C, respectively. Marked effects of temperature on forage grass seed germination were earlier observed by McGinnes (1960), Tadmore *et al*. (1969); and Hsu *et al*. (1985). No germination at the 36/36 regime and significantly lower total and rate of germination at the 36/29 regime than 29/22 regime after 42 days indicates a threshold germination temperature lower than 36°C for these grasses. This is in contrast to the findings of Hsu *et al*. (1985) where some warm season forage grasses germinated better at 36°C than at lower temperatures. Low threshold germination temperature may be associated with their adaptation to colder high elevation environments. This suggests that poor emergence may result from seeding these into dark mineral oberburden during midsummer when mid day temperatures can reach above 40°C.

The optimum temperatures of 22/15 and 29/22 for P. alpina and A. latiglume germination, respectively, are similar to those that give the best seed germination in many cultivated species at low elevations (Sayers and Ward 1966; Hsu et al. 1985). This indicates suitability of these nursery-grown seeds for low elevation propagation.

For P. alpina seed germination, the effect of the constant temperature regime (22/22) was similar to the fluctuating temperature regime (22/15). This was also observed in range grasses like bluebunch and beardless wheatgrass (Ellern and Tadmor 1967; Young et al. 1981). However, fluctuating temperatures (22/15) had a marked positive effect over constant temperatures (22/22) on A. latiglume seed germination as was observed in some warm and cool season grasses (Stubbendieck and McCully 1972; McElgunn 1974; Harty and Butler 1975; and Williams 1983). In general, P. alpina seeds germinated well over a wider range of temperatures than A. latiglume seeds.

Light had a significant effect on alpine grass seed germination. Poa alpina seeds germinated better in darkness than under 16 h photoperiod unlike P. annua, P. trivialis and Deschampsia caespitosa where light has a positive effect (Williams 1983). The seeds of A. latiglume germinated more and faster during early imbibition in darkness. However, final germination under the 16 h photoperiod exceeded germination in darkness. Such an effect of light and darkness was also observed in alpine T. spicatum by Sayers and Ward (1966). Early loss of seed dormancy under darkness caused by burial may be an adaptation of plants growing in fluctuating alpine conditions. Rapid loss of dormancy in seeds that imbibe water while on the surface receiving light, particularly at suboptimal tempera- tures, may lead to early death of seedlings in the unstable alpine environment. To avoid such consequences seeds exposed to light probably after-ripen slowly allowing germination only after a prolonged exposure to higher temperatures.

In P. alpina and A. latiglume the temperature regimes at which dark and light treatments had the biggest difference in seed germination were 8/8 and 22/22, respectively. The light and dark treatments had the least influence on germination at optimum temperature regimes for the two species. However, for rapid initial germination the recommendation is to use optimum temperature conditions for the species and complete darkness during imbibition. Faster germination in darkness also suggests that seed drilling will be more successful than broadcasting while establishing field plots.

Gradual germination of mature seeds after two months of harvest under optimal germination conditions indicates the presence of primary seed dormancy in the two test species. Faster germination of P. alpina seeds, 15 days to 90%, than the A. latiglume, 35 days to 90%, demonstrates a shorter after-ripening period for the former. The observed slow resumption of seed germination, 25% in 90 days, after moving 36/36 regime seeds to optimal conditons indicates the presence of induced secondary dormancy. Amen (1966) observed seed dormancy in other alpine species and concluded that this adaptive mechanism often confers a selective advantage in distribution and abundance of some alpine species.

High total and rates of germination observed in our nursery-grown seeds of alpine grasses, as was observed by Urbanska and Schutz (1986) in other alpine species, suggest the suitability of these grasses for agricultural situations. On the other hand, the ability of these nursery-grown seeds to acquire dormancy under unfavourable conditions indicates the preservation of their adaptation to alpine environments.

Populations originating in close proximity such as Agla 18 and Agla 19; Poal 22 and Poal 23 germinated differently in both species. Since the populations tested in these experiments were grown in one nursery, harvested during the same week after maturity and seeds were handled the same way, the effect could not have been confounded with external factors. The observation may partly be due to vegetative mode of reproduction, including production of apomictic seeds, in situ and the presence of physical barriers for germplasm exchange in mountainous regions. The self pollinating nature of <u>A. latiglume</u> may have enhanced the process of genotypic divergence among plant populations living in close proximity. The presence of variability for total and rate of germination among native populations suggests the possibility of genetic advance through selection for these traits. Significant population x temperature, and population x temperature x light interactions for both species suggests that a mechanical mixture of different types rather than a single homogeneous line will be required for successful reclamation of alpine and subalpine disturbances.

In conclusion, these experiments demonstrate the strong influence of environment on seed germination. They also indicate the presence of primary and secondary dormancy in the seeds of the two alpine grasses. These dormancies may be adaptive, allowing population survival under extreme environments, and therefore it will be necessary to take steps to preserve these traits in the breeding program. The variability for seed germination in alpine populations growing in close proximity is encouraging from the breeding standpoint.

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Links are associated with numbers below:

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