Divergence in germination traits among arctic and alpine populations of *Koenigia islandica*: light requirements

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Abstract Light is known to regulate conservative germination strategies and the formation of seed banks. Although these strategies are crucial to survival in tundra environments—especially for annuals—light requirements for germination in arctic–alpine species are seldom investigated. Furthermore, environmental differences between arctic and alpine regions are expected to lead to evolutionary divergence among conspecific populations in seed germination strategies. In this study, we report important differences in germination light requirements among six arctic and alpine populations of the annual *Koenigia islandica*. Light had little effect on germination of the seeds from Iqaluit (Nunavut, Canada), Yukon (Canada), and Jasper (Alberta, Canada), whereas the seeds from the most severe climates, Svalbard (Norway) and Colorado (USA), had strong light requirements. Stratification of the seeds had little influence on their germination light requirements, with the exception of the population from Dovre (Norway), in which it induced a strong light requirement. Possible adaptive explanations and some implications of these observed germination patterns are discussed.

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Introduction

Persistence of arctic and alpine annual plant species depends on reproduction by seed. This requires a successful seed production every year in an environment with short and unpredictable growing seasons. Successful seed reproduction is closely associated with the seasonal timing of germination (Baskin and Baskin 1988; Simons and Johnston 2006), and light, together with soil moisture and temperature, is among the most important environmental factors influencing the timing of seed germination (Baskin and Baskin 1998; Grime et al. 1981; Meyer et al. 1990) in arctic and alpine annuals. Specifically, the presence of a light requirement is one of the main elements of conservative germination strategies (Schütz 2002), and in the ability of seeds to postpone germination, i.e., to stay dormant in the soil and form seed banks (Kettenring et al. 2006; Milberg and Andersson 1997; Pons 1991), a trait posited as a "bet-hedging" strategy. This study tests whether genetically-based divergence exists in the germination light responses among the six widely distributed arctic and alpine populations of *Koenigia islandica*.

Conservative germination strategies are clearly of great importance in arctic and alpine environments, where the conditions for germination and seedling establishment might not be favorable every growth season (Bell and Bliss 1980; Körner 1999) and, in response, some species develop large and persistent seed banks (Cavieres and Arroyo 2001; Shimono and Kudo 2005). Environmental conditions, however, are far from homogeneous over the considerable range of tundra habitats (Billings 1973), and plant species growing in both arctic and alpine environments are expected to have diverged in germination traits, including light requirements. Because tundra environments are so adverse to seed reproduction, most tundra plants reproduce vegetatively. The few annual species of the tundra, however, are compelled to reproduce by seed every year. Because timing of germination can have strong fitness consequences (Simons and Johnston 2000) germination responses of these annuals may be especially highly adapted to available environmental cues, and to the sometimes subtle differences between arctic and alpine environments.

Despite its theoretical importance, there is no integrated concept of germination light requirements in arctic and alpine plant species (Shimono and Kudo 2005), and studies that investigate this topic are also scarce (Acharya 1989; Densmore 1997; Schütz 2002; Shimono and Kudo 2005). Arctic and alpine annuals may be especially vulnerable to effects of climate change if local adaptation is strong: reliance on cues is adaptive only as long as the cues are dependable indicators of environmental conditions. If the environmental conditions to which populations have adapted prove to be transient over longer time scales (Simons 2002), however, persistence depends on "adaptive tracking" of the changing conditions (Bell and Collins 2008; Franks et al. 2007).

Although interpopulation differences in light requirements for seed germination in temperate species have been the subject of several studies (Meyer et al. 1990; Milberg and Andersson 1998; Schütz and Milberg 1997), Mooney and Billings' (1961) seminal analysis on *Oxyria digyna*—a perennial species—is the only work that compares germination responses to light of arctic and alpine populations of a tundra plant. There are very few studies that investigate germination light responses in arctic–alpine annual species (Heide and Gauslaa

1999; Reynolds 1984a), and none that investigate within-species divergence in light requirements.

This study investigates differences in germination light requirements under differing stratification regimes in six arctic and alpine populations of the arctic–alpine annual *Koenigia islandica* L. (Polygonaceae). This species is the only annual plant in many tundra environments (Billings 1974). It has a wide, bipolar distribution, having populations mainly in the Arctic and in northern hemisphere, temperate mountain ranges (Hedberg 1997; Hultén 1971), but also an isolated, subantarctic population (Zuloaga and Morrone 1999). The general aim of the study is to assess the extent of genetic divergence among populations. Previous work on this species (Wagner and Simons 2008b) shows that population divergence in morphology, life-history and phenological traits is predicted by severity of local conditions rather than by arctic or alpine origin. Measures of site severity include mean summer temperature, extreme maximum and minimum temperatures, and duration of growing season (Table 1). Therefore, a further prediction here is that populations group with respect to light requirements for germination: specifically, those that experience more severe climates at their location of origin have stronger light requirements (Meyer et al. 1990). By using seeds produced under a common laboratory environment, the study can detect if the observed differences are evolved and genetically based.

Materials and methods

Plant material

Germination light requirements were tested for achenes (seeds) of six populations of *Koenigia islandica* from a wide range of arctic and alpine environments (Table 1). The plant material for the six populations is described in detail elsewhere (Wagner and Simons 2008a, b). Previous experiments showed no significant differences in seed germination among local subpopulations within the main populations (Wagner and Simons 2008a). Therefore, subpopulations (for the Svalbard, Jasper and Colorado populations; see Wagner and Simons 2008a, b) were pooled for the present work. After collection, the seeds were allowed to dry at room temperature and were stored for 2–3 months at 18°C until further use. An exception are

Table 1 Environmental characteristics of the sites of origin of the *Koenigia islandica* populations (after Wagner 2007; Wagner and Simons 2008b)

Population name	Svalbard	Iqaluit	Dovre	Yukon	Jasper	Colorado
Country	Norway	Canada	Norway	Canada	Canada	USA
Latitude	78°14′N	63°44′N	62°18′N	61°10′N	52°49′N	∼40°N
Longitude	15°35′E	68°34′W	9°36′E	138°25′W	118°08′W	∼105°42′W
Elevation (m a.s.l.)	10	15	900	783	∼2,300	∼3,650
Maximum photoperiod (light hours)	24	20.8	19.9	19.3	16.9	15
Summer photoperiod (Jun–Aug, light hours)	24–19.1	19.9–14.6	19.1–14.5	18.7–14.3	16.5–13.7	14.8–13.1
Mean annual temperature (°C)	**−6.7**[a]	**−9.8**[b]	**−0.1**[c]	**−3.8**[d]	–[e]	**−3.71**[f]
Mean summer temperature (Jun–Aug, °C)	4.2[a]	6.0[b]	9.1[c]	11.4[d]	7.5[e]	6.6[f]
Extreme maximum summer temperature (°C)	21.3[a]	25.8[b]	26.8[c]	31.7[d]	29.0[e]	19.0[g]
Extreme minimum summer temperature (°C)	−8.4[a]	−10.2[b]	−6.0[c]	−8.5[d]	−12.2[e]	−12.0[g]
Days/year with maximum temperatures >20°C	0.06[a]	1.2[b]	9.9[c]	28.1[d]	5.6[e]	0[g]
Mean annual precipitation (mm)	190[a]	412.1[b]	435[c]	279.7[d]	–[e]	930[f]
Mean summer precipitation (Jun–Aug, mm)	51[a]	160[b]	180[c]	158[d]	256[e]	172[f]
Mean growing season length (days/year with minimum temperatures >0°C)	99[a]	93[b]	140[c]	106.8[d]	–[e]	47[g]

Bold values represents the mean annual temperature of the study sites, an environmental characteristic that is considered the most significant in distinguishing environmental severity of the sites

Dash indicates data not available

[a] 1961–1990 Longyearbyen Airport, 28 m a.s.l., Norwegian Meteorological Institute

[b] 1971–2000 Iqaluit Airport, 33.5 m a.s.l., Environment Canada

[c] 1961–1990 Fokstugu Station, 972 m a.s.l., Norwegian Meteorological Institute

[d] 1971–2000 Burwash Airport, 807 m a.s.l., Environment Canada

[e] 1963–2003 Adams Creek, 2,210 m a.s.l., Environment Canada

[f] 1951–1985 Niwot Ridge D1 Station, 3,749 m a.s.l. (Greenland 1989)

[g] 1952–1970 Niwot Ridge D1 Station, 3,749 m a.s.l. (Barry 1973)

the seeds from Dovre, which belong to the same population as the one investigated in an earlier study on *K. islandica* (Heide and Gauslaa 1999), and had been previously stored for 23 years at −22°C before being propagated through a full generation for use in the present work (Wagner and Simons 2008a).

Laboratory seed propagation

In order to minimize maternal effects (Fenner 1991), only laboratory-obtained seeds were used. The tested seeds of the Svalbard, Iqaluit, Dovre, and Jasper populations were from plants grown through one generation in the laboratory. Because insufficient seeds from first generation plants were available for the Yukon and Colorado populations, seeds from plants grown through two laboratory generations were used for these populations. The field-collected seeds

were germinated in SG-30 Enconair germination chambers (BioChambers 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 resulting seedlings were transplanted to pots in a 1:8 mixture of sand and peat-based standard growing medium and grown in growth chambers (Enconair GC-40). *K. islandica* is self compatible and has mostly cleistogamous, self-pollinating flowers (Hedberg 1997); therefore, no cross-pollination was performed by hand in this study. The seeds were harvested, dried at room temperature and stored for up to 2 years at −18°C until further use.

Experimental procedures

Cold–wet seed stratification of seeds simulates over-wintering in the dark under snow cover. This treatment

insures that germination is not triggered by exposure to light in any of the seeds, given that *K. islandica* can germinate at very low temperatures. Light requirements for germination were tested for both dark-stratified (45 days at 4°C) and unstratified seeds. Work on this diminutive annual requires efficient use of materials. Stratification plates were assembled prior to the plates for the unstratified treatment (to coordinate the initiation of the light requirement experiment) using conservative sample size; numbers were increased slightly for the unstratified seeds. Six Petri dishes for each population were prepared containing either 20 unstratified seeds or 15 stratified seeds. For the dark treatment, half the dishes for each population and stratification treatment were wrapped in two layers of aluminum foil and, for the light treatment, the remainder of the dishes were wrapped in a layer of transparent plastic foil in order to avoid humidity differences between the two treatments. All dishes were placed in a germination chamber at continuous light and constant 27°C. The germinated seeds were counted and removed once every 2 days over a period of 60 days. Percent of germinated seeds (germination fraction) and the time from imbibition to germination (time to germination) were recorded. A number of seeds germinated in the Petri dishes during the stratification treatment (Svalbard 2.2%, Iqaluit 19.5%, Dovre 2.2%, Yukon 1.1%, Jasper 16.1%, and Colorado 4.4%); they were counted toward the germination fraction of that particular plate.

As germination light requirements of seeds of various species may be fulfilled by exposure to light of less than a minute (Milberg et al. 1996), it was insured that seeds of the dark treatment did not receive any photosynthetically active light after imbibition during the experiment: preparation of dishes and seed counts for the dark treatment was performed in a darkroom under a dim green darkroom light. Also, tests with miniature temperature loggers (iButtons, Maxim Integrated Products Inc., Sunnyvale, CA), placed inside Petri dishes indicated no discernible differences in temperatures inside dishes wrapped in aluminum versus transparent plastic foil.

In order to determine whether the remaining seeds did not germinate in the dark because of lack of light or because of other factors, the Petri dishes of the dark treatment were placed into light conditions for several weeks in the germination chamber following termination of the experiment to confirm viability.

Statistical analysis

To test the dependence of germination fraction on population, stratification treatment, light treatment and their interaction, a mixed model factorial analysis of variance (ANOVA) was used. The analysis was performed at the level of replicate Petri dishes, and germination fractions were transformed as $p' = $ arc-sine $(p^{0.5})$ prior to the analysis (Simons and Johnston 2006). Because none of the populations and treatments germinated in very low percentages (cf. to Wagner and Simons 2008a), an analysis of time to germination was possible with an ANOVA performed at the level of individual seeds. Randomly positioned replicate Petri plates are crucial to eliminate confounding this effect with treatment effects even though limited degrees of freedom precludes the inclusion of this factor in analyses. For both germination fraction and time to germination, post-hoc Tukey HSD-tests were performed to identify the differences among populations and treatments detected by the ANOVAs. All analyses were performed using JMP 7.0.2 (SAS Institute Inc 2007).

Results

The analyses of variance indicate that significant differences in germination light requirements exist among the six populations of *Koenigia islandica*. The effect of light, as well as its interactions with the population effect, is highly significant for both germination fraction (Table 2), and time to germination (Table 3). A post-hoc Tukey test reveals that two out of the six populations, Dovre and Yukon, are significantly influenced by the stratification treatment, for Dovre, in both germination fraction (Fig. 1) and time to germination (Table 4). Stratification, however, has no effect on the light requirements of most populations; the Light * stratification interaction term is nonsignificant for both germination fraction (Table 2) and time to germination (Table 3).

Responses to light were found to be divergent among the six arctic and alpine populations in both germination fraction (Fig. 1) and time to germination (Fig. 2). Light had no influence on the germination of seeds from Jasper, Iqaluit, and Yukon populations (Fig. 1). As in the previous germination tests with this species and these populations (Wagner 2007), the

Table 2 Analysis of variance of germination fraction in light and dark conditions of unstratified and stratified seeds of six populations of *Koenigia islandica*, from Svalbard, Iqaluit, Dovre, Yukon, Jasper, and Colorado

Source	df	MS	F	P
Population	5	0.424	18.989	<0.0001
Light	1	3.348	149.686	<0.0001
Stratification	1	0.008	0.397	0.5314
Population * light	5	0.386	17.287	<0.0001
Population * stratification	5	0.181	8.130	<0.0001
Light * stratification	1	0.041	1.854	0.1796
Population * stratification * light	5	0.142	6.352	0.0001

Table 3 Analysis of variance of time to germination in light and dark conditions of unstratified and stratified seeds of six populations of *Koenigia islandica*, from Svalbard, Iqaluit, Dovre, Yukon, Jasper, and Colorado

Source	df	MS	F	P
Population	5	5818.762	103.650	<0.0001
Light	1	6794.84	121.037	<0.0001
Stratification	1	0.00798	0.0001	0.9905
Population * light	5	1383.828	24.650	<0.0001
Population * stratification	5	575.991	10.260	<0.0001
Light * stratification	1	55.361	0.986	0.3209
Population * light * stratification	5	270.383	4.816	0.0002

Fig. 1 Germination fraction for unstratified and stratified seeds in six populations of *Koenigia islandica* at 27°C. *Solid lines* represent germination in dark conditions, *dotted lines* represent germination under light. *Different letters* (below for dark germination, above for light germination), indicate figure-wide significant differences according to post-hoc Tukey HSD-tests (see Table 2). Error bars indicate ±1 SD
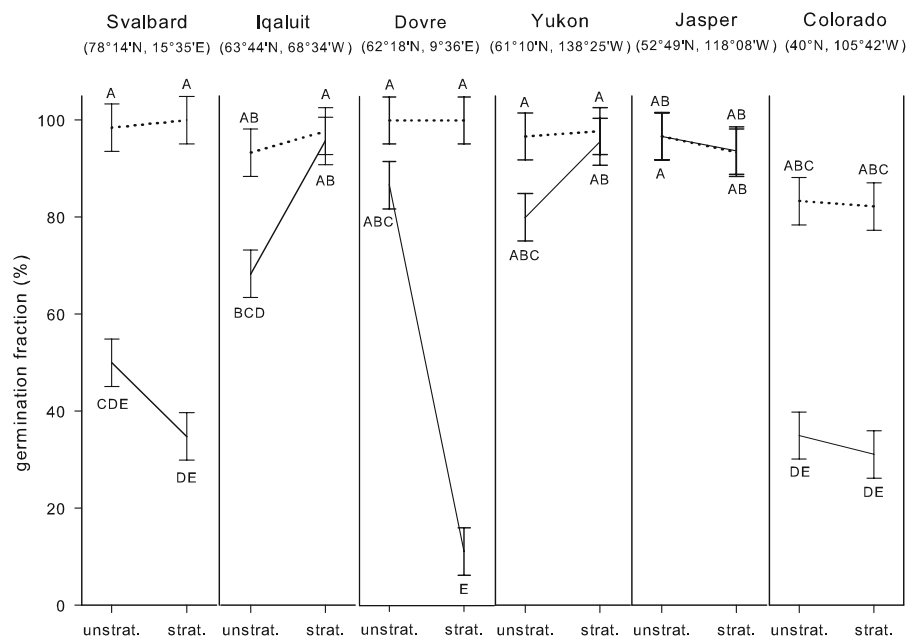
populations from the two extreme tundra environments, the high arctic Svalbard and the low latitude alpine population from Colorado, had very similar germination responses. Light strongly promoted germination in seeds of both populations, whereas stratification did not decrease their light requirement (Fig. 1). The Dovre population's germination response differed markedly: unstratified seeds in both light and dark, and stratified seeds in light germinated readily (Fig. 2) and in high percentage (Fig. 1). Cold stratification, however, induced a strong light requirement in the Dovre seeds; only 11% of the stratified seeds of this population germinated in the dark (Fig. 1).

Table 4 Mean time to germination (days) of unstratified and stratified seeds of six populations of *Koenigia islandica* in light and dark conditions

Populations	Dark		Light	
	Unstratified	Stratified	Unstratified	Stratified
Svalbard 78°14′N 15°35′E	28.76[AB]	35.81[A]	15.19[C]	13.42[CD]
Iqaluit 63°44′N 68°34′W	11.34[CDEFG]	5.93[FGHI]	5.46[HI]	2.72[I]
Dovre 62°18′N 9°36′E	5.67[GHI]	19.00[BCDE]	3.63[I]	8.11[DEFGHI]
Yukon 61°10′N 138°25′W	15.64[C]	9.16[DEFGH]	5.48[HI]	3.22[I]
Jasper 52°49′N 118°08′W	6.28[EFGHI]	5.40[HI]	5.25[HI]	3.28[HI]
Colorado ∼40°N ∼105°42′W	13.00[CDEF]	8.71[CDEFGHI]	11.94[CD]	12.81[CD]

Values with different letters indicate table-wide significant differences according to post-hoc Tukey HSD-tests (see Table 3)

Fig. 2 Trends in time to germination for unstratified and stratified seeds of six populations of *Koenigia islandica* at 27°C, in dark and light conditions. *Solid lines* represent germination in dark, *dotted lines* germination in light. *Thin lines* are for unstratified seeds, *bold lines* for stratified seeds
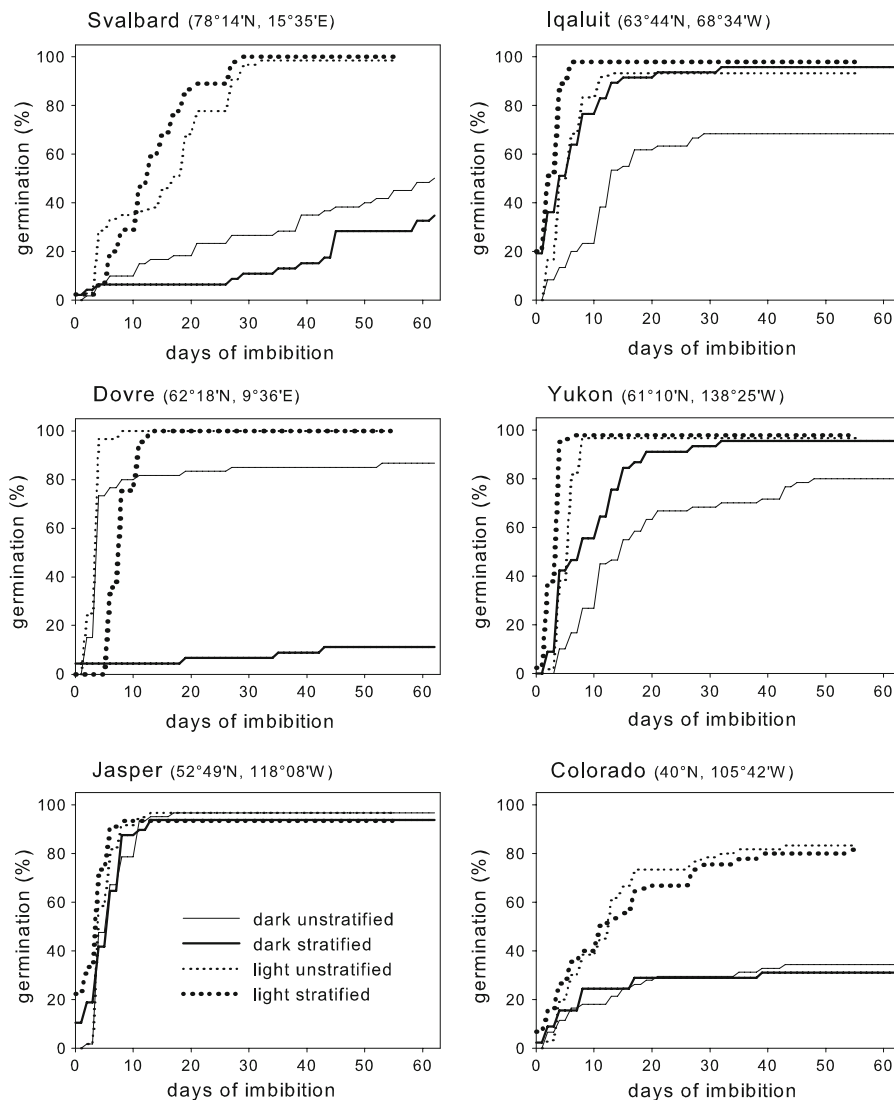
Table 5 Germination fractions of remaining ungerminated *Koenigia islandica* seeds of the dark treatment (see Table 3), 2 weeks after being moved into light conditions

	Svalbard	Iqaluit	Dovre	Colorado
Unstratified	80	57.14	62.50	44.44
Stratified	86.66	–	79.48	68.42

The lack of germination in dark conditions in some populations cannot be attributed entirely to dead or deeply dormant seeds; over 70% of the previously ungerminated seeds of the dark treatment germinated within 2 weeks of exposure to light in the germination chamber (Table 5), although some populations showed lower germination fractions.

Discussion

The results of the experiment indicate that significant differences exist among the six populations in the germination responses of their seeds to light, and in the effect of stratification on these light requirements. These differences were maintained over one or more generations of plants grown under laboratory conditions, indicating that the observed differences are genetically based.

The observed light germination responses are generally consistent with divergence in morphological, life-history and phenological traits (Wagner and Simons 2008b): differentiation occurs among populations differing in environmental characteristics related to severity, such as mean growth season temperatures, and extreme maximum and minimum summer temperatures. For example, despite originating from study sites situated at the extremes of the tundra gradient, the high arctic Svalbard population and the southern alpine population from Colorado have very similar germination responses to light and stratification. The two populations are from sites with especially severe climates (Wagner and Simons 2008b), and have the strictest light requirements which are undiminished by the stratification treatment. The finding in *K. islandica* that populations from sites with severe climates, according to the criteria used here, have stronger light requirements than populations from milder climates is in agreement with results of studies on the perennial sagebrush, *Artemisia tridentata* (Meyer et al. 1990).

The strong light requirement of the Svalbard and Colorado populations, even at the temperature at which their seeds normally reach their highest germination fraction (27°C; Wagner 2007), leads to another interesting consequence. Germination light requirement is considered to be one of the main factors that promote the formation of large soil seed banks (Kettenring et al. 2006; Milberg and Andersson 1997; Pons 1991; Shimono and Kudo 2005) and it is thus likely that these two *K. islandica* populations form important seed banks. This is suggested also by the fact that the climates these populations experience are marginal for the high germination temperature requirements of their seeds, especially in the case of the Svalbard populations (Wagner 2007). Unfortunately, there is little information on *K. islandica* soil seed banks (Cooper et al. 2004; Reynolds 1984b); the only study directly investigating *K. islandica* seed banks in the soil reports only a small residual seed bank for an alpine population from Montana (Reynolds 1984b). However, this population was also found not to have a germination light requirement (Reynolds 1984a), which is consistent with the observation that a light requirement for germination is necessary for the formation of large seed banks (see citations above). Further work is needed to investigate whether *K. islandica* populations with strong light requirements have important residual seed banks.

Previous studies reported that stratification diminishes the light requirement of seeds of spring germinators from temperate (Milberg and Andersson 1997; Schütz and Milberg 1997; Schütz and Rave 1999), as well as arctic and alpine regions (Densmore 1997; Schütz 2002; Shimono and Kudo 2005). The results of this experiment contradict these findings; the seeds of none of the analyzed populations germinated at significantly higher rates after stratification. It must be noted, however, that the temperature of 27°C used in this experiment is that at which the seeds of most of the investigated populations, including unstratified seeds, germinate best. The possibility exists that potential significant differences among stratification treatments in light and dark were hidden by the very high percentages of seed germination at this temperature. If tested for light requirements at suboptimal temperatures of, for example, 24°C, seeds of the Iqaluit and Yukon populations might reveal significant effects of stratification on light requirement.

Consistent with previous findings on other traits (Wagner 2007; Wagner and Simons 2008a), the most divergent germination responses were exhibited by the Dovre population. The strong light requirement for germination following stratification, together with the observed decrease in germinability at low temperatures following stratification (Wagner 2007) matches the germination syndrome of some autumn germinators (Milberg and Andersson 1998). This is a very surprising trait in a plant from an environment where all species are supposedly spring germinators. However, the possibility also exists that the low germination fraction of the seeds, i.e., their dormancy in the dark, was induced not by the stratification treatment, but by the dark condition itself (Pons 1991). Since light requirement induced by burial and dark conditions is another important mechanism of seed bank formation (Milberg and Andersson 1997; Pons 1991), it can be again hypothesized that the Dovre population too forms important seed banks in the soil. These issues merit future study.

This experiment presents evidence for divergence in germination light requirements among six arctic and alpine *K. islandica* populations, divergence that is genetically based. Differences appear to be related to climate severity but, because of the complex differences among the environmental characteristics of the sites of origin, the precise adaptive significance of the observed differences are not known. Nevertheless, it is cautioned that strong evolved differences among arctic and alpine populations of *K. islandica* are likely indicative of local adaptation which, in turn, signals particular sensitivity to an altered climate regime.

References

Acharya SN (1989) Germination response of two alpine grasses from the Rocky Mountains of Alberta. Can J Plant Sci 69:1165–1177

Barry RG (1973) A climatological transect on the east slope of the Front Range, Colorado. Arct Alp Res 5:89–110. doi: 10.2307/1550251

Baskin CC, Baskin JM (1988) Germination ecophysiology of herbaceous plant species in a temperate region. Am J Bot 75:286–305. doi:10.2307/2443896

Baskin CC, Baskin JM (1998) Seeds. Ecology, biogeography and evolution of dormancy and germination. Academic Press, San Diego

Bell KL, Bliss LC (1980) Plant reproduction in a high arctic environment. Arct Alp Res 12:1–10. doi:10.2307/1550585

Bell G, Collins S (2008) Adaptation, extinction and global change. Evol Appl 1:3–16. doi:10.1111/j.1752-4571.2007.00011.x

Billings WD (1973) Arctic and alpine vegetations: similarities, differences, and susceptibility to disturbance. Bioscience 23:697–704. doi:10.2307/1296827

Billings WD (1974) Arctic and alpine vegetation: plant adaptations to cold summer climates. In: Ives JD, Barry RG (eds) Arctic and alpine environments. Methuen, London, pp 371–402

Cavieres LA, Arroyo MTK (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). J Ecol 89:31–39. doi: 10.1046/j.1365-2745.2001.00514.x

Cooper EJ, Alsos IG, Hagen D, Smith FM, Coulson SJ, Hodkinson ID (2004) Plant recruitment in the High Arctic: seed bank and seedling emergence on Svalbard. J Veg Sci 15:115–124. doi:10.1658/1100-9233(2004)015[0115:PRITHA]2.0.CO;2

Densmore RV (1997) Effect of day length on germination of seeds collected in Alaska. Am J Bot 84:274–278. doi: 10.2307/2446088

Fenner M (1991) The effect of the parent environment on seed germinability. Seed Sci Res 1:75–84

Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proc Natl Acad Sci USA 104:1278–1282. doi: 10.1073/pnas.0608379104

Greenland D (1989) The climate of Niwot Ridge, Front Range, Colorado, USA. Arct Alp Res 21:380–391. doi:10.2307/1551647

Grime JP, Mason G, Curtis AV, Rodman J, Band SR (1981) A comparative study of germination characteristics in a local flora. J Ecol 69:1017–1059. doi:10.2307/2259651

Hedberg O (1997) The genus *Koenigia* L. emend. Hedberg (Polygonaceae). Bot J Linn Soc 124:295–330

Heide OM, Gauslaa Y (1999) Developmental strategies of *Koenigia islandica*, a high-arctic annual plant. Ecography 22:637–642. doi:10.1111/j.1600-0587.1999.tb00512.x

Hultén E (1971) The circumpolar plants. II. Dicotyledons. Almqvist & Wiksell, Stockholm

Kettenring KM, Gardner G, Galatowitsch SM (2006) Effect of light on seed germination of eight wetland *Carex* species. Ann Bot (Lond) 98:869–874. doi:10.1093/aob/mcl170

Körner C (1999) Alpine plant life: functional plant ecology of high mountain ecosystems. Springer, Berlin

Meyer SE, Monsen SB, Mcarthur ED (1990) Germination response of *Artemisia tridentata* (Asteraceae) to light and chill: patterns of between-population variation. Bot Gaz 151:176–183. doi:10.1086/337817

Milberg P, Andersson L (1997) Seasonal variation in dormancy and light sensitivity in buried seeds of eight annual weed species. Can J Bot 75:1998–2004

Milberg P, Andersson L (1998) Does cold stratification level out differences in seed germinability between populations? Plant Ecol 134:225–234. doi:10.1023/A:1009793119466

Milberg P, Andersson L, Noronha A (1996) Seed germination after short-duration light exposure: implications for the photo-control of weeds. J Appl Ecol 33:1469–1478. doi:10.2307/2404785

Mooney HA, Billings WD (1961) Comparative physiological ecology of arctic and alpine populations of *Oxyria digyna*. Ecol Monogr 31:1–29. doi:10.2307/1950744

Pons TL (1991) Induction of dark dormancy in seeds: its importance for the seed bank in the soil. Funct Ecol 5:669–675. doi:10.2307/2389487

Reynolds DN (1984a) Alpine annual plants: phenology, germination, photosynthesis, and growth of three Rocky Mountain species. Ecology 65:759–766. doi:10.2307/1938048

Reynolds DN (1984b) Populational dynamics of three annual species of alpine plants in the Rocky Mountains. Oecologia 62:250–255. doi:10.1007/BF00379022

SAS Institute Inc (2007) JMP statistics and graphics guide. SAS Institute, Carry

Schütz W (2002) Dormancy characteristics and germination timing in two alpine *Carex* species. Basic Appl Ecol 3:125–134. doi:10.1078/1439-1791-00090

Schütz W, Milberg P (1997) Seed dormancy in *Carex canescens*: regional differences and ecological consequences. Oikos 78:420–428. doi:10.2307/3545604

Schütz W, Rave G (1999) The effect of cold stratification and light on the seed germination of temperate sedges (*Carex*) from various habitats and implications for regenerative strategies. Plant Ecol 144:215–230. doi:10.1023/A:1009892004730

Shimono Y, Kudo G (2005) Comparisons of germination traits of alpine plants between fellfield and snowbed habitats. Ecol Res 20:189–197. doi:10.1007/s11284-004-0031-8

Simons AM (2002) The continuity of microevolution and macroevolution. J Evol Biol 15:688–701. doi:10.1046/j.1420-9101.2002.00437.x

Simons AM, Johnston MO (2000) Variation in seed traits of *Lobelia inflata* (Campanulaceae): sources and fitness consequences. Am J Bot 87:124–132. doi:10.2307/2656690

Simons AM, Johnston MO (2006) Environmental and genetic sources of diversification in the timing of seed germination: implications for the evolution of bet hedging. Evolution 60:2280–2292

Wagner I (2007) A comparison of life-history characters of arctic and alpine populations of the annual *Koenigia islandica*. PhD thesis, Carleton University, Ottawa

Wagner I, Simons AM (2008a) Intraspecific divergence in seed germination traits between high and low latitude populations of the arctic–alpine annual *Koenigia islandica*. Arct Antarct Alp Res 40:233–239. doi:10.1657/1523-0430(07-003)[WAGNER]2.0.CO;2

Wagner I, Simons AM (2008b) Divergence among arctic and alpine populations of the annual, *Koenigia islandica*: morphology, life-history, and phenology. Ecography. doi:10.1111/j.1600-0587.2008.05497.x

Zuloaga FO, Morrone O (1999) Catálogo de las plantas vasculares de la República Argentina. II. In: Monographs in systematic botany, vol 74. Missouri Botanical Garden, USA, pp 1–1269