Effect of light, temperature, salinity and maternal habitat on seed germination of *Aeluropus lagopoides* (Poaceae): an economically important halophyte of arid Arabian deserts

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<td>Carón, María ; Universidad Nacional de Salta-CONICET, Av. Bolivia 5150, 4400 Salta, Argentina, IMBIV</td>
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<td>Santo, Andrea; Via dei gladioli 16 C, 09047 Selargius, Cagliari, Italy</td>
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Effect of light, temperature, salinity and maternal habitat on seed germination of *Aeluropus lagopoides* (Poaceae): an economically important halophyte of arid Arabian deserts

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Running Head: Effect of environmental condition and maternal habitat on seed germination of *Aeluropus lagopoides*

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Abstract

In the present study, salt tolerance during germination of *A. lagopoides* was tested for fresh seeds collected from three different maternal habitats under three thermoperiods and two light regimes. Additionally, the ability of non-germinated seeds at the different NaCl conditions to recover their germination in distilled water was tested. The results showed a significant effect of seed source, temperature and salinity and some of their two- and three-way interactions on, final germination and recovery percentage. The seeds from non-saline provenances had the highest germination (ca. 79%) under the 35/25°C temperature regime while the lowest germination (ca. 21%) was recorded in seeds from saline conditions under the 25/15°C treatment. Additionally, the germination decreased from seeds incubated under non-saline solutions - control (0 mM NaCl) and warmer conditions (35/25°C) to saline solutions (100, 200, 400 and 600 mM NaCl) and colder conditions (15/25°C). The highest recovery percentage was recorded for seeds of the hyper-saline habitat incubated at 35/25°C. Thus, seeds maintained their viability despite experiencing a range of saline conditions and were able to germinate upon the arrival of suitable conditions, which can be an adaptation to its saline arid desert habitat.

**Keywords:** *Aeluropus lagopoides*; germination recovery; maternal habitat; photoperiod; salinity; thermoperiod
Introduction

Desert plants generally experience extreme aridity, large fluctuations of water availability and a relatively short growing season (Omar and Bhat 2008). In several desert plants, light, temperature and water availability are the main environmental factors influencing seed germination, plant growth and survival (Weber 2009; Chen and Jiang 2010; El-Keblawy and Bhatt 2015; Bhatt et al. 2016a, b, c, d; Bhatt et al. 2019). In particular, photoperiod contributes to determine when and where germination will take place (Fenner and Thompson 2005), although seeds of different plants show species-specific responses (e.g. some species require only light or darkness to germinate, while other germinate equally well in light and darkness (Baskin and Baskin 2014). Temperatures play an important role on seed germination timing and seedling establishment in desert plants (Baskin and Baskin 2014). Moreover, interaction of light and temperature can modify the sensitivity of seeds to both factors (Sugahara and Takaki 2004; Baskin and Baskin 2014). However, it is known that different populations can show local adaptations in response to the spatial variability of environmental conditions, such as climatic and edaphic parameters (Leimu and Fischer 2008; Youssef 2009; Stanton-Geddes et al. 2012; Santo et al. 2017; El-Keblawy et al. 2018; Elnaggar et al. 2019). This could be controlled through factors prevailing during seed production and germination (Sambatti and Rice 2006).

Soil salinity level has been also defined as one of the most important variables influencing seed dormancy and germination of desert plants (Khan and Ungar 1996). Previous studies reported that salinity tolerance of halophytic grasses is species-specific and varies with the ecotype, habitat of provenance and in relation to specific environmental factors (Gulzar et al. 2003b; Poddà et al. 2017). Different studies showed that interactions between parental plants and environmental conditions during seed development and maturation can affect seed dormancy and consequently the germination process (Fenner 1991b; Wulff 1995). Therefore, a better knowledge of the role of the maternal salinity could be helpful in identifying suitable habitats that can produce seeds with low dormancy for future restoration programs. The inter-population variability of seeds germination requirements (Murru et al. 2015; El-Keblawy et al. 2016, 2017, 2018; Murru et al. 2017) has a genetic base, but often is imputed to different phenotypic plasticity, frequently caused by the local environmental conditions during seed maturation (Gutterman 2000). In fact, both genotype and parental environmental conditions, such as maternal habitat and time of seed development on the mother plant (Wulff 1995; Gutterman 2000; El-Keblawy et al. 2017, 2018, 2019), are reported to play an important role in
determining seed dormancy, germination characteristics and germination requirements in several species (Fenner 1991a; Donohue and Schmitt 1998; Paolini et al. 1999; Galloway 2001a, b).

*Aeluropus lagopoides* (L.) Trin. (Poaceae), is a perennial halophytic grass growing in northern Africa, eastern Mediterranean region, Middle East, Arabian Peninsula and central Asia. In the United Arab Emirates (UAE), it is locally common in coastal areas, sandy soils and saline grounds. *A. lagopoides* has a wide occurrence on coastal zones all over the UAE, and it was also recorded from three inland wadis (unpublished data). The ability of *A. lagopoides* to grow in habitats that differ in salinity offers a good opportunity for studying the interactive effects of maternal habitat and salt exposition during germination. The UAE has a sub-tropical arid climate with sporadic and erratic rainfall, which mainly occurs from November to March, when average temperatures are lowest. In fact, the studied species shows several adaptive features (e.g. vigorous seed production, slow vegetative propagation, strong network of roots, salt secreting habitus and small leaves) necessary to survive both in habitat with high drought and under salt stress (Mohsenzadeh et al. 2006). *A. lagopoides* is known to be of economic importance: it is utilized as a fodder in arid areas and a good soil/sand dunes stabilizer (Gulzar et al. 2003a). Furthermore, this species has the potential to be used for landscaping the urban areas of desert regions (Phondani et al. 2016).

The effects of temperature, light and salinity on the seed germination of *A. lagopoides* has been investigated (Gulzar and Khan 2001; Khan and Gulzar 2003; Gulzar et al. 2003a), but the different studies were conducted on seeds from a single population/habitat and did not evaluate the inter-population variability. Furthermore, the influence of saline environments experienced by the mother plant on the germination of offspring seeds of *A. lagopoides* has not been studied yet. However, it is known that seeds from different habitats where the species is surviving may have different adaptation strategies to specific environmental conditions during germination. Therefore, the present study aimed to investigate the seed germination ecophysiology of *A. lagopoides* from different habitats of arid deserts of UAE. The specific goals of this research were to test the effect of germination response, salinity tolerance and germination recovery to temperature and photoperiod of seeds collected from three different maternal habitats (hyper-saline, saline and non-saline soils).

**Materials and Methods**

**Seed collection and storage**
Mature caryopses (hereafter referred to as seeds) of *A. lagopoides* were collected at the time of natural dispersal (May-July) from three populations experiencing different soil salinity levels (see Table 1). The tested populations were from a hyper-saline (Kalba: 25° 0' 18.02'' N; 56° 20' 55.81'' E), saline (Al Mergab: 25° 23' 30.40'' N; 55° 25' 47.44'' E) and non-saline soils (Al Hamriyah: 25° 29' 8.90'' N; 55° 30' 8.14'' E) in Sharjah Emirate, UAE (Table 1). In each population, seeds were randomly collected from 150-200 plants, cleaned and pooled in order to represent the local genetic diversity. After collection, seeds were stored at room temperature (20 ± 2°C) for 3 weeks until the beginning of the experiments. The mean seed mass was determined for seeds lots from each habitat by weighing three replicates each of 100 seeds (Table 1).

A soil analysis was conducted to identify pH and salinity of the soil from the three study sites. Five soil samples were collected randomly from each site at a depth of about 15 cm (excluding the surface crust). These samples were then pooled together to form one composite sample, air-dried, and thoroughly mixed for the analysis. Soil-deionized water extracts (1:5) were prepared in triplicate for the determination of electrical conductivity (EC) and pH. Conical flasks with soil suspensions were swirled in an orbital shaker for 15 minutes, and then allowed to settle for 5 minutes. After the prescribed settling time, EC and pH was determined using a Hanna soil pH/EC/TDS tester (Model: HI98130, Hanna Instruments).

**Effect of light, temperature and provenance on seed germination**

To investigate the effect of light and temperature on germination, seeds from each tested habitat were sown with distilled water at three daily temperature regimes of 25/15, 30/20 and 35/25°C in both continuous darkness and alternating 12 h light/12 h darkness. The incubation temperatures were set to simulate the temperature fluctuations in the natural habitats during the seasons of seed germination. For the dark treatment, the Petri-dishes were wrapped in two layers of aluminum foils to prevent any exposure to light. Seeds were germinated in 9-cm tight-fitting Petri-dishes containing three disks of Whatman No. 1 filter paper moistened with 10 ml of distilled water. Three replicates, each with 25 seeds per habitat, were used for each treatment. Seeds were considered to be germinated with the emergence of the radicle (≥ 2 mm). Germinated seeds were counted and removed daily for 30 days. Seeds incubated in the dark were only checked at the end of the total germination trial (30 days).

At the end of the germination tests, all the still un-germinated seeds were punctured and then categorized as mouldy or healthy. The mouldy seeds were considered as dead. However, the non-mouldy seeds were considered as
either dead or viable. The viability of these seeds was tested after soaking them in 1% tetrazolium chloride solution for 24 h and then the cut seeds were examined under a binocular microscope (data not shown).

**Effect of salinity, temperature and provenance on seed germination**

In order to determine salinity tolerance during germination, three replicates of 25 seeds per seed lot from each habitat were sown at each of five salinity levels (0, 100, 200, 400 and 600 mM NaCl) using the same temperature treatments mentioned above. Seeds were germinated in 9-cm Petri dishes on a layer of Whatman no.1 filter paper and moistened with 10 ml of different concentrations of NaCl solution. Petri dishes were sealed by plastic film to prevent evaporation. Germinated seeds were counted and removed daily from the dishes for 30 days (end of experiment). All seeds that failed to germinate under different NaCl concentrations were removed at the end of the trial, rinsed three times in distilled water and then incubated in distilled water for 15 days. Recovery percentages (RP) were evaluated for seeds that fail to germinate under different salt solutions.

**Data analyses**

Mean germination time (MGT) was calculated using the formula: 

\[ MGT = \frac{\sum DN}{\sum N} \]

where \( D \) is the number of days counted from the date of sowing and \( N \) is the number of seeds germinated on day \( D \) (Ellis and Roberts 1981). Recovery percentage (RP) was calculated using the formula: 

\[ RP = \frac{[a-b] \times 100}{c-b} \]

where \( a \) is the total number of seeds germinated in the saline solutions plus those that recovered and germinated in distilled water, \( b \) is the total number of seeds germinated in saline solutions, and \( c \) is the total number of seeds. The germination of seeds incubated with distilled water recorded under different light and temperature conditions was analyzed as a function of the seeds’ provenance and incubation conditions (i.e. light and temperature) with Generalized Linear Model (GLM) with binomial error structures. Additionally, seed germination, mean germination time (MGT) and recovery percentage (RP) of seeds incubated under different temperatures and saline solutions were analyzed as a function of the provenance, salinity level and temperature, using GLM with binomial (germination) and Gaussian error structures (MGT and RP) with the nlme package in R version 3.1.2 (R Core Team 2014). RP data was arcsine square root transformed to achieve normality and homogeneity of variance prior to analysis. For all the analyzed variables, first the full model was fitted with all the factors and interactions included, after which models were simplified by dropping
first the least significant interaction and then the least significant individual variable at each step. The comparison between models was based on the likelihood ratio test (LRT) for the binomial data and on the scaled deviance for the Gaussian data, until all the remaining terms were significant (Zuur et al. 2009).

Results

Effect of provenance, light and temperature on seed germination

The final germination of *A. lagopoides* seeds varied according to the seeds’ provenance and the incubation temperature (Table 2 and Supplementary Table S1). Temperature significantly influenced the germination, and a decrease from warmer (25/35 °C) to colder (15/25 °C) conditions was recorded. Additionally, the three-and two-ways interactions between and among factors influenced seed germination of this species (Table 2, Fig. 1). The seeds from non-saline provenances showed a high germination (ca. 79%) under the 35/25°C temperature regime while lowest germination (ca. 21%) was recorded in seeds from saline conditions germinated under the 25/15°C treatment (the interaction Provenance × Temperature was significant, Fig. 1). The interaction between light conditions and temperature was also significant, with the germination decreasing from 81.8% at the 35/25°C under cycles of light, to 17.3% and 3.9% at 25/15°C treatment under darkness, respectively.

Effects of provenance, salinity and temperature on seed germination

All the main factors (i.e. provenance, salinity and temperature) significantly affected germination (Table 3 and Supplementary Table S2). The germination increased from cooler to warmer temperatures and from the highest salinity level (600 mM NaCl) to control (0 mM NaCl).

The interaction between provenance and salinity was significant (*P*<0.001; Table 3). Seeds from hyper-saline habitat did not germinate under the different levels of salinity tested, but seeds of the non-saline or saline habitats attained some germination under saline conditions. Additionally, the interaction between provenance and temperature was significant (*P*<0.01; Table 3). Considering all the salinity treatments together, the highest germination (18.5%) was recorded in seeds from non-saline provenances incubated at 35/25°C, while the lowest germination (4.8%) was recorded in seed from hyper-saline provenances incubated at 25/15°C (Fig. 2). The interaction between temperature and salinity was significant, indicating that salinity tolerance during germination depended on temperature of
incubation. The germination decreased from seeds incubated under non-saline solutions - control (0 mM NaCl) and warmer conditions (35/25°C) to saline solutions (100, 200, 400 and 600 mM NaCl) and colder conditions (25/15°C)(Table 2).

**Mean Germination time**

The mean germination time (MGT) was independent of the seeds’ provenance but varied as a function of the salinity and temperature (Table 3). However, due to the strong negative influence of salinity on germination the results of MGT as function of salinity should be considered with caution. The MGT decreased (see Supplementary Table S3) with increasing temperatures (i.e. seeds incubated under warmer conditions germinated faster than seeds germinated under colder conditions; Fig. 3). The interactions between salinity and both provenance and temperature were significant indicating that the germination speeds depended on both maternal salinity and temperature of seed incubation (Table 3).

**Germination Recovery**

Recovery percentages varied as a function of all the main factors (provenance, temperature and salinity) (Table 3 and Supplementary Table S4). Recovery percentages were also influenced by the two-way interactions between habitat and temperature and temperature and salinity while the interaction between habitat and salinity was not significant (Table 3). The highest recovery percentage was recorded for seeds of the hyper-saline habitat incubated at 35/25°C and the lowest was in seeds from the same habitat at 25/15°C and seeds of saline habitats incubated at 25/15°C (Fig. 4 and Supplementary Table S4). In addition, the highest value of recovery percentage was recorded in seeds germinated in lower salinity level (100 mM NaCl) and higher temperatures 35/25°C, while the lowest germination recovery percentage was recorded in seeds germinated under the highest salinity (600 mM NaCl) and lower temperatures25/15°C (Fig. 5). Viability testing showed that most of the seeds were, however, viable but did not recover from the highest salinity at low temperature.

**Discussion**

Environmental conditions at the maternal source showed a strong influence on seed germination requirements. This probably could be linked to differences in soil mineral and nutrient concentrations, temperature
and water availability. In the present study, freshly matured seeds of *A. lagopoides* have low innate dormancy; final germination reached high levels (up to 80% in distilled water), especially at high temperatures. However, seeds entered a salinity induced dormancy even at low concentrations of salinity (i.e., 100 mM NaCl). Similar results have been reported earlier for *Aeluropus lagopoides* and other desert grasses such as *Sporobolus arabicus*, *Sporobolus ioclados*, *Cenchrus ciliaris*, *Dichanthium annulatum*, *Halopyrum mucronatum*, *Pennisetum divisum*, *Lasiurus scindicus*, and *Urochondra setulosa* (Khan and Gulzar 2002; El-Keblawy 2006; El-Keblawy et al. 2011). Seeds entering an enforced dormancy at low concentrations of salinity indicate that the plants postpone the germination until the precipitation of heavy rainfall that reduce the soil salinity to less than 100 mM NaCl. This ensures that seedlings will emerge at the proper time of the year in the presence of enough water to ensure successful seedling establishment and survival (El-Keblawy et al. 2018; Elnaggar et al. 2019). In the absence of rainfall, *A. lagopoides* seeds might enter the soil seed bank and stay dormant (Bhatt and Pérez-Garcia 2016). It has been reported that *A. lagopoides* maintains a transient seed bank in coastal salt marshes of the subtropical climate of Pakistan (Khan and Gul 1999). In several habitat indifferent halophytes (i.e., grow well in both saline and non-salty soils) has shown differences in germination and such difference in the germination of seeds from different habitat types has been linked to the combined influence of genetic and environmental factors (El-Keblawy et al. 2016; El-Keblawy et al. 2017; El-Keblawy et al. 2018).

In the present study, provenance significantly affected final germination in both distilled water and saline solution. Interestingly, seeds of non-saline habitats germinated significantly more in distilled water at both 30/20°C and 35/25°C, as compared to seeds from both saline and hyper-saline habitats incubated under colder conditions. In addition, seeds from the non-saline habitat attained some germination in 100-400 mM NaCl, but those from plants of saline and hyper-saline habitats virtually did not germinate in salt solutions. El-Keblawy et al. (2018) interpreted the low germination of seeds from plants of the saline habitats to the accumulation of high levels of ABA in the plants of these habitats under the salinity stress. Such high levels of ABA could probably have carried over to the seeds and affected their final germination and tolerance to salinity stress (Boyko and Kovalchuk 2011; Migicovsky et al. 2014). Several reports have shown that high levels of ABA or lower GA/ABA ratio could induce dormancy (Kucera et al. 2005). In seeds from plants of the non-salty habitats, however, low levels of ABA and high levels of GA (i.e., higher GA/ABA ratio) are expected (El-Keblawy et al. 2018). The assessment of the different phytohormones in seeds from plants growing in habitats that differ in salinity levels is very important to understand their role in germination regulation and controlling salinity stress.
The light requirement for germination varied with the tested temperature regimes, indicating that seeds respond to particular combinations of light and temperature to germinate, as reported for several other species (Pons 1992; El-Keblawy and Al-Rawai 2005). Buried seeds (dark conditions simulated here) are able to germinate better at high (25/35°C) or moderate (20/30°C) temperature regimes under distillated water. This data suggest that germination will occur once rain events leach the soil salinity, which usually occurs between December to March in the study area. At this time of the year, the average monthly temperature is around 20-27.9 °C and the chances of rainfall are high (Böer 1997; Islam et al. 2009). However, if *A. lagopoides* seeds remain at the surface, where they face higher fluctuation in light and day/night temperatures, they would have light and the higher temperature requirements (El-Keblawy and Al-Shamsi 2008; El-Keblawy et al. 2017). However, it is important to consider that the seeds of *A. lagopoides* are small and contain limited amounts of storage reserves for early development. Therefore, when seeds germinate deeper into the soil their reserves may be exhausted before the seedlings emerge (ISTA 2003).

Our results showed that seeds collected from habitats with different salinity germinated significantly better at higher (35/25°C) than at lower temperatures (25/15°C). Therefore, the fluctuating temperatures between 35/25°C can be considered as the most optimal for successful germination of this species, regardless of the provenance. The higher germination under warmer conditions might be linked to some eco-physiological processes such as increasing membrane permeability, activity of membrane-bound proteins and cytosol enzymes, which increase the ability of seeds to germinate (Bewley and Black 1994). The ability of seeds of *A. lagopoides* to germinate at high temperatures indicates that they are able to germinate if rainfall events take place by the end of the growing seasons (i.e., March – May). Germinated seedlings could be affected by the high temperatures of summer that can reach up to 50°C on some days. Therefore, seedlings and plants may die unless they develop proper mechanisms to cope with high salinity of soils, high temperatures and water scarcity. Naz et al. (2009) investigated structural and functional modifications in three differently adapted ecotypes of *A. lagopoides* and concluded that long-term exposure of these ecotypes to their specific habitats imposed changes in their genetic makeup, which ensure their successful survival in their respective habitats.

Seed germination is a crucial stage in life history of a plant, and coastal plants are expected to exhibit some tolerance to salinity (Woodell 1985). Variations in salinity tolerance during germination might be attributed to other environmental factors characterizing the maternal habitat, such as changing in soil composition, local rainfall pattern.
etc. (Baskin and Baskin 2014; Bhatt et al. 2016 a, e; El-Keblawy et al. 2016; El-Keblawy et al. 2017). For example, previous studies show that soil texture and soil depth can influence the moisture regime in arid environments with episodic rainfall, which could affect seed development that in turn affect seed dormancy and germination response to a particular soil water stress (Fenner 1991b; Refka et al. 2013; Bhatt and Santo 2017a, b). Therefore, we assumed that maternal habitat plays an important role in determining the salinity tolerance of A. lagopoides seeds, but such results should be considered cautiously because this was not true for seeds from hyper-saline habitats. Similar to our findings, Gulzar et al. (2003b) reported that salinity tolerance of halophytic grasses varies with the ecotype, species, habitat and other environmental factors. Therefore more environmental aspects should be included to determine more clearly which factor is the most important for seed germination and salinity tolerance of the studies species.

Lower salinities and higher temperatures decreased the MGT in A. lagopoides seeds, indicating that the increase in salinity would delay germination, which is probably linked to a prevention of water absorption that is essential for seed imbibition and starting the germination process. However, these results should be considered with caution due to the overall low germination reported under the different saline solutions. Moreover, to verify this aspect it would be important to test the effect of osmolarity with polyethylene glycol. Faster germination in low salinity, irrespective of habitat type, might be an adaptation to establish seedlings immediately after the rainfall period. Similar results have been reported for A. lagopoides by Gulzar and Khan (2001) and for Phragmites australis by Xianzhao et al. (2013).

Aeluropus lagopoides seeds showed variation in recovery percentage when transferred from saline solutions to distilled water. Seeds of hyper-saline habitats showed the highest recovery rate at higher temperatures compared to seeds collected from the other two habitats under the same temperature conditions. These finding concur with the study of Gulzar and Khan (2001), who reported that the germination recovery of A. lagopoides was greater at higher temperature.

In conclusion, our results showed that seeds of A. lagopoides are sensitive to salinity and therefore seed germination in nature will be difficult unless natural soil salinity is reduced by rainfall. This kind of study, although not common, can provide useful information for environmental restoration activities, because it allowed us to highlight the different ranges of environmental conditions that seeds of species from different habitats/ source can tolerate, increasing the probability of in situ germination success.
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Table 1: Habitat characteristics and mean seed weight of *A. lagopoides*.

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<th>Soil pH</th>
<th>Soil electrical conductivity (mS/cm)</th>
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<td>Hyper-saline (Kalba)</td>
<td><em>Suaeda aegyptiaca</em>&lt;br&gt;<em>Heliotropium kotschyi</em>&lt;br&gt;<em>Launaea capitata</em>&lt;br&gt;<em>Salsola drummondii</em>&lt;br&gt;<em>Zygophyllum qatarens</em></td>
<td>15.1 ± 0.40</td>
<td>8.12</td>
<td>5.50</td>
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<td>Saline (Al Mergab)</td>
<td><em>Sporobolus spicatus</em>&lt;br&gt;<em>Sesuvium verrucosum</em>&lt;br&gt;<em>Cyperus arenarius</em>&lt;br&gt;<em>Phragmites australis</em>&lt;br&gt;<em>Suaeda vermiculata</em></td>
<td>8.6 ± 0.10</td>
<td>8.37</td>
<td>3.01</td>
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<td>Non saline (Al Hamriya)</td>
<td><em>Crotalaria persica</em>&lt;br&gt;<em>Lotus garcinii</em>&lt;br&gt;<em>Heliotropium kotschyi</em></td>
<td>14.2 ± 0.07</td>
<td>8.61</td>
<td>1.56</td>
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Table 2 - Effect of provenance, light, temperature and their interactions on final germination percentage of *A. lagopoides* seeds

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<th>Pr (&gt;Chi)</th>
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<td>Provenance (P)</td>
<td>2</td>
<td>6.304e-11 ***</td>
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<tr>
<td>Light (L)</td>
<td>1</td>
<td>0.3713 n.s.</td>
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<tr>
<td>Temperature (T)</td>
<td>2</td>
<td>&lt; 2.2e-16 ***</td>
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<tr>
<td>L × P</td>
<td>2</td>
<td>0.1987438 n.s.</td>
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<tr>
<td>L × T</td>
<td>2</td>
<td>3.839e-11 ***</td>
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<tr>
<td>P × T</td>
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<td>0.0001613 ***</td>
</tr>
<tr>
<td>P × L × T</td>
<td>4</td>
<td>0.001985 **</td>
</tr>
</tbody>
</table>

ns, ** and *** are *P* values for insignificant, <0.01 and 0.001, respectively, according to the likelihood ratio test.
Table 3 – Effects of provenance (P), salinity levels (S), temperature (T) and their interactions on final germination, mean germination time (MGT) and germination recovery of *Aeluropus lagopoides* seeds

<table>
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<tr>
<th>Predictor</th>
<th>Df</th>
<th>Pr(&gt;Chi)</th>
<th>Df</th>
<th>Pr(&gt;Chi)</th>
<th>Df</th>
<th>Pr(&gt;Chi)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Provenance (P)</td>
<td>2</td>
<td>4.667e-10***</td>
<td>2</td>
<td>0.4791 n.s.</td>
<td>2</td>
<td>0.02 *</td>
</tr>
<tr>
<td>Salinity (S)</td>
<td>1</td>
<td>&lt; 2.2e-16 ***</td>
<td>1</td>
<td>0.0002088 ***</td>
<td>1</td>
<td>4.249e-11 ***</td>
</tr>
<tr>
<td>Temperature (T)</td>
<td>2</td>
<td>&lt; 2.2e-16 ***</td>
<td>2</td>
<td>1.73e-05 ***</td>
<td>2</td>
<td>4.517e-07 ***</td>
</tr>
<tr>
<td>P × T</td>
<td>4</td>
<td>0.006795 **</td>
<td>4</td>
<td>0.003958 **</td>
<td>4</td>
<td>0.001495 **</td>
</tr>
<tr>
<td>T × S</td>
<td>2</td>
<td>1.183e-05 ***</td>
<td>2</td>
<td>0.195831 n.s.</td>
<td>2</td>
<td>0.0863702 n.s.</td>
</tr>
<tr>
<td>P × S</td>
<td>2</td>
<td>1.701e-15 ***</td>
<td>2</td>
<td>0.036453 *</td>
<td>2</td>
<td>0.017971 *</td>
</tr>
<tr>
<td>P × T × S</td>
<td>4</td>
<td>5.6e-15 ***</td>
<td>4</td>
<td>0.2333 n.s.</td>
<td>4</td>
<td>0.1284 n.s.</td>
</tr>
</tbody>
</table>

ns, *, ** and *** are P values for insignificant, <0.05, <0.01 and 0.001, respectively, according to the comparison of scaled de
Figure captions

**Fig. 1.** Germination percentages as a function of provenance, light and temperature conditions. Cycles of light indicates the 12/12 hours photoperiod. Error bars indicate standard error (SE).

**Fig. 2.** Seed germination as a function of the provenance, saline concentration and temperature of incubation.

**Fig. 3.** Average germination of seeds from the three selected habitats at each time point along the experiment and as a function of the salinity concentrations (top panel) and the temperatures of incubation (bottom panel). Error bars are not shown to avoid overlapping.

**Fig. 4.** Germination recovery as a function of provenance and temperature.

**Fig. 5.** Germination recovery as a function of the temperature and saline solutions.
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