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Author(s)	Tsuyuzaki, Shiro
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3 **The Seed Germination of Berry-Producing Ericaceous Shrubs in**  
4 **Relation to Dispersal by Hare**

5 Shiro Tsuyuzaki

6 Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-

7 0810 Japan

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10 **CONTACT** **Shiro Tsuyuzaki.** ✉ e-mail: [tsuyu@ees.hokudai.ac.jp](mailto:tsuyu@ees.hokudai.ac.jp)

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13 **ABSTRACT**

14 Hare pellets contribute greatly to the seed dispersal of a berry-producing shrub,  
15 *Gaultheria miqueliana* Takeda (Ericaceae), on Mount Koma, northern Japan.  
16 Numerous seeds of *G. miqueliana* germinated from the hare pellets ( $122.2 \pm 7.3$ /pellet,  
17 mean  $\pm$  SE), confirming that the pellets potentially had a role in the seed dispersal. Lab-  
18 experiments confirmed that the seeds of *G. miqueliana* needed light for full germination  
19 without cold stratification. Besides, hare pellets were collected from a post-mined  
20 peatland in Sarobetsu Mire, northern Japan, where *G. miqueliana* was not distributed but  
21 two berry-producing ericaceous species were distributed. No seeds germinated on the  
22 pellets collected from the Mire. These results suggested that the tight relationships  
23 between hare and berry-producing shrubs were species-specific.

24

25 **Keywords**

26 Berry fruit; Hare pellet; Light; Seed dispersal and germination; Volcano; Wetland

27

## 28 Introduction

29 The potential of seeds dispersed through mammalian guts, i.e., endozoochory, often  
30 determines plant population dynamics, even though the seed survival is reduced by the  
31 digestion (Cosyns et al. 2005). Of the mammals, hares (*Lepus* spp.) act as seed  
32 dispersers of *Retama raetum* (Fabaceae) in the east Mediterranean deserts (Izhaki and  
33 Ne'eman 1997). A dwarf shrub, *Gaultheria miqueliana* Takeda, produces berries  
34 containing numerous seeds that are dispersed by mountain hare (*Lepus timidus ainu*) on  
35 Mount Koma, northern Japan, and the hare pellets facilitate delayed seed germination,  
36 i.e., seed germination occurs with the degradation of pellets for long-term to avoid risks  
37 such as drought (Nomura and Tsuyuzaki 2015). Therefore, the hare and shrub, *G.*  
38 *miqueliana*, are more mutually evolved than previously thought.

39 Since light and cold stratification are two major determinants on seedbank  
40 development and delayed seed germination (Baskin and Baskin 2014), further lab-  
41 experiments were performed to confirm the effects of light and cold stratification on the  
42 seed germination of *G. miqueliana*. *G. miqueliana* is distributed in northern Japan,  
43 Sakhalin, Kuril Islands and Aleutian Islands (Satake et al. 1981), while hare (*Lepus*  
44 *timidus*) is distributed in the arctic, subarctic and boreal regions of the Old Continent  
45 (Thulin 2003). *L. t. ainu* is endemic subspecies to Hokkaido (Yamada et al. 2002).  
46 Therefore, a distributional gap between the shrub and hare exists. Due to the behaviors  
47 of animals, the dispersal distances of endozoochorous seeds are determined (Jordano  
48 2017). The seeds of *G. miqueliana* dispersed by a migrant bird, *Turdus naumanni*,  
49 which moves between Siberia and southern China via Japan, has been reported (Nishi and  
50 Tsuyuzaki 2004). The home ranges of *L. t. ainu* are a few tens of hectares (Chapman  
51 and Flux 1990). Therefore, the short-distance seed dispersal by hare that maintains the  
52 population of *G. miqueliana* is expected, as compared with the migrant bird.

53 Ericaceous shrubs often establish in nutrient-poor habitats, such as volcanoes and  
54 bogs, using symbiotic mycorrhizal fungi (Keddy 2007). A post-mined peatland in

55 Sarobetsu Mire, where nutrients were poor (Nishimura and Tsuyuzaki 2015), allows the  
56 establishment of two ericaceous shrub species producing berries, *Empetrum nigrum* L.  
57 and *Vaccinium oxycoccos* L., but lacks *G. miqueliana* (Egawa et al. 2017). Therefore,  
58 pellets collected from the post-mined peatland were also investigated to examine if  
59 germinable seeds were available in the pellets. The seed dormancy types of these three  
60 species are categorized into physiological dormancy with firm seed coats (Vander Kloet  
61 and Hill 2000; Tsuyuzaki and Miyoshi 2009; Baskin and Baskin 2014). Therefore, the  
62 seed characteristics of these three species were expected to be comparable.

63 Using the seed germination tests of hare pellets and fruits collected from the volcano  
64 and pellets collected from the peatland, I reported: 1) the responses of *G. miqueliana*  
65 seeds to light and cold stratification; and 2) species-specific interactions between hare  
66 pellets and berry-producing shrubs. Although this study did not examine the seasonal  
67 and annual variations of seed production, it detected that species-specific relationships  
68 between hare and berry-producing shrubs were present.

69

## 70 **Methods**

### 71 ***Sampling sites in relation to berry-producing ericaceous shrubs***

72 The samples were collected from the two locations, Mount Koma and Sarobetsu Mire,  
73 northern Japan. Mount Koma is an andesite stratovolcano of which last catastrophic  
74 eruption occurred in 1929 (Table 1). The revegetation progresses slowly by *Larix*  
75 *kaempferi* (Lam.) Carr. but the nutrients are still poor (Kwon and Tsuyuzaki 2016).  
76 Although seven ericaceous species are recorded from Mount Koma (Tsuyuzaki et al.  
77 2001), all species except for *G. miqueliana* produce capsules.

78 Sarobetsu Mire, occupied mostly by bog, is distributed in the northernmost part of  
79 Hokkaido, Japan (Table 1). In the mire where *Sphagnum* mosses were predominant,  
80 peat mining was conducted from 1970 until 2003. The succession after peat mining  
81 starts with pioneer sedges, such as *Rhynchospora alba* (L.) Vahl. (Nishimura and

82 Tsuyuzaki 2014). Four ericaceous species establish in this post-mined peatland (Egawa  
83 et al. 2017). Of the four species, *E. nigrum* and *V. oxycoccos* produce berries.

84

#### 85 ***Sample preparations and seed germination experiments***

86 The pellets were collected from the southwestern slope of Mount Koma in May 5 2001  
87 and from the post-mined peatlands of Sarobetsu Mire in early April 2019. The pellets  
88 were collected from different locations that were apart more than 5 m to each other. The  
89 timings of pellet collections were just after snowmelt in both sites. The hare  
90 infrequently utilizes grassy habitats, including Sarobetsu Mire, during snow season to  
91 avoid the predators (Abe and Ota 1987). The three berry-producing shrubs, *G.*  
92 *miqueliana*, *V. oxycoccos* and *E. nigrum*, produce their fruits during middle summer to  
93 late autumn. Since the hare pellets were collected in early spring before the fruit  
94 production began in the current year, seeds in the pellets should be produced in the last  
95 year or earlier if available. In addition, most seeds were exposed naturally to cold  
96 stratification for more than a few months.

97 The inter-annual variations of fruit production are often observed for berry-  
98 producing shrubs, including these three examined species (Nestby et al. 2019).  
99 However, annual monitoring on Mount Koma and Sarobetsu Mire to date confirms that  
100 the fruit production of the examined species is not poor every year (Tsuyuzaki and Hase  
101 2005, Nishimura and Tsuyuzaki 2014). The food of hare, *L. t. ainu*, is diverse among  
102 seasons and among regions (Chapman and Flux 1990). When numerous seeds  
103 germinated from the pellets, the results also suggested that the hare depend the food on  
104 the berries.

105 The seed germination test of pellets collected from Mount Koma started on May 12  
106 2001. A pellet crushed gently by hands was placed on a moistened three-layered filter  
107 paper (Whatman #1) in a petri dish. Thirty replications of pellets were used. The  
108 pellets in dishes were kept at a 5°C/25°C cycle with continuous light in an incubator.

109 Distilled water was poured into the petri dishes when the pellet surface was slightly dried.  
110 Seed germination was counted every day until the peak of germination and thereafter at  
111 ever few days until no seeds germinated for one week for all the seed germination  
112 experiments. Pellets collected from Sarobetsu Mire were treated as the same way with  
113 these collected from Mount Koma except for the temperatures. Two treatments were  
114 conducted, i.e., 10°C/25°C (12h/12h) with continuous light and 5°C/20°C (12h/12h) with  
115 discontinuous light (12h/12h). Ten replications were used in each treatment. When  
116 each experiment was completed, the pellets on all petri dishes were observed under a  
117 binocular microscope to check if viable seeds remained.

118 The mature fruits of *G. miqueliana* on Mount Koma were collected from more than  
119 20 shoots, which were apart more than 5 m to each other, on the southwestern slope in  
120 the end of October 2001. About five fruits were collected from each shoot. Seeds were  
121 removed gently from the fruits soon after the collection and kept in a paper bag at room  
122 temperature for one month until use. In each petri dish, 50 seeds were sown on a  
123 moistened three-layered filter paper without any pre-treatments on November 26 2001.  
124 The seeds were randomly selected from the paper bag. The remainders of seeds were  
125 sown after cold stratification at 2°C for one month under the darkness. Then, the seeds  
126 were placed into an incubator with light and with darkness on December 26 2001. On  
127 each combination of treatments (light × cold stratification), 50 seeds were placed into  
128 each dish and 10 replications were used. While the germination was recorded under dim  
129 green light on the dark treatment, it was done under fluorescent light on the light treatment.  
130 Soon after completing the experiment, the viability of ungerminated seeds was estimated  
131 from the extent to which they were firm and intact (Ishikawa-Goto and Tsuyuzaki 2004).

132 Final germination (FG; %) and the time to onset of germination ( $t_0$ ; d) were  
133 calculated for each petri dish. Final germination was calculated as germination  
134 percentage in relation to total viable seeds and  $t_0$  was the day for the first germination.  
135 Differences in the final seed germination between the treatments were examined by a

136 generalized linear model (GLM) with a binomial distribution and logit-link function (R  
137 version 3.6.1) (R Core Team 2019). The equation is:

138 
$$P(g) = 1/(1 + \exp(-A)), \text{ and}$$

139 
$$A = \alpha_c \cdot \log t + \alpha_l \cdot \log l + \alpha_{c \times l} \cdot (\log c \times \log l) + \beta,$$

140 where  $P(g)$  is the probability of seed germination rate;  $c$  and  $l$  indicate cold stratification  
141 and light, respectively. Cross symbols ( $\times$ ) indicate interactions.  $\alpha_i$  is the slope of each  
142 explanatory variable; and  $\beta$  is the intercept. In the same way, differences in  $t_0$  was  
143 investigated by GLM with and without light and cold stratification, respectively, with the  
144 assumption of binomial distribution and logit-link function.

145

## 146 **Results**

147 In total, 3853 seeds germinated from the 30 pellets for five months. The number of  
148 germinated seeds per pellet averaged  $122.2 \pm 7.3$  (mean with SE; range: 64-210 seeds).  
149 The first seeds germinated 13 days after sowing but was *Anaphalis margaritacea* Benth.  
150 et Hook. fil. var. *angustior* Nakai. Except this seeding, all the seeds were *G. miqueliana*.  
151 The  $t_0$  of *G. miqueliana* averaged  $18.9 \pm 0.3$  days after sowing the seeds (Figure 1).  
152 Thereafter, the seed germination occurred enormously for two weeks and ceased 119 days  
153 after sowing the seeds.

154 The pellets collected from Sarobetsu Mire did not show any seeds germinated for  
155 five months under the two temperature fluctuation patterns with continuous and  
156 discontinuous light. The microscopic observations of pellets after completing the seed  
157 germination experiments conducted by the pellets collected from Mount Koma and  
158 Sarobetsu Mire confirmed that germinable or viable seeds were least in the pellets,  
159 showing that most seeds germinated by the experiments.

160 On the seeds of *G. miqueliana* removed from fruits,  $t_0$  of all the treatments averaged  
161  $13.9 \pm 0.5$  days. The  $t_0$  indicated that the cold-stratified seeds germinated earlier  
162 (GLM, slope = -1.143,  $P < 0.01$ ), while  $t_0$  did not changed by light exposure ( $p = 0.365$ ).



163 The interaction was not significant ( $p = 0.447$ ). These results showed that the cold  
164 stratification promoted early germination and the light did not. The final seed  
165 germination percentage was  $86.2\% \pm 1.8$  under the light and  $29.2\% \pm 2.7$  under the  
166 darkness when the seeds were not exposed to cold stratification (Figure 2). When the  
167 seeds experienced cold stratification, the percentages were  $85.0\% \pm 1.2$  and  $46.4\% \pm 3.5$   
168 under the light and darkness, respectively. The seed germination percentages were  
169 affected by light but not by cold stratification (intercept = +1.742, significant at  $P < 0.001$ ),  
170 viz; the seed germination was decreased by the darkness (slope = -1.887,  $P < 0.001$ ) and  
171 was not affected by cold stratification ( $P = 0.618$ ). The interaction between light and  
172 cold stratification was also significant (slope = -0.783,  $P < 0.001$ ), showing that the cold  
173 stratification enhanced the seed germination under the darkness. The microscopic  
174 observations after the experiments confirmed that 1.9 and 0.6 seeds per dish had been  
175 rotten in average with and without light, respectively. Therefore, nearly all seeds  
176 germinated with light and 1/2 or less seeds were still dormant without light.

177

178

## 179 **Discussion**

180 The pellets collected from Mount Koma in early spring emerged 64 seedlings or more per  
181 pellet, indicating that the hare has a high potential role in the seed dispersal of *G.*  
182 *miqueliana*. Even though the seed survival is decreased after mammalian digestion  
183 (Cosyns et al. 2005), the hare should be considered to contribute to the seed dispersal of  
184 *G. miqueliana* on Mount Koma. Concurrently, these meant that the hare depended its  
185 food greatly on the berries of *G. miqueliana* in late spring. In contrast, no seeds  
186 germinated from the pellets collected in early spring on Sarobetsu Mire. Since the  
187 pellets collected from the mire, where the two berry-producing ericaceous species  
188 established, did not contain viable seeds, the diet of hare should be examined (Green et  
189 al. 2013). The seeds of *G. miqueliana* required light for full germination and did not

190 require cold stratification, although the seed germination became earlier by the cold  
191 stratification. This meant that the cold stratification promoted the seeds germinate  
192 quickly so that seedlings are large before dry summer.

193 By contrast, the hare pellets prolong the seed germination period when the pellets  
194 degraded slowly, because of no light in the inside. The decay rates of *Lepus americanus*  
195 pellets, of which decay is defined as visually disappeared, are 1-14% per year, increase  
196 with soil moisture in a tundra shrubland (Prugh and Krebs 2004). Since moisture in the  
197 volcanic deposits of Mount Koma is dry in summer (Uesaka and Tsuyuzaki 2004), the  
198 decay rates should be lower. This seed germination strategy is not observed on other  
199 species and/or in other regions, including Sarobetsu Mire, although berry-producing  
200 ericaceous species establish well in the mire. The responses of sedge seeds to cold  
201 stratification and daily temperature fluctuation differ greatly between wetland and  
202 dryland species (Schutz and Rave 1999). As the soil moisture is different between the  
203 volcano and peatland, the different seedbank development in hare pellets is possible.  
204 Therefore, the optimal seed germination timings and patterns seemed to be determined  
205 by a balance between seed germination shortened by cold stratification and prolonged by  
206 burial in the hare pellets.

207 In Sarobetsu Mire, the two ericaceous species usually produce numerous berries.  
208 However, these seeds were not present in the hare pellets collected in early spring. The  
209 two species in Sarobetsu Mire do not develop seedbanks in the pellets, as shown in this  
210 study, and in the peat on the post-mined peatland (Egawa et al. 2009). The hares in  
211 Sarobetsu Mire do not rely on ericaceous berries as food resources. In contrast, the  
212 seedlings of *E. nigrum* emerge from scats provided by passerine, gull, mink and fox in a  
213 wide range of Nova Scotia (Hill et al. 2012). These results suggest that the behaviors of  
214 hare, related to the development of seedbank in pellets, are different between the habitats  
215 or regions.

216 Numerous *G. miqueliana* seeds were viable in the pellets collected from Mount

217 Koma. The  $t_0$  was a few days earlier for the seeds removed from fruits than for the seeds  
218 germinated from the pellets. These results suggested that the digestion by hare damaged  
219 less seeds. Hare pellets contribute to the dispersal and accumulation of nutrients through  
220 mineral cycling in nutrient-poor ecosystems such as tundra and then increase shrub  
221 growth (Krebs et al. 2001). Nutrients are poor in the volcanic ejecta and *Sphagnum* peat.  
222 In fact, nitrogen and phosphorus are poor on the volcanic bareground (Uesaka and  
223 Tsuyuzaki 2004) and the post-mined peatland (Nishimura and Tsuyuzaki 2014). The  
224 nutrient supply from pellets is likely to contribute to the establishment and growth of *G.*  
225 *miqueliana*. In conclusion, the firm interactions between the shrub and hare on the  
226 volcano and the least interactions between them on the mire show the regional and species  
227 differences in interspecific interactions between the plants and hares.

228

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234

#### 235 **Notes on contributors**

236 *Shiro Tsuyuzaki* is a plant ecologist working at Graduate School of Environmental Earth  
237 Science, Hokkaido University, Japan. He is interested in structure and function of  
238 ecosystems after disturbances, including seed ecology. *Contribution*: contributed to all  
239 the parts of manuscript as a single author.

240

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319 *Genetic Syst* 77(2): 107-116  
320

321 Table 1. The characteristics of study sites, Mount Koma and Sarobetsu Mire in northern  
 322 Japan .

323

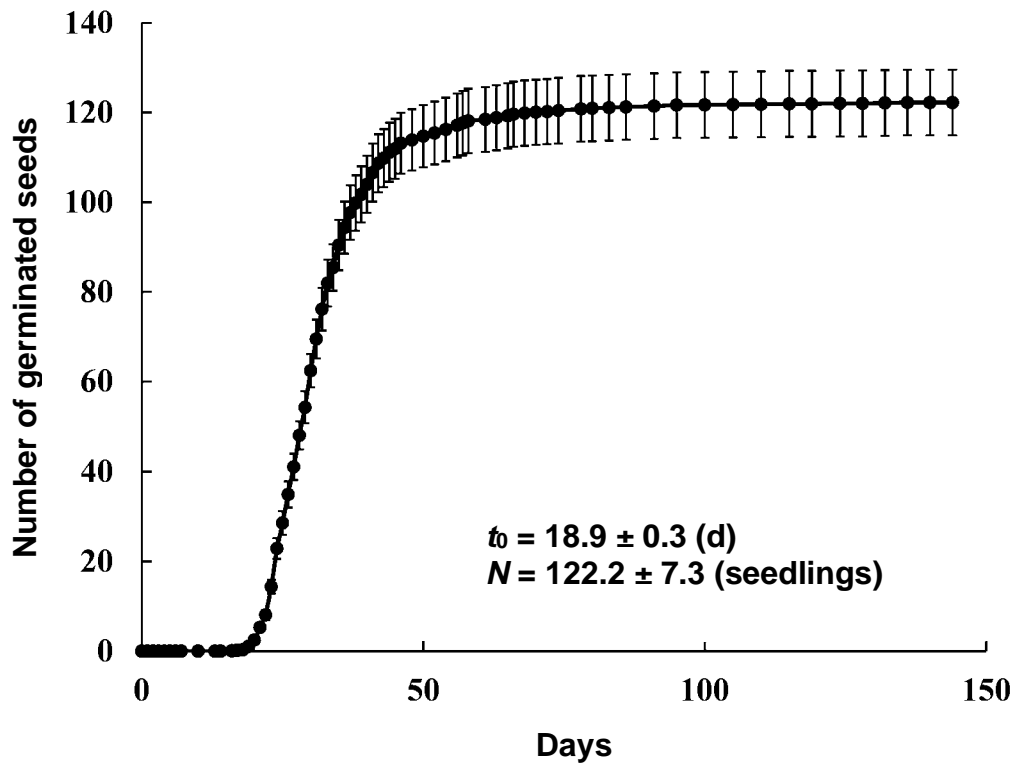
Study site	Mount Koma	Sarobetsu Mire
Latitude	42°03'N	45°06'N
Longitude	140°40'E	141°42'E
Elevation (m)	650-450 <sup>(a)</sup>	7
Mean annual temperature (°C)	10.2 <sup>(b)</sup>	12.3 <sup>(b)</sup>
Mean annual precipitation (mm)	1072.5 <sup>(b)</sup>	1097.3 <sup>(b)</sup>
Disturbance	Eruption in 1929	Peat mining during 1970 to 2003
Number of ericaceous species	7	4
Ericaceous species producing berry	<i>Galutheria miqueliana</i>	<i>Empetrum nigrum</i> <i>Vaccinium oxycoccos</i>

324 a) the top of mountain is 1133 m a.s.l. The study area is located on the southwestern  
 325 slope of mountain.

326 b) the mean annual temperature and mean annual precipitation calculated for the period  
 327 from 1981 and 2010 on weather stations located in Mori Town (7 km from Mount Koma,  
 328 10 m a.s.l.) and in Toyotomi Town (5 km far from Sarobetsu Mire, 16 m a.s.l.) (Japan  
 329 Meteorological Agency 2019).

330

1



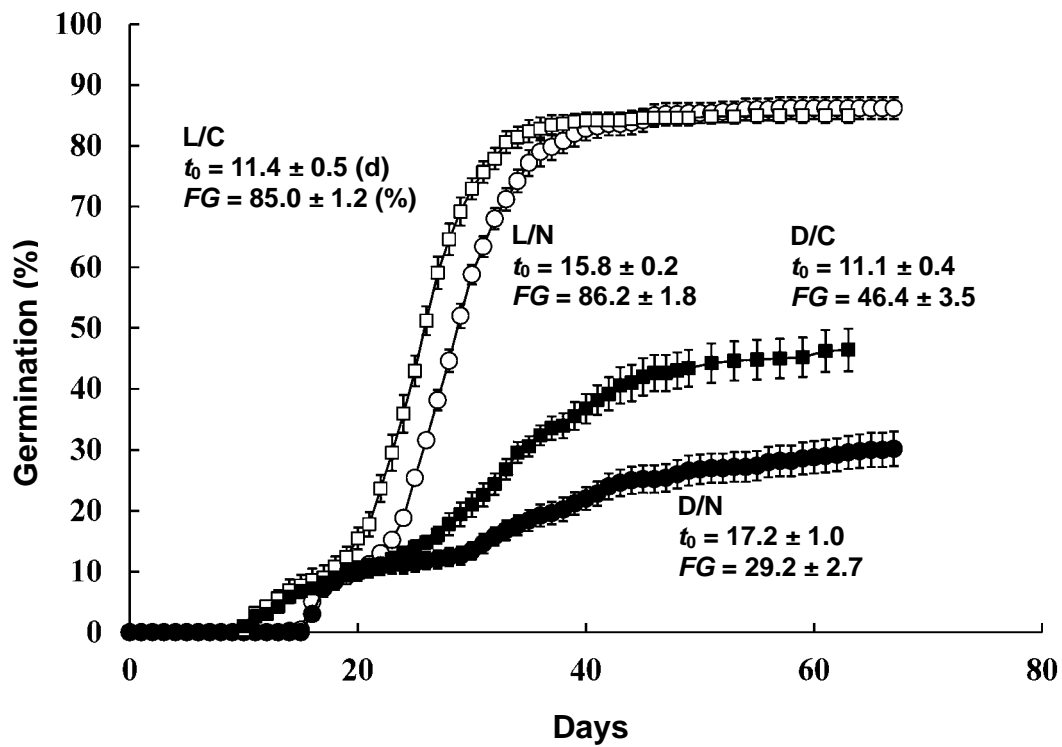
2

3

4 Figure 1. Cumulative number of seedling emergence of *Gaultheria miqueliana* by 30  
5 hare pellets collected on May 5 2001 from Mount Koma. The lab-experiment started on  
6 May 12 2001 and ceased on September 20 2001. The mean of cumulative number of  
7 seedling emergence is shown with standard error (vertical bars).  $N$  = number of seeds  
8 germinated at the final investigation (mean  $\pm$  SE).

9





1

2

3 Figure 2. The cumulative germination percentage of *G. miqueliana* seeds treated by  
 4 cold stratification and light, confirmed by lab-experiments. The mean number of ten  
 5 replicates at each treatment is shown with standard error (vertical bars). Open and  
 6 closed symbols indicate seeds under light (L) and darkness (D), respectively. Circles  
 7 and squares indicate non-cold (N) and cold (C) stratification, respectively. On the  
 8 statistical results, see in the text.