

Intraspecific Divergence in Seed Germination Traits between High- and Low-Latitude Populations of the Arctic-Alpine Annual *Koenigia islandica*

Authors: Wagner, Ioan, and Simons, Andrew M.

Source: Arctic, Antarctic, and Alpine Research, 40(1) : 233-239

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(07-003\)\[WAGNER\]2.0.CO;2](https://doi.org/10.1657/1523-0430(07-003)[WAGNER]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Intraspecific Divergence in Seed Germination Traits between High- and Low-Latitude Populations of the Arctic-Alpine Annual *Koenigia islandica*

Ioan Wagner*† and
Andrew M. Simons*

*Department of Biology, Carleton
University, 1125 Colonel By Drive,
Ottawa, Ontario, K1S 5B6, Canada

†Corresponding author:
jwagner@ccs.carleton.ca

Abstract

Populations of arctic-alpine plant species inhabit a range of environments, to which their life-history characters are expected to have adapted; yet geographic differentiation among populations is seldom studied. Brief growing seasons mean that germination characters are critical fitness traits, especially for annual species. In this study, striking differences in germination traits among three geographically distinct populations of the widely distributed arctic-alpine annual *Koenigia islandica* are found. The seeds (achenes) of the Colorado population, which experience the lowest summer temperatures, are conditionally dormant; only scarification breaks dormancy. This germination pattern is consistent in all four investigated subpopulations from Colorado, with no significant differences among them. In contrast, seeds originating in the Yukon, which experience extreme winter temperatures but a relatively warm summer, germinate readily after cold stratification, a pattern consistent with that of summer annuals. Seeds from the Norway population, which experience the mildest climate, germinate readily even if untreated. Cold stratification decreases germination fraction in the Norway population, a pattern characteristic of winter annuals. The strong population differentiation found here provides evidence for divergent selection operating among arctic-alpine habitats and suggests that further investigation of its adaptive significance is merited.

DOI: 10.1657/1523-0430(07-003)[WAGNER]2.0.CO;2

Introduction

The timing of germination is of major importance in seedling survival of plant populations inhabiting seasonal environments (Baskin and Baskin, 1988; Simons and Johnston, 2006) and is crucial for plant establishment in arctic and alpine tundra environments, characterized by low temperatures and a short and sometimes unpredictable growing season (Billings and Mooney, 1968). In these environments, dominated by slow-growing perennials reproducing predominantly by vegetative means (Billings and Mooney, 1968; Bliss, 1971), the germination characteristics of the few annual species, which reproduce exclusively by seeds, must be under particularly strong selective pressure. In the northern hemisphere, tundra environments occupy broad areas in the high-latitude, arctic regions of the continents as well as in the high-altitude, alpine regions of the temperate mountain systems of North America and Eurasia. Despite similarities between arctic and alpine environments, the gradients of latitude and elevation along this extensive range create important differences in environmental characteristics of tundra, differences to which arctic-alpine plant species germinating in these different tundra environments, including arctic-alpine annuals, should have adapted (Bliss, 1956). The most important environmental dissimilarities are photoperiod and temperature, but precipitation regime and length of growing season may also be critical. Differences in germination characteristics of populations of the same species inhabiting dissimilar environments are a widespread feature (Milberg and Andersson, 1998), and adaptations of seed germination to latitudinal and altitudinal climatic differences are well documented in polycarpic perennials

(Mooney and Billings, 1961; Meyer et al., 1989; Meyer and Monsen, 1991; Schütz and Milberg, 1997; Vandvik and Vange, 2003; Gimenez-Benavides et al., 2005).

However, in spite of the theoretical importance of arctic and alpine annuals, there has been little research on the germination responses of these interesting species, and virtually none on intraspecific differences in germination of arctic-alpine annuals. Some of the few studies on germination of arctic and alpine annuals have either addressed only interspecific differences (Reynolds, 1984) or have studied a single population (Heide and Gauslaa, 1999). Moreover, most of the previous studies on interpopulation germination differences were conducted on seeds collected directly from natural populations from the field, not allowing for the separation of genetic and environmental components in germination responses (Fenner, 1991). A comparative study on interpopulation variation of germination responses of an arctic-alpine annual, conducted on seeds produced in the laboratory under uniform conditions (Quinn and Colosi, 1977) appeared therefore desirable.

Annual plant species are rare in arctic and alpine regions, presumably because of the difficulties of growing sufficiently large and completing their life cycle in one growing season in these extreme environments (Billings, 1974). In most arctic and alpine habitats, annual species constitute only 1–2% of the flora (Billings and Mooney, 1968). *Koenigia islandica* L. (Polygonaceae) is probably the most widespread arctic-alpine annual, having an almost continuous Arctic circumpolar distribution with offshoots in several temperate mountain ranges (Hultén, 1971; Hedberg, 1997), as well as a disjunct population in the southern hemisphere, in southernmost South America (Zuloaga and Morrone, 1999).

TABLE 1

Environmental characteristics of the sites of origin of the *Koenigia islandica* populations.

Population:	Norway	Yukon	Colorado
Latitude	62°18'N	61°10'N	~40°N
Longitude	9°36'E	138°25'W	~105°40'W
Elevation (m a.s.l.)	900	783	~3600
Mean annual temperature (°C)	-0.1 ^a	-3.8 ^b	-3.71 ^c
Mean summer temperature (Jun–Aug, °C)	9.1 ^a	11.4 ^b	6.63 ^c
Mean January temperature (°C)	-8.8 ^a	-22 ^b	-13.15 ^c
Extreme maximum winter temperature (°C)	8.8 ^a	13.5 ^b	5 ^d
Extreme minimum winter temperature (°C)	-32.4 ^a	-55 ^b	-37 ^d
Mean annual precipitation (mm)	435 ^a	279.7 ^b	930 ^c
Mean summer precipitation (Jun–Aug, mm)	180 ^a	158.2 ^b	172.1 ^c

^a 1961–1990 Fokstugu Station, 972 m a.s.l., Norwegian Meteorological Institute.

^b 1971–2000 Burwash Airport, 807 m a.s.l., Environment Canada.

^c 1951–1985 Niwot Ridge D1 Station, 3749 m a.s.l. (Greenland, 1989).

^d 1952–1970 Niwot Ridge D1 Station, 3749 m a.s.l. (Barry, 1973).

In this study we investigate differences in germination characteristics of populations of *K. islandica* inhabiting three markedly different environments. Although all three habitats are considered alpine, they occur at vastly different latitudes, and there are significant differences in their environmental characteristics. Previous studies have found that populations from more severe climates have deeper dormancies that require longer periods of cold stratification to overcome it (Meyer et al., 1989; Meyer and Monsen, 1991; Cavieres and Arroyo, 2000, 2001). The study aimed to test this hypothesis and characterize differences in germination pattern in these *K. islandica* populations, test the effect of scarification and different length of cold stratification on seed germination, and advance preliminary adaptive explanations for these differences. By using seeds obtained under uniform laboratory conditions for the experiment, the study may detect genetically based differences.

Materials and Methods

PLANT MATERIAL

The achenes used in the germination experiments (hereafter referred to as seeds) were obtained from *K. islandica* populations and subpopulations from sites in Colorado, Yukon, and southern Norway, which are exposed to dissimilar environmental conditions in many respects (Table 1).

The seeds from Norway (Norway population) were donated by O. M. Heide from the Agricultural University of Norway and belong to the same population as those used in his study on *K. islandica* (Heide and Gauslaa, 1999). The seeds were collected on Kongsvoll in the Dovre Mountains (Oppdal, southern Norway) and were previously stored for 23 years at -20 °C before being propagated in the lab for the present work. The seeds from southwestern Yukon (Yukon population) were collected (by Mary Vetter) in 2003 from a population at Rat Lake, in close proximity to Kluane Lake, from plants growing on a marshy lakeshore among small *Scirpus* sp. and *Carex* sp. plants. The seeds from Colorado (Colorado population) were collected (by I. Wagner) in 2003 from four subpopulations from the Front Range as follows: two subpopulations were from the Mount Evans Wilderness; the first collection was from plants growing in wet gravel on the shores of Summit Lake near Mount Evans at an elevation of 3910 m a.s.l. (Mount Evans subpopulation) and the other from plants on the

shores of a small stream in wet gravel near Guanella Pass Campground, at an elevation of 3459 m a.s.l. (Guanella subpopulation). The other two subpopulations were from Rocky Mountain National Park; the first was situated on the north side of the drainage of the saddle between Toll Memorial and Sundance Mountain at an elevation of 3548 m a.s.l. (Toll Memorial subpopulation), and collections were made from plants growing on peat in a marshy area. Seeds from the final subpopulation were collected from the southeastern slope of Sundance Mountain at an elevation of 3627 m a.s.l., from plants growing in a small spring in gravel and organic material (Sundance subpopulation).

The seeds were dried at room temperature and stored at -18 °C until used.

LABORATORY SEED PROPAGATION

In order to eliminate possible maternal effects (Quinn and Colosi, 1977; Simons and Johnston, 2006), all populations were grown for one generation in the laboratory under uniform conditions. The seeds were germinated in germination chambers (Enconair SG-30, Enconair Ecological Chambers Inc., Winnipeg, Manitoba) under long day (LD) photoperiod (15:9) at 24 °C day and 17 °C night temperatures on wet filter paper in Petri dishes. The germinating seedlings were transplanted to pots in a mixture of sand and peat-based standard growing medium and grown in growth chambers (Enconair GC-40) under LD (15:9) photoperiod at 15 °C day and 10 °C night temperatures. The resulting seeds were harvested, dried at room temperature and stored at -18 °C for further use.

GERMINATION EXPERIMENTS

Two replicate germination experiments—with some minor differences outlined below—were conducted using seeds produced in the laboratory; one in July 2004 (trial 1), and the second in January 2005 (trial 2). In both germination trials 400 seeds for each population were split between the following four treatments: 100 seeds were scarified by slitting open the seed coat (actually the pericarp) with a scalpel, 100 were stratified in the dark at 4 °C on wet filter paper in Petri dishes wrapped in two layers of aluminum foil, 100 seeds per population received both scarification and stratification treatments, and the final 100 seeds remained untreated. To eliminate the possible confounding influence of positional or Petri dish effects, the 100 seeds for each treatment were divided among 4 Petri dishes. Because seeds from Colorado were derived from four subpopulations, 25 seeds of each of the subpopulations were used in each treatment and were each split between two of the four Petri dishes. The two germination experiments differed only in that the stratification period for the first trial was 6 weeks, whereas it was 20 weeks for the second trial. This allows for at least a crude appraisal of the additional effect of stratification duration on germination characteristics. The seeds were germinated in an SG-30 germination chamber under a LD (15:9) photoperiod (ca. 50 μmol m⁻² s⁻¹ photosynthetic photon flux density) and 24 °C day and 17 °C night temperatures. The choice of 24 °C as germination temperature follows Heide and Gauslaa's finding (1999) that this temperature is optimal for the germination of *K. islandica*. Time from imbibition to germination (time to germination) for individual seeds was determined by counting germinated seeds daily over a 28-day period, and cumulative final germination

TABLE 2

Analysis of variance of germination fraction for three populations of *Koenigia islandica* from Norway, Yukon, and Colorado. Experimental trial effect, also included in the model, and all of its interactions were found to be nonsignificant ($P > 0.05$) and are not presented.

Source	MS	df	F	P
Scarification	14.100	1	5739.841	0.008
Stratification	0.240	1	31.144	0.112
Population	4.335	2	1081.096	0.000
Scarification*Population	1.144	2	25.983	0.037
Stratification*Population	1.466	2	47.823	0.020
Scarification*Stratification	0.042	1	4.089	0.292
Scarification*Stratification*Population	1.108	2	48.858	0.020

percentages (germination fraction) were recorded at the end of the experiment.

STATISTICAL ANALYSIS

We used a mixed model factorial analysis of variance (ANOVA) to test the dependence of germination fraction on population, seed treatment, germination trial, and their interaction. Because we are interested in the independent effects of scarification and stratification (as well as their interaction), these were considered two factors, each with two levels, in the analysis. To account for possible differences between the two germination experiments, experimental trial (length of stratification period) was included as an additional factor along with its interaction terms. Experimental trial was considered to be a random effect, whereas all other effects were fixed. Neither the experimental trial effect nor any of its interactions were found to be statistically significant ($P > 0.05$) and, for clarity, are not presented. Because germination fractions (p) are proportional measurements and cannot be measured at the individual level, analyses were performed at the level of replicated Petri plates (see “GERMINATION EXPERIMENTS” above). Germination fractions were transformed as $p' = \arcsin(p^{0.5})$ prior to all analyses. When ANOVA indicated significant effects ($P \leq 0.05$), post-hoc Tukey HSD tests were performed to further examine the differences detected. Additional ANOVA and Tukey HSD analyses were performed in an identical manner to ask whether germination characters differ among the Colorado subpopulations.

Data from individual seeds (days from imbibition to germination) were used in the assessment of time to germination. Although seeds that do not germinate are valid data for analyses of germination fractions, they constitute missing data in analyses of time to germination. Germination time constitutes time-to-event data which are appropriately treated with time-series or failure-rate analysis (Vange et al., 2004) in which nongerminated seeds are missing or “censored” data. However, for numerous population and treatment combinations, germination fraction was low. Although survival analysis is designed to handle censored data that occur randomly among treatments or groups, the

extreme inequality of proportion of censored data among treatments and populations in the present data set would lead to systematic bias in results. Thus, no statistical tests were applied to time to germination data, and the assessment of trends in time to germination, included for the interested reader, should be interpreted with due caution.

Results

Analysis of variance reveals general differences in overall germination fractions among populations as well as significant effects of the various seed treatments. It also shows that response to these seed treatments is population dependent, as indicated by significant population by stratification, and population by scarification interaction terms (Table 2). The post-hoc Tukey tests provide more specific insight into where these significant differences occur (Table 3).

Scarification had a positive general effect on germination fraction, but the germination pattern of untreated seeds revealed strong differences among populations (Fig. 1). For example, a significantly greater fraction of untreated seeds of the Norway population germinated than those of other populations (Table 3). Untreated seeds from the other two populations that germinated in a lower percentage also appeared to reach their maximum germination percentage later (Fig. 2), although this difference in time to germination was not tested statistically (see “Materials and Methods”).

A small number of the seeds germinated during the stratification treatment at 4 °C in the dark: 5% of the seeds of the Norway population, only 0.5% of the seeds from Yukon, and 0.25% of the seeds from Colorado. Cold stratification alone had very different effects on the germination fraction of the seeds of the three populations (Fig. 1). Neither stratification nor its duration had a significant effect on the germination of the Colorado seeds, whereas cold stratification of the Yukon seeds significantly improved their germination (Table 3). Cold stratification significantly reduced the germinability of the seeds from the Norway population (Table 3) and also appeared to increase the time to germination for the seeds from Norway (Fig. 2). Overall, germination patterns of the two experimental trials conducted six

TABLE 3

Differentiation in germination fraction of seeds of three populations of *Koenigia islandica* subjected to various treatments. Trial 1—July 2004; Trial 2—January 2005. Different letters indicate table-wide significant differences according to post-hoc Tukey HSD tests (see Table 2).

Treatment	Norway		Yukon		Colorado	
	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
Untreated	A	A	CDE	EF	F	EF
Stratified	BC	CD	AB	A	EF	DEF
Scarified	A	A	A	A	A	A
Stratified and scarified	A	A	A	A	A	A

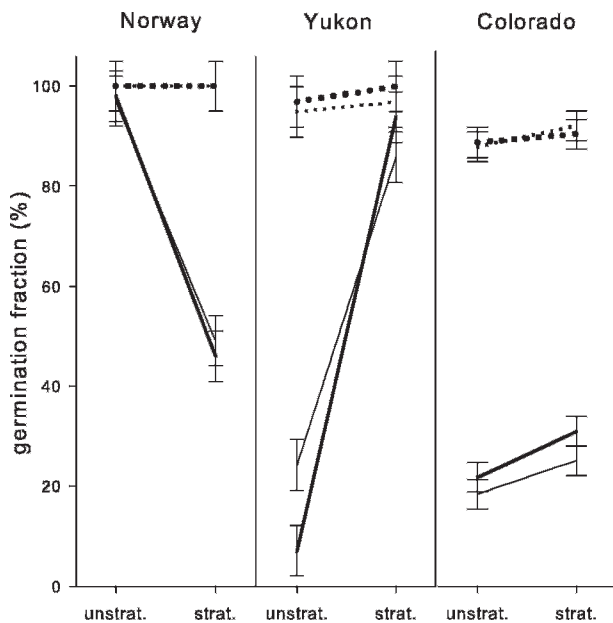


FIGURE 1. Germination fraction for unstratified and stratified seeds in three populations of *Koenigia islandica* at 24 °C. Broken lines represent germination of scarified seeds; solid lines represent germination of unscarified seeds. Thin lines represent trial 1 (July 2004—stratification of 6 weeks); bold lines represent trial 2 (January 2005—stratification of 20 weeks). Error bars indicate $\pm 1SD$.

months apart were consistent, with no significant differences between the trials (Fig. 1).

Scarification of the seed coat resulted in significantly higher germination fractions for all population trials except those for Norway (Fig. 1). Again, although time to germination was not compared statistically, the trends suggest that treatments that tend to increase germination fraction also shorten times to germination (Fig. 2).

The analysis of the four subpopulations from Colorado revealed a consistent germination pattern among subpopulations (Table 4), with the only statistically significant differences being among seed treatment main effects. All seeds of the Colorado subpopulations germinated in very low percentages if untreated; stratification did not result in a significantly higher germination percentage in any of the subpopulations, and germination in all subpopulations was strongly promoted by scarification (Fig. 3).

Discussion

Likely because the growing season is short, annual plants are rare in arctic and alpine habitats. Those annual species that do persist, then, are expected to show phenological adaptations associated with the seasonal constraints imposed. In particular, seed germination is expected to have evolved to respond to available cues such that the effective length of the potential growing season is maximized and, at the same time, the risk of germination outside the narrow window appropriate for seedling

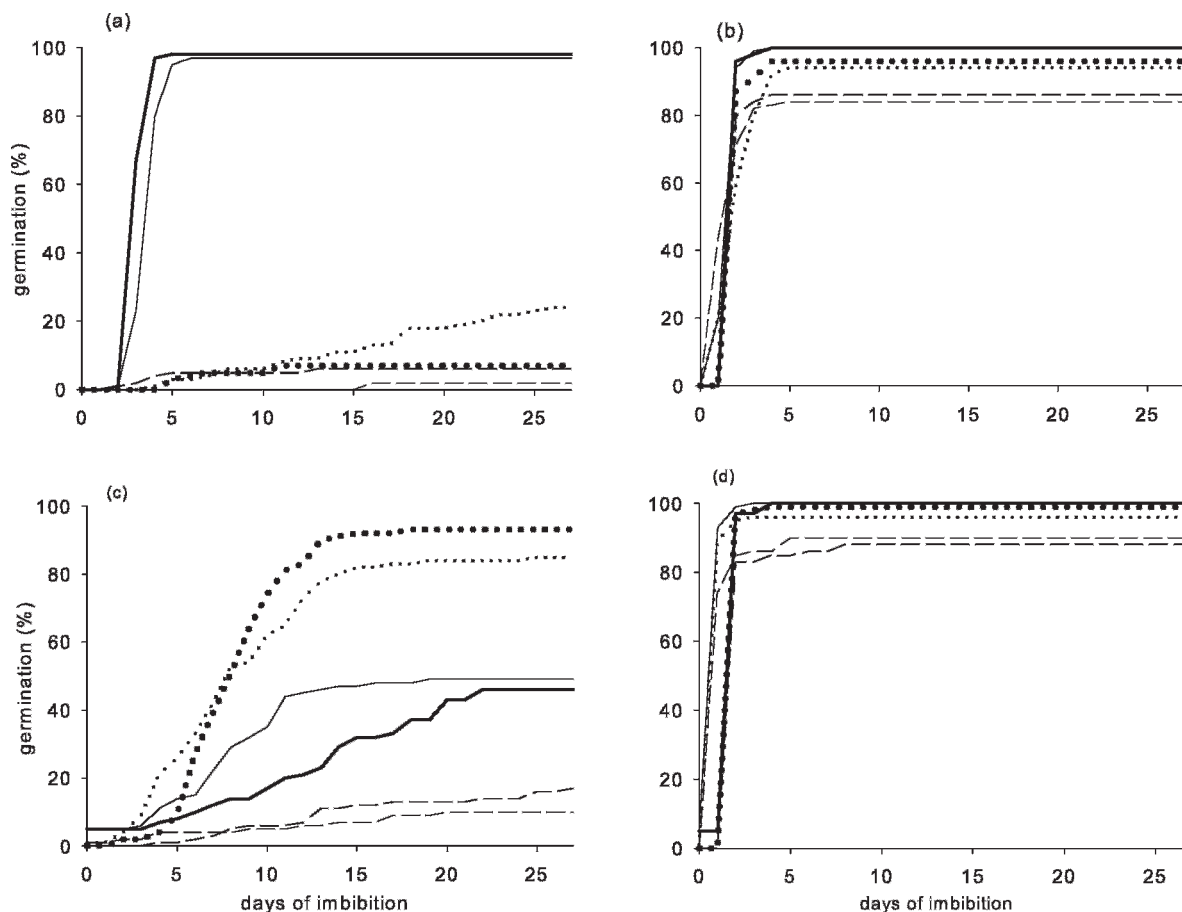


FIGURE 2. Trends in time to germination for seeds of three populations of *Koenigia islandica* at 24 °C. (a) Untreated seeds, (b) scarified seeds, (c) stratified seeds, and (d) scarified and stratified seeds. Solid line: Norway; dotted line: Yukon; broken line: Colorado. Thin lines represent trial 1 (July 2004—stratification of 6 weeks); bold lines represent trial 2 (January 2005—stratification of 20 weeks). Because statistical comparisons among populations and treatments could not be performed (see “Materials and Methods”), results are intended to represent general trends only.

TABLE 4

Analysis of variance of germination fraction for four subpopulations of *Koenigia islandica* from Colorado. Experimental trial effect, also included in the model, and all of its interactions were found to be nonsignificant ($P > 0.05$) and are not presented.

Source	MS	df	F	P
Scarification	17.685	1	573.364	0.026
Stratification	0.230	1	201.486	0.044
Subpopulation	0.135	3	4.488	0.124
Scarification*Subpopulation	0.015	3	0.217	0.879
Stratification*Subpopulation	0.082	3	1.895	0.306
Scarification*Stratification	0.087	1	98.714	0.063
Scarification*Stratification*Subpopulation	0.019	3	0.855	0.549

survival and growth is minimized. In this set of experiments, we ask whether genetically based differentiation exists in germination traits of three populations of the arctic-alpine annual *Koenigia islandica* originating from widely divergent latitudes and altitudes.

The results of the germination experiments indicate that important differences in germination characteristics exist among the investigated populations of *K. islandica*. The fact that these differences are maintained through a generation grown under a common garden environment in the laboratory indicates that these are evolved differences. Also, the consistency of the observed patterns over two independent germination trials lends confidence to the reliability of the tests. Furthermore, the fact that little difference is observed among the four geographically close subpopulations from Colorado suggests that the germination patterns are locally adapted.

The germination of seeds not subjected to a period of cold stratification simulates the germination of freshly matured seeds late in the same growing season. At 24 °C, at which the unstratified, seemingly non-dormant seeds of the Norway populations readily germinate in high percentage, the unstratified seeds from Yukon and Colorado reach only a modest germination fraction in both trials; this indicates at least a conditional dormancy (Shimono and Kudo, 2005) that could be overcome by cold stratification in the Yukon population, and in a much lesser extent in the Colorado population (Fig. 1). The finding that cold stratification improves the germinability of seeds from tundra environments is consistent with results of previous work on arctic and alpine species (Bell and Bliss, 1980; Marchand and Roach,

1980; Reynolds, 1984; Densmore, 1997; Cavieres and Arroyo, 2000) and confirms the initial hypothesis that seeds of populations from severe winter sites are less likely to germinate under autumn and early winter thaw conditions than seeds from regions with milder winters (Meyer and Monsen, 1991).

The relative inhibition of germination of unstratified seeds from Yukon might be an important adaptation to the severe and unpredictable climate there, with extreme negative winter temperatures alternating with short periods of positive temperatures and thaw that might induce the germination of seeds lacking dormancy. This observation is similar to the finding of Vandvik and Vange (2003), that populations from an environment with higher probabilities of repeated freeze-thaw events have deeper dormancies. The increase in germination percentage following wet-cold stratification in the Yukon population is consistent with a summer annual's germination pattern in which seed dispersal occurs in the first summer/fall, a seed overwinters under snow cover, and germinates, grows, and sets seed in late summer or autumn (Baskin and Baskin, 1988). The Colorado population, on the other hand, originating from a high-altitude environment with the most severe growing season among the studied populations, is characterized by germination that is little improved by cold stratification of any length. This observation is similar to those of Amen (1966) and Dorne (1981): seed germination fractions generally decrease with increasing latitude or elevation of origin; that is, with the increasing severity of the climate.

As in the study of Dorne (1981), the relative dormancy of the Colorado seeds might be due to the seed coat: their dormancy was

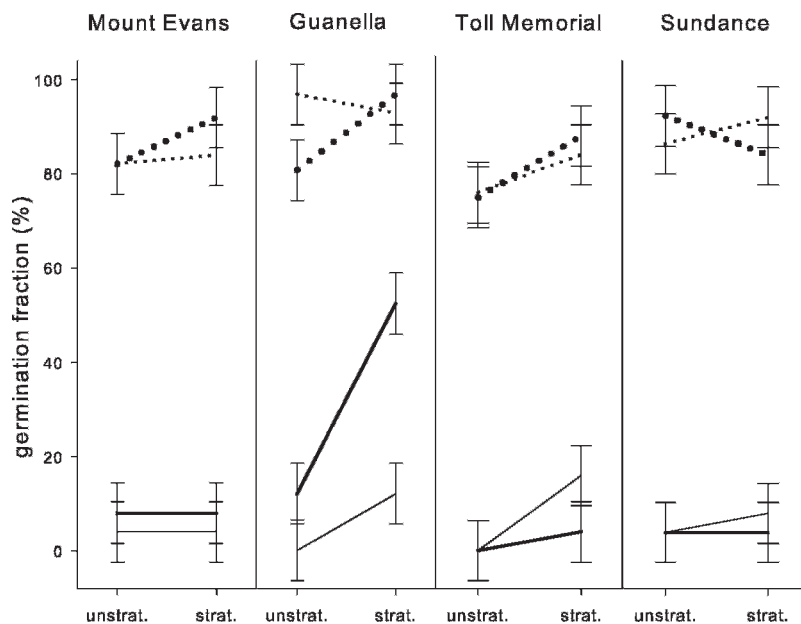


FIGURE 3. Germination fraction for unstratified and stratified seeds in four subpopulations of *Koenigia islandica* from Colorado at 24 °C. Broken lines represent germination of scarified seeds; solid lines represent germination of unscarified seeds. Thin lines represent trial 1 (July 2004—stratification of 6 weeks); bold lines represent trial 2 (January 2005—stratification of 20 weeks). Error bars indicate $\pm 1SD$.

broken by seed scarification and their germination fraction greatly improved and time to germination decreased following this treatment (Figs. 1, 2). The breaking of dormancy through mechanical seed coat scarification is likely a treatment that the seeds of the Colorado population receive in their natural habitat when they are rolled in coarse sand and gravel of the small streams and ponds they usually inhabit. Seed germination fractions were increased by scarification in the Norway and Yukon populations as well (Fig. 1), consistent with the finding that seed dormancy of alpine plants is overcome by scarification (Pelton, 1956). Likewise, germination fraction was improved and time to germination of *K. islandica* decreased by scarification in Heide and Gauslaa's study (1999).

Previous work on germination variation among populations along an elevation gradient found that populations normally encountering long periods of snow cover and adverse winter conditions would require longer periods of cold stratification for germination than those exposed to milder winters (Meyer and Monsen, 1991; Cavieres and Arroyo, 2000). Our observations that the longer stratification period failed to significantly improve the germinability of the seeds from Colorado (Fig. 1) do not seem to reinforce these previous findings and are similar to the results of Schütz and Milberg (1997), that longer cold stratification did not improve the seed germination of populations from a harsher climate.

The most divergent results were provided by the germination of the Norway population of *K. islandica*. Virtually all of the seeds of this population germinated readily if untreated, which supports our hypothesis that seeds of populations from milder climates are less dormant. Following cold stratification, however, the Norway seeds experienced a significant reduction in germination fraction and an increase in time to germination. A reduction in germination fraction following a longer stratification period, together with the ability of unstratified seeds to germinate at low temperatures (including during the stratification treatment itself) is consistent with the germination characteristics of some winter annuals, but is a surprising trait for an arctic-alpine annual. This finding is, however, reinforced by the observation that the cold stratified seeds of this population also show a decreased temperature range for germination (Simons and Wagner, 2007) and an increased light requirement for germination (Wagner and Simons, unpublished), which are again typical traits of most winter annuals (Milberg and Andersson, 1998). A winter annual is a plant which germinates in the autumn, passes the winter in vegetative state under the snow cover, and flowers, sets seed, and dies in the following spring or summer (Baskin and Baskin, 1988). In the case of *K. islandica* from Dovre Mountains in southern Norway, however, it is difficult to imagine how seedlings that had germinated in the previous season would persist for more than six months under the snow cover in this alpine region. On the other hand, the flora of southern Scandinavia, in a mild oceanic climate, is known to have many winter annual plant species (Milberg and Andersson, 1998). Further field observations are required to shed light on this question.

It is beyond the scope of the present study to unequivocally assess the adaptive significance of the particular germination patterns found. However, this work implies that important differences in the selective forces exist among habitats of conspecific populations which have resulted in strong and genetically based population differentiation in life-history characters.

Acknowledgments

We thank Ola Heide from the Norwegian University of Life Sciences for providing the seeds from southern Norway and Mary Vetter from the University of Regina for collecting the seeds of the

Yukon population. We would also like to thank Steve Popovich for permission to collect seeds in the Mount Evans Wilderness and for assistance in field, Terry Terrell for permission to work in the Rocky Mountain National Park, Richard Bray for assistance with collecting seeds, and Lennart Nilsen for help with the climate data. We thank two anonymous reviewers for comments that improved the manuscript. This work was supported by a Natural Sciences and Engineering Research Council (NSERC) of Canada Discovery grant to Simons.

References Cited

- Amen, R. D., 1966: Extent and role of seed dormancy in alpine plants. *Quarterly Review of Biology*, 41: 271–281.
- Barry, R. G., 1973: A climatological transect on the east slope of the Front Range, Colorado. *Arctic and Alpine Research*, 5: 89–110.
- Baskin, C. C., and Baskin, J. M., 1988: Germination ecophysiology of herbaceous plant-species in a temperate region. *American Journal of Botany*, 75: 286–305.
- Bell, K. L., and Bliss, L. C., 1980: Plant reproduction in a high arctic environment. *Arctic and Alpine Research*, 12: 1–10.
- Billings, W. D., 1974: Arctic and alpine vegetation: plant adaptations to cold summer climates. In Ives, J. D., and Barry, R. G. (eds.), *Arctic and Alpine Environments*. London: Methuen, 371–402.
- Billings, W. D., and Mooney, H. A., 1968: The ecology of arctic and alpine plants. *Biological Reviews of the Cambridge Philosophical Society*, 43: 481–529.
- Bliss, L. C., 1956: A comparison of plant development in microenvironments of arctic and alpine tundras. *Ecological Monographs*, 26: 303–337.
- Bliss, L. C., 1971: Arctic and alpine life cycles. *Annual Review of Ecology and Systematics*, 2: 405–438.
- Cavieres, L. A., and Arroyo, M. T. K., 2000: Seed germination response to cold stratification period and thermal regime in *Phacelia secunda* (Hydrophyllaceae)—Altitudinal variation in the mediterranean Andes of central Chile. *Plant Ecology*, 149: 1–8.
- Cavieres, L. A., and Arroyo, M. T. K., 2001: Persistent soil seed banks in *Phacelia secunda* (Hydrophyllaceae): experimental detection of variation along an altitudinal gradient in the Andes of central Chile (33°S). *Journal of Ecology*, 89: 31–39.
- Densmore, R. V., 1997: Effect of day length on germination of seeds collected in Alaska. *American Journal of Botany*, 84: 274–278.
- Dorne, A. J., 1981: Variation in seed germination inhibition of *Chenopodium bonus-henricus* in relation to altitude of plant growth. *Canadian Journal of Botany—Revue Canadienne de Botanique*, 59: 1893–1901.
- Fenner, M., 1991: The effect of the parent environment on seed germinability. *Seed Science Research*, 1: 75–84.
- Gimenez-Benavides, L., Escudero, A., and Perez-Garcia, F., 2005: Seed germination of high mountain Mediterranean species: altitudinal, interpopulation and interannual variability. *Ecological Research*, 20: 433–444.
- Greenland, D., 1989: The climate of Niwot Ridge, Front Range, Colorado, USA. *Arctic and Alpine Research*, 21: 380–391.
- Hedberg, O., 1997: The genus *Koenigia* L. emend. Hedberg (Polygonaceae). *Botanical Journal of the Linnean Society*, 124: 295–330.
- Heide, O. M., and Gauslaa, Y., 1999: Developmental strategies of *Koenigia islandica*, a high-arctic annual plant. *Ecography*, 22: 637–642.
- Hultén, E., 1971: *The Circumpolar Plants. II. Dicotyledons*. Stockholm: Almqvist & Wiksell, 463 pp.
- Marchand, P. J., and Roach, D. A., 1980: Reproductive strategies of pioneering alpine species—Seed production, dispersal, and germination. *Arctic and Alpine Research*, 12: 137–146.

- Meyer, S. E., and Monsen, S. B., 1991: Habitat-correlated variation in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) seed-germination patterns. *Ecology*, 72: 739–742.
- Meyer, S. E., McArthur, E. D., and Jorgensen, G. L., 1989: Variation in germination response to temperature in rubber rabbitbrush (*Chrysothamnus nauseosus*, Asteraceae) and its ecological implications. *American Journal of Botany*, 76: 981–991.
- Milberg, P., and Andersson, L., 1998: Does cold stratification level out differences in seed germinability between populations? *Plant Ecology*, 134: 225–234.
- Mooney, H. A., and Billings, W. D., 1961: Comparative Physiological ecology of arctic and alpine populations of *Oxyria digyna*. *Ecological Monographs*, 31: 1–29.
- Pelton, J., 1956: A study of seed dormancy in eighteen species of high altitude Colorado plants. *Butler University Botanical Studies*, 13: 74–84.
- Quinn, J. A., and Colosi, J. C., 1977: Separating genotype from environment in germination ecology studies. *American Midland Naturalist*, 97: 484–489.
- Reynolds, D. N., 1984: Alpine annual plants—Phenology, germination, photosynthesis, and growth of 3 Rocky-Mountain species. *Ecology*, 65: 759–766.
- Schütz, W., and Milberg, P., 1997: Seed dormancy in *Carex canescens*: regional differences and ecological consequences. *Oikos*, 78: 420–428.
- Shimono, Y., and Kudo, G., 2005: Comparisons of germination traits of alpine plants between fellfield and snowbed habitats. *Ecological Research*, 20: 189–197.
- Simons, A. M., and Johnston, M. O., 2006: Environmental and genetic sources of diversification in the timing of seed germination: implications for the evolution of bet hedging. *Evolution*, 60: 2280–2292.
- Simons, A. M., and Wagner, I., 2007: The characterization of complex continuous norms of reaction. *Oikos*, 116: 986–994.
- Vandvik, V., and Vange, V., 2003: Germination ecology of the clonal herb *Knautia arvensis*: regeneration strategy and geographic variation. *Journal of Vegetation Science*, 14: 591–600.
- Vange, V., Heuch, I., and Vandvik, V., 2004: Do seed mass and family affect germination and juvenile performance in *Knautia arvensis*? A study using failure-time methods. *Acta Oecologica—International Journal of Ecology*, 25: 169–178.
- Zuloaga, F. O., and Morrone, O., 1999: Catálogo de las plantas vasculares de la República Argentina. II. *Monographs in Systematic Botany from the Missouri Botanical Garden*, 74: 1–1269.

Ms accepted May 2007