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ORIGINAL PAPER

Germinating seeds or bulbils in 87 of 113 tested Arctic species indicate potential for ex situ seed bank storage

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Abstract Arctic plant species are expected to lose range due to climate change. One approach to preserve the genetic and species diversity for the future is to store propagules in seed vaults. However, germinability of seeds is assumed to be low for Arctic species. We evaluated ex situ storage potential of 113 of the 161 native angiosperms of Svalbard by studying seed ripening and germination. Seeds or bulbils were collected, and germinability was tested after one winter of storage in the Svalbard Global Seed Vault. Twenty-six of the species did not produce ripe propagules, 8 produced bulbils, and 79 produced seeds. Bulbils sprouted to high percentages. Seeds of 10 species did not germinate, 22 had low germination $(\leq 20 \%)$, 34 had germination of 21–70 %, and 13 had high germination percentages $(>70 \%)$. More than 70 % of the species belonging to Asteraceae, Brassicaceae, Caryophyllaceae, Juncaceae, Rosaceae, and Saxifragaceae germinated. Cold tolerant, common species had higher germination percentages than relatively thermophilous, rare species. Germination percentages were six times higher than observed

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in 1969 ($n = 51$) and 0.7 times that observed in 2008 $(n = 22)$, indicating that recent climate warming improves germination in the Arctic. While in situ conservation is of vital importance, ex situ conservation in seed banks is a potential complementary conservation strategy for the majority of Arctic vascular plant species. For species that did not germinate, other methods for ex situ conservation should be sought, for example, growing in botanical gardens.

Keywords Arctic · Bulbils · Conservation · Seed germination · Rare · Red List

Introduction

Climate change, invasive species, land use, and other human impact may threaten a large part of the words flora (Sala et al. [2000;](#page-12-0) Pimentel [2011;](#page-12-0) Thuiller et al. [2011](#page-13-0)). To meet these challenges, many nations now collect and bank seeds for restoration purposes, ex situ conservation, and relocation (Vitt et al. [2010](#page-13-0)). While large efforts are made to bank the entire flora of, for example, the USA and UK [\(http://www.nps.gov/plants/sos/,](http://www.nps.gov/plants/sos/) [http://www.kew.org/\)](http://www.kew.org/), the Arctic flora is so far underrepresented in these seed banks. A relatively low proportion of the Arctic flora is rare and considered endangered (Talbot et al. [1999](#page-13-0); Elven et al. [2011](#page-12-0)); however, even common species may be threatened as the expected profound changes in Arctic climate (ACIA [2006](#page-11-0)) may reduce species ranges by 40 % followed by considerable loss of genetic diversity (Alsos et al. [2012a](#page-11-0)). Also, increased human activities combined with climate change increase the risk of establishment of alien species (Ware et al. [2012](#page-13-0)), which may have negative effect on the native flora. A prerequisite for storing seeds is that they are

viable, but knowledge of germinability of seeds and bulbils of the Arctic flora is still scarce. In earlier studies, the proportion of species producing viable seeds and their germination percentages were found to be lower in the Arctic than in other regions (Sørensen [1941](#page-12-0); Bliss [1958](#page-11-0); Eurola [1972](#page-12-0); Bell and Bliss [1980\)](#page-11-0). However, a recent study of 22 Arctic species indicated increased germination, partly owing to increased temperature (Müller et al. [2011](#page-12-0)). Knowledge of germinability of seeds and bulbils for more species is required to evaluate if Arctic flora can be additionally conserved ex situ in seed vaults.

Many factors are likely to influence seed production and viability in the Arctic. Two main factors are the short growing season and the low temperatures, which are especially pertinent for relatively thermophilous species that may only be able to set viable seeds in infrequent years of high summer temperatures (Sørensen [1941](#page-12-0); Wookey et al. [1995](#page-13-0); Alsos et al. [2003\)](#page-11-0). Low temperatures also reduce pollinator activity (Hodkinson et al. [1998\)](#page-12-0) and drive the reproduction mode towards asexuality (Peck et al. [1998\)](#page-12-0), which may influence successful reproduction and seed set. Although some species reproduce with asexual (apomictic) seeds, many essentially rely on runners or bulbils for dispersal (Wehrmeister and Bonde [1977](#page-13-0); Murray [1987](#page-12-0); Dormann et al. [2002](#page-12-0)). Bulbils are analogous to seeds in terms of dispersal, but they are generally more vulnerable as they lack the protection of a seed coat. Thus, their prospects for long-term storage may be low (Walck et al. [2010](#page-13-0)). However, while asexual reproduction is successful and important in the Arctic flora, it is rarely exclusive, and ripe seeds of most species may be found in favourable sites or years, even for those species mainly reproducing by bulbils (Murray [1987](#page-12-0)).

The flora of the Arctic archipelago Svalbard is typical for the mid-to-high Arctic flora as insect-pollinated herbs, in terms of species number, are dominating (Brochmann and Steen [1999](#page-11-0)). Different from most low-to-mid Arctic sites, there are no bumble bees on the archipelago, and pollination is mainly by flies (Diptera) [\(http://svalbardin](http://svalbardinsects.net/)[sects.net/](http://svalbardinsects.net/), Coulson and Refseth [2004\)](#page-12-0). It is assumed that 97 of 161 angiosperms in Svalbard reproduce mainly sexually (Brochmann and Steen [1999](#page-11-0)). In the most comprehensive study on germination from Svalbard, 19 of 63 mainly common species did not germinate, whereas those that did germinate generally had low germination rates (Eurola [1972\)](#page-12-0). However, more recent studies on five (Hagen [2002\)](#page-12-0) and 22 (Müller et al. 2011), mainly common species, show higher germination rates. Very rare $(1-4$ localities) and rare (5–25 localities) species constitute 36 % of the flora of Svalbard (Brochmann and Steen [1999](#page-11-0)). Due to the geographic isolation of the archipelago, a separate evaluation of threats to the species has been made, and 54 of them have been redlisted; 10 as critically endangered, 10 as endangered, and 17 as near threatened (Solstad et al. [2010](#page-12-0)). The majority of rare species are relatively thermophilous (Elven and Elvebakk [1996](#page-12-0); Engelskjøn et al. [2003](#page-12-0)). These may have colonized the archipelago during the Holocene hypsithermal 8000–4000 BP (Alsos et al. [2002,](#page-11-0) [2007](#page-11-0)), when the climate was $1-2$ °C warmer than today (Birks et al. [1994\)](#page-11-0), and may persist in the current climate predominately by clonal growth (Alsos et al. [2002\)](#page-11-0). With a warming climate, recruitment of the thermophilous species may also increase, as has been observed for common Arctic species (Müller et al. [2011\)](#page-12-0).

The aims of this study were to (1) collect seeds or bulbils from as many species as possible of Svalbard's native vascular flora, (2) test whether germinability of species is appropriate for ex situ conservation in seed banks, (3) test whether germinability is related to thermal requirements, rarity, or ability to reproduce clonally, and (4) compare with earlier studies to see if germination has recently increased. New test of germination is planned again after 5 and 10 years. However, as we present data on 55 species not studied in Svalbard before, and as this is the largest study of germination in Arctic plants since Sørensen's studies in Greenland (Sørensen [1941](#page-12-0)), we present the results of germination after 1 year of storage here.

Materials and methods

Collection and storage of seeds

Seeds were collected in paper bags between 27 August and 19 September 2008 in the Isfjorden area of Svalbard (Appendix 1 of Electronic supplementary material, Fig. [1](#page-4-0)). If possible, seeds were shaken out of the plants to ensure that only mature seeds were collected. However, if the plants were wet, seed capsules were collected and left in paper bags at $5-8$ °C in 35 % relative humidity (RH) to dry. Seeds that were obviously not ripe were not collected. Seeds of species which did not seem 100 % ripe (Arnica angustifolia, Carex glacialis, Carex marina ssp. pseudolagopina, Coptidium pallasii, Micranthes hieracifolia ssp. hieracifolia, Petasites frigidus ssp. frigidus, and Ranunculus wilanderi) were left in paper bags at $5-8$ °C until 19 September to permit ripening, after which they were assumed to be ripe. Nuts of Empetrum nigrum were washed out of the berries. Herbarium vouchers were collected and deposited at Tromsø University Museum (TROM).

For this first germination test following one winter of storage, and also for each of two tests planned for the future, seeds were counted and placed in sealed aluminium bags. The bags were placed at -2 °C on 15 or 24 September 2008 and stored outside at about -6 °C from 1 October. A temperature logger (Tinytag Plus 2 TGP-4020)

Fig. 1 Sites where seeds were collected for studies of germination and for long-term storage in the Svalbard Global Seed Vault

was placed in one of the boxes 2 October. The temperature dropped to -10 °C during the night of 2 October. On 3 October, the seed boxes were placed in the Svalbard Global Seed Vault where the temperature was about -14 °C. The box with the seeds for germination trials was taken out of the Svalbard Global Seed Vault on 27 April 2009. Thus, this first year of storage resembles what seeds of Arctic species experience under natural conditions as they ripe in autumn and normally do not germinate within the season they are produced (Söyrinki [1939;](#page-13-0) Sørensen [1941\)](#page-12-0). As a period of frost usually enhance germination in Arctic species (Söyrinki [1939\)](#page-13-0), no fresh seeds were germinated.

Stratification and germination of seeds

Usually 3×50 seeds of each species were put in Petri dishes (9 cm in diameter) with 10 % agar solution and covered with a lid to ensure high moisture conditions. Thereafter, the seeds were either stratified for a period at 1 °C, or put directly to germination at 24 h 10 °C, 24 h 20 °C, or 12 h 10 °C and 12 h 20 °C (Appendix 2 of Electronic supplementary material). Stratification and germination conditions selected for each species were based on an extensive review of seed germination trials of the same species or genera (not shown), or after recommendations from Lindsay Robb at the Millenium Seed Vault (personal communication). The light temperature was 4,000 K (Osram 35 W, 840 HE) and the brightness was 3,300 lm (manufacturer's information). The proton flux was approximately 40 µmol per square meter per second measured with a quantum flux sensor at the level of the seeds. If the germination percentage obtained was low, but the seeds still seemed viable, a new germination test was attempted following an additional period of stratification (Appendix 2 of Electronic supplementary material). Only final germination percentages are given in Table 1.

Table 1 Germination percentages of species from the Arctic Archipelago of Svalbard

Species	$\%$
Alopecurus borealis	Ω
Arabis alpina	6.6
Arctagrostis latifolia (EN)	
Arctophila fulva	
Arenaria pseudofrigida	30.5
Arnica angustifolia	0.7
Betula nana var. tundrarum (NT)	Ω
Bistorta vivipara ^a	100.0
Braya glabella ssp. purpurascens	60.3
Calamagrostis neglecta ssp. groenlandica	
Campanula rotundifolia ssp. gieseckiana (VU)	
Cardamine polemonioides	
Carex bigelowii ssp. ensifolia (CR)	
Carex fuliginosa ssp. misandra	Ω
Carex glacialis (VU)	8.1
Carex krausei (VU)	67.1
Carex lachenalii	14.1
Carex lidii (VU)	
Carex marina ssp. pseudolagopina (VU)	Ω
Carex maritima	2.7
Carex nardina ssp. hepburnii	Ω
Carex parallela ssp. parallela	
Carex rupestris	2.0
Carex saxatilis ssp. laxa	

Table 1 continued

for all species. Rarity in Svalbard (very rare $= 1-4$

populations, rare $= 5-25$ populations, and common) was given according to Elven and Elvebakk ([1996\)](#page-12-0) except for two species where the taxonomy later has been clarified; Carex bigelowii ssp. ensifolia is found one place (Solstad et al. [2010](#page-12-0)) and F. edlundia is common (Alsos et al. [2012a](#page-11-0)). We classified the species into five groups of thermophily (strongly, distinctly, moderately, weakly, indifferent) according to Elvebakk [\(1989](#page-12-0)) except for species not classified by him: Carex krausei, Eriophorum \times soerensenii, Festuca edlundia, Ranuculus wilanderi, Saxifraga rivularis ssp. rivularis, and S. svalbardensis. For these species, we used Elvebakk's criteria combined with known distribution (Alsos et al. [2012a](#page-11-0)). Clonal modes of propagations were according to Brochmann and Steen ([1999\)](#page-11-0) except for C. bigelowii ssp. ensifolia which was according to Brooker et al. [\(2001](#page-12-0)). Species producing runners, stolons, or bulbils were classified as clonal, and others as nonclonal (including species with apomictic seeds). No data on reproduction were available for *Eriophorum* \times *sorensenii*. Nomenclature follows Elven et al. [\(2011](#page-12-0)).

Comparison with other studies

There are four previous studies on germination from Svalbard that includes a minimum of three species. Eurola [\(1972](#page-12-0)) collected seeds in the vicinity of Longyearbyen and the climatically similar location Svea in 1969. In addition, he collected some seeds along altitudinal gradients. His mean values from Longyearbyen and Svea are used if he collected the species there; otherwise, data from other sites were used. Hagen (2002) (2002) (2002) and Müller et al. (2011) (2011) collected seeds in the vicinity of Longyearbyen in 1998 and 2008, respectively. For Müller, germination percentages obtained at 18 \degree C in the phytotron were used. Hagen ([2002\)](#page-12-0) displays the germination in graphs and no exact percentages are given. Alsos et al. [\(2003](#page-11-0)) collected seeds of three thermophilous species in Colesdalen; none of them germinated.

To compare with another Arctic region of similar climate, we used the data of Sørensen ([1941\)](#page-12-0). He collected seeds of 99 species in 1934 at Eskimonæs, Northeastern Greenland, and germinated them in the field at the same site. He further collected bulbils of two species and noted lack of ripe seeds in 22 species. This is the only extensive germination study we are aware of which is in the same bioclimatic subzone (subzone C) as the sampling sites in Svalbard. Comparisons were done at species level ignoring that for some species different subspecies occur in the two regions.

Statistics

To test the strength of association between family and thermophily, we initially applied a linear model. However, as the model fit was very poor, we treated thermophily as a variable with five categories and applied a Cramer's V (Acock and Gordon [1979\)](#page-11-0). To test the strength of other two-way association between rarity, thermophily, family, and clonality, we applied Chi square tests for $2 \times X$ contingency tables. Only families with at least three species represented were included. Standard deviations for germination percentages of each species were calculated with a formula for binomial data (Collett [2003](#page-12-0)).

To assess the effect of propagule type, thermophily, rarity, clonality, and family on germination, we applied generalized linear models (GLM) with a quasibinomial error distribution. Each GLM was set up with one predictor variable. Further, to test the influence of the above-mentioned predictor variables also on the proportion of species with ripe seeds, each species that germinated was marked as successful and each species that did not germinate, or for which no seed was initially found, was marked as not successful.

To test for interactions between predictor variables and estimate the biological effect of these variables on germination, a linear mixed effect model (LME) with a binomial error distribution was fitted to the data. As rarity and thermophily was associated, we choose the predictor variable with less levels (rarity). Rarity (levels: rare and common) and main reproduction mode (levels: clonal reproduction present and clonal reproduction absent) were used as categorical predictor variables with fixed effects and plant family as random effect with species nested within family as random effect. For these, the R package lme 4 version 0.999999-0 ([http://lme4.r-forge.r-project.org/\)](http://lme4.r-forge.r-project.org/) was used. All calculations were done in R 2.14.0 (R Core Team [2012](#page-12-0)).

Results

Of the 113 species observed in this study, 79 had ripe seeds and 8 had bulbils (Table [1](#page-4-0)). In addition, 26 species were without ripe seeds (Table [1\)](#page-4-0). All species with bulbils germinated at high percentages (71–100 %).

Of the 79 species with seeds, seeds of 10 species did not germinate; 12 species had very low germination $(\leq 10 \%)$; 10 had low germination (10–20 %); 23 had intermediate germination $(21-50\%)$; 11 had high germination $(51–70 \%)$; and 13 had very high germination ($>70 \%$, Table [1](#page-4-0)). The mean germination was 35 %.

Of the 24 species that germinated to >50 %, all are common in Svalbard with the exception of two species (Appendix 3 of Electronic supplementary material). Five of the 13 species showing very high $(>70 \%)$ germination were of the genus Draba. Surprisingly, the two strongly thermophilous species Juncus albescens and Carex krausei had germination percentages of 91 and 67 %, respectively.

Among the 36 species that either did not germinate or for which no ripe seeds were observed, 22 were strongly or

distinctly thermophilous species, and seven were rare, and six very rare (Appendix 3 of Electronic supplementary material). Of the ten species that did not germinate, there were three species of *Carex*, two of *Coptidium*, one graminoid (Alopecurus borealis), one shrub (Betula nana var. tundrarum), one Asteraceae (Petasites frigidus ssp. frigidus), and the hemiparasites Euphrasia wettsteinii and Pedicularis dasyantha var. dasyantha (Table [1](#page-4-0)).

We found seeds in all except four non-clonal species: Deschampsia sukatschewii ssp. borealis, Minuartia biflora, Polemonium boreale, and Saxifraga aizoides (Table [1,](#page-4-0) Appendix 3 of Electronic supplementary material). Further, seeds of six non-clonal species did not germinate. Seven of the non-clonal species without germinable seeds were common, one rare, and two very rare (Appendix 3 of Electronic supplementary material).

Assumed ripe seeds were found in 12 redlisted species and seeds of eight of these germinated. Another eight redlisted species were examined but had no ripe seeds (Table [1](#page-4-0)).

Effect of species characteristics

There was an association between thermophily and rarity $(\chi^2 = 43.80, df = 5, p < 0.001)$, as all rare species were strongly thermophilous or distinctly thermophilous (Appendix 3 of Electronic supplementary material). There was also an association between thermophily and family (Cramer's V = 0.43, M; $N = 10$; 5, $p = 0.042$). There was no association between family and rarity ($\chi^2 = 7.16$, $df = 9$, $p = 0.620$. Further, there was no association between clonality and rarity ($\chi^2 = 0.012$, $df = 1$, $p = 0.913$, family ($\chi^2 = 15.08$, $df = 9$, $p = 0.089$), or thermophily ($\chi^2 = 4.55$, $df = 4$, $p = 0.337$).

Plant family had a significant influence on germination percentages (Table 2). The applied GLM with plant family as predictor variable for germination percentages had the lowest deviance of all used models (Table 2), and thus, plant family had a comparatively high influence on germinability of seeds. The family that had the highest germination rate was Brassicaceae (57 %), followed by Caryophyllaceae (46 %) and Juncaceae (44 %). Scrophulariaceae (6 %) had the lowest germination percentages, followed by Asteraceae (18%) and Cyperaceae (20%) ; Fig. 2; Table 2). Germination, however, increased with increasing cold tolerance of the species. Also germination percentages were higher for common species than for rare species (Fig. 2; Table 2). Thermophile species either did not produce seeds (e.g. Betula nana and Rubus chamaemorus) or germinated to comparatively low percentages (e.g. Arnica angustifolia and Carex glacialis,

Table 2 Effect of species characteristics on germination percentages of seeds from Svalbard

Predictor variable	Level	Germination $(\%)$	Lower SE	Upper SE	Number of Species	\boldsymbol{n}	df	Residual deviance	F value p	
Propagules	Bulbils	94.09	90.24	96.48	8	23		254 5,509.6	87.54	< 0.001
	Seeds	35.03	33.09	37.01	79	233				
Clonal reproduction	Clonal	25.32	21.87	29.12	20	233		231 5,213.4	8.26	0.004
	Non-clonal	38.32	35.99	40.71	59					
Thermophily	Continuous 1-5	$4.4x + 15.87^{\circ}$	$12.78^{\rm a}$	$19.54^{\rm a}$	79	233	231	4,957.1	22.03	< 0.001
Rarity	Rare	20.46	16.77	24.72	15	43	231	5,129.6	12.58	< 0.001
	Common	38.26	36.03	40.54	64	190				
Family ^b	Asteraceae	18.32	12.21	26.55	$\overline{4}$	11	216	3,966.6	5.43	< 0.001
	Brassicaceae	56.98	51.72	62.08	10	30				
	Caryophyllaceae	46.32	41.02	51.71	10	29				
	Cyperaceae	20.15	16.31	24.62	11	33				
	Juncaceae	43.84	36.63	51.31	5	15				
	Poaceae	35.02	30.43	39.90	12	36				
	Ranunculaceae	29.98	23.26	37.69	6	16				
	Rosaceae	52.06	42.47	61.51	3	9				
	Saxifragaceae	31.10	25.57	37.23	7	21				
	Scrophulariaceae	5.91	2.70	12.41	3	9				

Test statistics for generalized linear models (GLMs) with quasibinomial error distribution are given for all characteristics. Species indicates the number of species included in the particular level, n is the total number of replicates included at a particular level. Test statistics is ANOVA with F tests. Species reproducing by bulbils are only included in the first test, whereas species without ripe seeds in the year of study were excluded from all tests. Germination percentages and SE were backtransformed from the quasibinomial models

^a Germination percentage and SE of the intercept

^b Plant families with less than three species are excluded

Fig. 2 Effect of species traits on the proportion of species germinating ($n < 113$) as well as mean germination percentage of species with ripe seeds ($n \le 79$). a Rarity in Svalbard, **b** thermal requirements, c ability to reproduce clonally, and d plant family (only families with at least three species included, see Table [1\)](#page-4-0). Effect of traits on species

germination was tested separately for the proportion of species germinating and mean germination percentages. Significant effects $(p<0.05,$ Table 3) are indicated by stars. The star in d applies to mean germination only

Table 3 Effect of rarity, clonal reproduction, family, and species on germination in 79 species from Svalbard analysed by linear mixed effect model (LME)

No.	Model term	df	Deviance	AIC	BIC		
	$y \sim$ Rarity * Clonal + (1 Family/Species)		753.50	782.1	803.4		
	$y \sim$ Rarity + Clonal + (1 Family/Species)		754.80	781.7	799.5	1.621	0.203

Model simplification for the given data with two predictor variables (fixed effects) and Family as random effect and Species nested in Family as random effect. No. model number, df degree of freedom, AIC Akaike information criterion, BIC Bayesian Information Criterion, χ^2 for model comparison. The AIC, BIC, and number of variables show that model 2 fits the data best

Appendix 3 of Electronic supplementary material). Similarly, the proportion of species that germinated was higher in common than rare species ($z = -2.008$; $p = 0.045$) as well as non-clonal than clonal species $(z = -2.800,$ $p = 0.005$, whereas there was no effect of the thermophily or family on the proportion of species that germinated $(p>0.05,$ Fig. 2).

No interaction between the predictor variables was found and the interaction term was removed from the model without significant differences between the models (Table 3). The result of the final model is that the predictor variable (rarity) had a significant influence on germination proportions (Table 3). The proportion of germinated seeds in rare species was significantly lower than the proportion of seeds germinating from common species $(z$ value $=$

 -2.680 ; $p = 0.007$). The second predictor variable (main reproduction mode) had also a significant influence on germination proportions. A significantly larger proportion of the seeds germinated from species that is not reproducing clonally compared to the proportion of seeds that germinated from species with a clonal reproduction option (z value $= -2.113$; $p = 0.035$). Overall, the uniform result of the GLMs and the LME (Tables [2](#page-7-0), 3) is, beside the strong influence of species and family traits, that rarity has the strongest influence on seed germination.

Comparison with other studies

In total, 51 of the species studied here had also been studied by Eurola ([1972\)](#page-12-0). The following species characterized as

having no viable seeds based on a tetrazodium test by Eurola [\(1972](#page-12-0)), germinated in our study: Carex lachenalii (14 %), C. ursina (62%) , Hierochloë alpina (14%) , and Stellaria humifusa (94 %); in contrast, no ripe seeds of Poa glauca, Poa pratensis ssp. alpigena, Polemonium boreale, or Stellaria longipes were found in either of the studies (Appendix 3 of Electronic supplementary material). In addition, the following species that did not germinate in the study by Eurola ([1972\)](#page-12-0) did germinate in our study: Cassiope tetragona ssp. tetragona, Dryas octopetala, Minuartia rubella, Ranuculus nivalis, Micranthes hieracifolia ssp. hieracifolia, and Saxifraga hirculus ssp. compacta. The mean germination percentages for the 51 species were six times higher in our study (36 %) compared to Eurola (6 %).

The mean germination percentages were higher in the study by Müller et al. (49 %) than in this study (34 %, $n = 22$). Lack of germination in three thermophilous species as observed by Alsos et al. ([2003\)](#page-11-0) was also observed in this study. Germination percentages were similar to Hagen [\(2002](#page-12-0)) for Bistorta vivipara and Dryas octopetala, but lower in our study for the three other species (Appendix 3 of Electronic supplementary material).

There were 67 species also studied by Sørensen [\(1941](#page-12-0)). All 37 species that germinated in Sørensen's study also germinated in our study except Betula nana, Euphrasia wettsteinii, and Minuartia biflora. Ten of 15 species that did not germinate in Sørensens's study germinated in our study. In addition, six of 15 species were Sørensen found no ripe seeds, germinated in our study (Appendix 3 of Electronic supplementary material).

Discussion

The proportion of species with viable propagules (79 with seeds and eight with bulbils of 113 species) and the germination percentages obtained (mean 35 %) are both high compared to some previous studies from Svalbard (Appendix 3 of Electronic supplementary material) and other Arctic regions (Sørensen [1941;](#page-12-0) Bliss [1958](#page-11-0)), and more in accordance with other reports from the Arctic (Mooney and Billings [1961;](#page-12-0) Bliss and Gold [1999](#page-11-0); Müller et al. [2011\)](#page-12-0). Thus, the ability to bank propagules of Arctic species for future restoration and conservation purposes is generally high. The low proportion $(<50 \%)$ of rare species germinating is of concern, as they are of highest conservation need, and alternative management strategies to seed banking and in situ conservation must be sought.

The generally improved germination observed in this study compared to Eurola [\(1972](#page-12-0)) could be partly due to improved stratification and germination treatment technique applied in our study, but also due to a greater temperature sum during the year of our study (1 May–30 September 2008, 489.6 K, mean 3.2 ° C) in comparison with Eurola (1 May–30 September 1969, 376.0 K, mean 2.5 °C). Also, the higher proportion of species that germinated in our study compared to Sørensen's study (Sørensen [1941\)](#page-12-0) strengthens the view that germination in Arctic species is increasing due to current climate warming (Müller et al. 2011).

Germination in relation to rarity, thermal requirements, and clonality

The strong association between rarity and thermophily suggests that thermal requirements limit recruitment in rare plants, which in turn limit their distribution. Rare and thermophilous species also do not germinate from natural Arctic seed banks (Cooper et al. [2004\)](#page-12-0). However, germinability may vary strongly among years (Laine et al. [1995](#page-12-0)), and sexual reproduction may occur only in infrequent, favourable years, as indicated by the levels of genetic diversity found in some rare, thermophilous species (Alsos et al. [2002](#page-11-0)). For some species, poor recruitment could be due to factors other than thermal constrains. In the species of assumed hybrid origin, Carex lidii and Eriopho $rum \times sorensenii$, lack of seeds could be due to problems with chromosome paring as observed in other hybrids (Comai [2005](#page-12-0)). In Carex marina ssp. pseudolagopina and Coptidium pallasii, lack of germination may be due to difficulties in breaking dormancy, as physiological and morphophysiological dormancy probably is evident in each of these species, respectively (Baskin and Baskin [2001](#page-11-0)). In the hemiparasite Euphrasia wettsteinii, which most regularly set ripe seeds in Svalbard as it is annual, host stimulus is not required but germination may be sensitive to stratification conditions (Liebst and Schneller [2008](#page-12-0)).

In contrast, the unexpected high germination percentages recorded in some rare and thermophilous species indicate that distribution of rare species may be limited by factors other than germinability of seeds. Juncus albescens, of which 91 % seeds germinated in this study, could be limited by factors such as availability of rich mire sites (cf. (Elvebakk [1994](#page-12-0))), whereas Carex krausei, which had a germination rate of 67 %, could be a recent immigrant that has further dispersal potential as it has only recently been discovered at two sites in Svalbard (Artsdatabanken [2010](#page-11-0)). The relatively high germination percentage (28 %) of the endemic, assumed apomictic species Ranuculus wilanderi (Jonsell [2001](#page-12-0)), is based on 18 seeds only: due to the small population size (Artsdatabanken [2010\)](#page-11-0), the total seed production is low and may constrain any spread of this endangered species. For all three species, also the seedling survival stage may be limiting, as seedling survival may be low even in common species (Karsdóttir and Aradóttir [2006](#page-12-0)). Low seedling survival in nature may, however, not be a problem for management purposes as high survival rates may be obtained in horticulture as observed for R. wilanderi, which is now conserved ex situ in Tromsø Arctic-Alpine Botanical Garden.

As we have collected seeds mainly in the warmest sites of Svalbard, we missed rare species that are cold tolerant. However, most rare species are thermophilous. Among the 54 species on the redlist for Svalbard (Artsdatabanken [2010\)](#page-11-0), 30 are classified as strongly thermophilous, 11 as distinctly thermophilous, and two as moderately thermophilous (Elvebakk [1989\)](#page-12-0). Further, four are classified as weakly thermophilous and five are unclassified by Elvebakk [\(1989](#page-12-0)). Only Draba pauciflora and Puccinellia vahliana, both near threatened, are classified as temperature indifferent. The latter germinated to 52 % in our study indicating that cold tolerant rare species may be limited by other factors than temperature.

Lack of germinable seeds in 23 common species was unexpected. It is unlikely that they obtained their current distribution in Svalbard (Alsos et al. [2012a\)](#page-11-0) by vegetative reproduction alone. Exceptions are Cerastium regelii, Puccinellia phryganodes ssp. villfoidea, and Stellaria longipes, which achieve efficient dispersal by shoots (and possible Poa pratensis ssp. alpigena, where the relationship between viviparous and seminiferous forms is unclear, Elven et al. [2011](#page-12-0)). Although ten of the species are somewhat thermophilous and may only reproduce infrequently (Carex parallela ssp. parallela, C. saxatilis, ssp. laxa, Coptidium lapponicum, Eriophorum triste, Deschampsia sukatschewii ssp. borealis, Poa glauca, Polemonium boreale, Salix reticulata, Petasites frigidus ssp. frigidus, and Pedicularis dasyantha var. dasyantha), the other ten are rather hardy and thus not expected to be constrained by the current climate. For Carex nardina ssp. hepburnii and C. fuliginosa ssp. misandra, the germination failure may be related to breaking of dormancy, as this can be problematic in sedges generally (Budelsky and Galatowitsch [1999](#page-12-0); Schütz [2000](#page-12-0)). Five of the species, Alopecurus borealis, Festuca rubra ssp. richardsonii, Minuartia biflora, Pedicularis dasyantha var. dasyantha, and Saxifraga platysepala, germinated to low percentages from seeds or seed banks in other studies from Svalbard (Eurola [1972](#page-12-0); Cooper et al. 2004 ; Müller et al. 2011), indicating that the lack of ripe seeds or germination in our study may be due to, for example, annual variation. Similarly, for Arctophila fulva, Cardamine polemonioides, and Saxifraga aizoides, lack of ripe seeds can also be a result of annual variation, although we are not aware of any other germination tests of these species from Svalbard. For the latter one, sexual reproduction must take place as it has no means of clonal reproduction.

The higher proportion of non-clonal than clonal species germinating was expected as non-clonal species rely on reproduction by seeds for long-term survival, and due to the trade-off between biomass investment in generative and vegetative plant structure (Herben et al. [2012\)](#page-12-0). Lack of germinable seeds in ten non-clonal may be related to unripe seeds in the year of study or difficulties of breaking dormancy as discussed above. Also, delimitation of clonality is not straightforward (Klimešová and Doležal [2011](#page-12-0)), and even species that we classified as non-clonal following Brochmann and Steen ([1999\)](#page-11-0) may regenerate by short lateral shoots as, for example, the tussock forming grass Deschampsia sukatschewii ssp. borealis. Species may also survive for long periods due to high age as, for example, Betula nana (up to 147 years, Miller [1975\)](#page-12-0) and may therefore sustain a population even with infrequent reproduction.

Perspectives for seed banking

The overall high germination rate $(71–100\%)$ of bulbils confirms that this is an efficient means of recruitment. Thus, bulbils may be useful at least for short-term storage. For the bulbil producing species studied here, storing seeds may not be an alternative as no seeds of these species have been observed in Svalbard (Brochmann and Håpnes [2001](#page-11-0); Alsos et al. [2012a\)](#page-11-0). Only Poa pratensis is commonly semeniferous, but no ripe seeds were found (Table [1](#page-4-0)). Thus, future test should be undertaken to determine if the bulbils remain viable even after some years of storage and are thus useful for ex situ conservation in seed vaults.

Of the species for which seeds were found but germination failed or was low, the viability of the seeds should be checked, for example, using a Tetrazodium test (Peters [2007](#page-12-0)). If the seeds are viable, different stratification and germination conditions should be tested. While the majority of cold adapted species produced viable seeds and thus are relatively easy to collect for a seed bank, most thermophilous species failed to produce viable seeds. To overcome the limitations caused by low temperatures, successful seed production could be obtained by artificially warming the plants using, for example, open top chambers (Klady et al. [2011](#page-12-0)). Although we expect that global warming on the long term will have a positive effect on recruitment in most of these species as it may increase seed production and viability (Klady et al. [2011](#page-12-0)), there is a risk that the species will get lost under current climate if both population sizes and/or levels of genetic diversity are low (Alsos et al. [2002](#page-11-0), [2007](#page-11-0); Frankham et al. [2009](#page-12-0)). Thus, ex situ conservation in, for example, botanical gardens should be used to conserve the current genetic diversity found in Arctic populations. As this requires a large effort per species, species should be prioritized according to Red List status.

For non-clonal species without viable seeds, ex situ conservation in, for example, botanical gardens may be

challenging. However, seeds may ripe in botanical gardens due to more optimal conditions. Also, propagation of new plants from cuttings is a well-established method in horticulture and has been successful also for non-clonal species from the Arctic (Hagen [2002](#page-12-0)).

The longevity of seeds should be tested repeatedly. Seeds from cool, wet conditions are shorter lived than those from hot, dry environments (Probert et al. [2009](#page-12-0)), and germinability is reduced over time in alpine species (Mondoni et al. [2011\)](#page-12-0). In seeds of Arctic species, however, germinability may be retained over long periods by seed storage at freezing temperatures (Billings and Mooney 1968), although the report of germination of 10,000 year old Lupinus arcticus seeds (Porsild et al. [1967](#page-12-0)) is disputed (Godwin [1968;](#page-12-0) Gugerli [2008\)](#page-12-0).

For species with low germination percentages, whether this is due to low proportion of viable embryos or due to lack of knowledge of adequate germination methods, larger amount of seeds should be collected to ensure sufficient amount of seeds that are likely to germinate. To account for annual variation, collections should be done over several seasons. Also, for all species seeds from more populations should be collected to obtain a representative cover of the total genetic diversity of the species. While ideally seeds from the entire range should be collected, populations likely to go extinct due to climate change, as identified by, for example, species distribution models (Alsos et al. 2012b), should be targeted (Vitt et al. [2010\)](#page-13-0). For Arctic species, species distribution modelling indicates that these will mainly be populations at the southern parts of their ranges (Parmesan [2006;](#page-12-0) Alsos et al. 2012b).

Conclusions

As the proportion of species germinating and their germination percentages were higher than assumed by many previous studies, seed banks may be a viable strategy for ex situ conservation also of the Arctic flora. Improved knowledge of seed ecology and ongoing climate warming are two factors that likely contribute to the high germination. Sampling of seeds should cover a broad geographical range, paying especially attention to regions where populations are expected to extirpate due to climate change, to obtain seeds representative for the majority of the genetic diversity within species. For species without viable seeds, alternative methods of ex situ conservation need to be evaluated.

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Species	Coll. date	Collection place	Habitat	Collector	Latitude	Longitude
Alopecurus borealis	$09-Sep$	Bjørndalen	Moist grassland	HEP, CJW, ASc	78.226	15.328
Arabis alpina	$06-Sep$	Kapp Smith	Fine gravel below bird cliff	IGA, SWS, TW, KJ	78.660	15.116
Arctagrostis latifolia	$02-Sep$	Kapp Thordsen	Salix polaris/ Saxifraga oppositifolia heath	IGA	78.458	15.476
Arctophila fulva	$04-Sep$	Bohemanflya	Wet grassy area with slowly flowing water	IGA, EM	78.414	14.676
Arenaria pseudofrigida	$12-Sep$	Hotellneset	Silene acaulis tundra	EM, SSS, HEP, ASc, SL	78.249	15.508
Arnica angustifolia	08 and 09 Sep	Colesdalen	S exposed rocky slope	EM, AS, CH, AB	78.106	15.126
Betula nana var. tundrarum	$09-Sep$	Colesdalen	S slope in depressions	EM, AS, CH, ASC	78.104	15.131
Bistorta vivipara	$27-Aug$	Endalen	Snow bed and river bank	EM, CJW, JV, IGA	78.197	15.810
Braya glabella ssp. purpurascens	$05-Sep$	Bohemanflya	Sandy moraine ridges	IGA, PBE	78.470	14.509
Calamagrostis neglecta ssp. groenlandica	$18-Sep$	Hotellneset	Moist grassland	EM	78.249	15.508
Campanula rotundifolia ssp. gieseckiana	$09-Sep$	Colesdalen	S exposed slope with gravel	EM	78.105	15.124
Cardamine polemonioides	$09-Sep$	Colesdalen	Moist mire beside open flowing water	EM	78.107	15.064
Carex bigelowii ssp. ensifolia	12 -Sep	Hotellneset	Mire	IGA	78.243	15.488
Carex fuliginosa ssp. misandra	$09-Sep$	Sassendalen	Dryas heath	SSS, REP, InGA	78.343	16.947
Carex glacialis	$06-Sep$	Kapp Smith	Open steep scree below bird cliff	IGA, SWS	78.660	15.115
Carex krausei	$09-Aug$	Kapp Smith	Steep scree below bird cliff	IGA, SWS, BES	78.662	15.125
Carex lachenalii	$10-Sep$	Colesdalen	Mire with some open water	EM	78.098	15.146
Carex lidii	09 and 10 Sep	Kapp Thordsen, Sassendalen	Rich mire	IGA, SL	78.458, 78.322	15.505, 17.035
Carex marina ssp. pseudolagopina	$10-Sep$	Sassendalen	Rich mire	IGA, UBM	78.342	16.950
Carex maritima	$10-Sep$	Sassendalen	Rich mire	InGA, REP, SSS, UBM	78.342, 78.322	16.950, 17.035
Carex nardina ssp. hepburnii	$10-Sep$	Sassendalen	Dry calcareous ridge	IGA, SSS, UBM	78.353	16.927

Appendix 1. Collection data for seeds. All seeds were collected in 2008 except *Carex krausei* which was collected in 2009.

AB - Allan Buras AS - Anders Søyland ASc - Andrea Schmidt CH - Charmain Hamilton CJW – Chris J. Ware EM - Eike Müller HEP - Hanne Eik Pilskog IGA - Inger Greve Alsos InGA - Ingvild Greve Alsos JV – Jochem Veenboer KJ – Kåre Johansen KK – Kim Klein MTD - Martin Torp Dahl PBE - Pernille Bronken Eidesen REP - Roman Egorovich Petrov SL - Sylvi Lundgren SSS - Sergey Semyonovich Sivtsev SWS - Snorre Winger Steen TW – Torunn Winsnes UBM - Ulf B. Mikalsen

Appendix 2. Overview of applied stratification (strat.) and germination methods.

Appendix 3. Germination percentages and species characteristics of Arctic species from Svalbard tested for germination. Reproduction (R) by seeds (s) or bulbils (b), or no ripe seeds found (ns). Rarity (1 = scattered or at least locally common, $2 =$ rare (5-25 localities known), $3 =$ very rare (1-4 localities), Thermophily (Ther, $1 =$ strongly, $2 =$ distinctly, $3 =$ moderately, $4 =$ weakly, and $5 =$ indifferent), Vegetative means of reproduction (Veg, $A =$ asexual seeds, $B =$ bulbils, $N =$ no vegetative reproduction, $R =$ runners, $S =$ shoots), $n =$ number of seeds germinated, % germ = percentage of germinated seeds, and sd = standard deviation. For comparison, mean germination percentages obtained by other studies are given: Eurola (1972) are given as germination/Tetrazodium test, Müller et al 2011 (germination at 18°C), other Svalbard (A = Alsos et al. 2003, H = Hagen 2002), and Sørensen 1941 (ns = no ripe seeds found, $0 =$ no seeds germinated, $(+)$ poor germination, $+$ = germination).

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