

Parental Plant Elevation Does Not Affect Nonnative *Poa annua*'s Seed Germination and Propagation Potential

Authors: Deschenes, Elise, Caubel, Eloise, and Sirois, Luc

Source: Natural Areas Journal, 39(3) : 333-338

Published By: Natural Areas Association

URL: <https://doi.org/10.3375/043.039.0305>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

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

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

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

Parental Plant Elevation Does Not Affect Nonnative *Poa annua*'s Seed Germination and Propagation Potential

Elise Deschenes¹

¹ Université du Québec à Rimouski
300 Allée des Ursulines
Rimouski, QC G5L 3A1
Canada

Eloise Caubel¹

Luc Sirois^{1,2}

² Corresponding author:
luc_sirois@uqar.ca; 1-418-723-1986

Associate editor: Mike Jenkins

Natural Areas Journal 39:333–338

ABSTRACT: Nonnative species are a threat to biodiversity as their numbers are increasing in protected areas globally, impacting many ecological processes such as hydrological cycles, fire regimes, and competition. These species possess traits that ease their progression into alpine habitats, which could be a threat to rare and endemic plants in these areas. A prime example of this is in the Gaspésie National Park (Québec) where many nonnative species, such as *Poa annua*, are progressing in elevation, establishing in alpine habitats inhabited by rare and endemic species. In the case of this study, the impacts of elevation on parental plants and date of collection on seed germinability was determined for mature seeds of *P. annua* on three mountains in the Gaspésie National Park. Elevation as well as the date of collection did not influence germination of seeds of *P. annua*, and total germination remained very high (>80%) at high elevations. Therefore, because seed germination is not affected by maternal plant elevation, we assume that the abundance of *P. annua* may increase in disturbed alpine areas, and management strategies should be developed to counter or mitigate the effects of these invasions.

Index terms: elevation, invasive, maturation, *Poa annua*, seed

INTRODUCTION

By competing with and potentially eliminating rare and endemic species, nonnative species are a threat to biodiversity (Peña et al. 2008; Powell et al. 2011; Vila et al. 2011). They can modify fire regimes, hydrological cycles, and soil conditions, and shift plant species composition, thus affecting animal habitats (Peña et al. 2008; Pauchard et al. 2009). These impacts are particularly alarming in alpine ecosystems, where mountains have a particular flora with a large proportion of rare and endemic species (Kollmaier et al. 2005).

The harsh abiotic conditions of mountains and low rates of human-mediated propagation generally limit the capacity of plants to invade these ecosystems (Arevalo et al. 2005; Becker et al. 2005; Molina-Montenegro et al. 2012), which could explain the apparent resistance of many high-elevation areas to invasions (Pauchard et al. 2009; Barros and Pickering 2013). Regardless, many nonnative species have colonized high-elevation environments and have already had major impacts on mountain ecosystems, affecting biodiversity as well as ecosystem services (Becker et al. 2005; Daehler 2005; Peña et al. 2008). According to Pauchard et al. (2009), there are four main drivers that promote plant invasions: (1) pre-adaptation of nonnative species to abiotic conditions (Davidson et al. 2011; Gallagher et al. 2014); (2) disturbances, especially anthropogenic (Lembrechts et al. 2016); (3) low biotic resistance of native communities (Levine et al. 2004); and (4) high propagule pressure (Lockwood et al. 2005; Colautti et al. 2006). In fact, many

nonnative plants can establish, grow, and reproduce high above their current limits in cold mountains (Lembrechts et al. 2016), indicating that climate is most likely not the main limiting factor, but rather time, as most nonnative species are still moving toward higher elevations (Pysek et al. 2011).

Considering the current progression of nonnative species into higher elevations, as well as the negative impacts caused by these species, it is of particular importance to determine and quantify the risk of invasions into areas not yet colonized by nonnative species. This study determined the impact of maternal (seed-producing) plant elevation on *Poa annua* L. seed germinability for three mountains in the Gaspésie National Park (GNP; Québec, Canada), to determine if elevation can limit the propagation of the species in alpine habitats. The mother plant is thought to have a significant influence over seed traits, such as seed size, dormancy, and germination. Environmental conditions during seed set have a major influence on seed germinability, which is thought to increase with higher temperatures, shorter days, drought, as well as high soil nitrogen levels (Fenner 1991; Penfield and MacGregor 2016). There does not yet seem to be a consistent relationship identified between germinability and changes in elevation (Vera 1997; Giménez-Benavides et al. 2005). *P. annua* is considered one of the most widespread invaders worldwide, especially in protected areas as well as in the Antarctic (Williams et al. 2016; Foxcroft et al. 2017). Therefore, the study of *P. annua* propagation potential is necessary for conservation in sensitive alpine ecosystems where the species is a

threat (Foxcroft et al. 2017). Germinability is expected to decrease with increased maternal plant elevation, due to the harsher climate, limiting seed maturation, although this trend is variable across species (Vera 1997; Giménez-Benavides et al. 2005). Later date of collection is expected to increase germination, as day length is shorter and seeds have had more time to mature (Fenner 1991).

MATERIAL AND METHODS

Study Area

The study is centered on the GNP (48.9474°N, 66.1224°W) and the surrounding region, a highland area in eastern Québec, Canada, where elevations vary from sea level to 1270 m. The Mont Albert, Mont Sainte-Anne, and Mont Jacques-Cartier mountains are only accessible via hiking paths. The climate is greatly influenced by the proximity to the Gulf of Saint Lawrence, these mountains receiving the highest precipitation in all of Québec (1849 mm), 56% of which is snowfall (Environment Canada 2018). Thermal sum (degree-days above 5 °C, DD) for the years 2015–2017 averaged 1497 DD and 827 DD at the lower end and at the upper end of the elevation gradient, respectively (L. Sirois, unpubl. data). The vegetation in the Gaspésie National Park varies according to elevation, with three main levels: the montane level, the subalpine level, and the alpine level. The montane level (<900m) is dominated by dense canopies of balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* Moench), whereas the subalpine level (900–1050 m) is characterized by krummholz stands interspersed with late-melting snowbeds, alpine prairies, and fens. The alpine level (>1050m) is the domain of the treeless tundra (Boudreau 1981). This region qualifies as a botanical hotspot due to a biological richness that is unlike anywhere else in Québec. The endemic and disjunct cordilleran flora of the alpine level in the GNP was already noticed by Fernald (1925). Four of these species are considered threatened: *Salix chlorolepis*, *Solidago chlorolepis*, *Cherleria marcescens*, and *Polystichum scopulinum* (MDDELCC 2018).

Methods

Visibly mature seeds of *P. annua* ($n = 43$ plants, each at a unique elevation), as well as *Hieracium caespitosum* ($n = 26$), *Hieracium pilosella* ($n = 26$), *Hieracium vulgatum* ($n = 20$), *Plantago major* ($n = 17$), and *Ranunculus acris* ($n = 18$) were collected between 15 July and 4 September 2017 at various elevations (0–1200 m) along the hiking paths on the Mont Albert (1151 m), Mont Jacques Cartier (1268 m), and Mont Sainte-Anne (1147 m) mountains as well as along the road in the Sainte-Anne valley for lower elevations (0–200 m; Figure 1).

For *P. annua* and *P. major*, seeds were collected when their reproductive tissues were stramineous, whereas for the three *Hieracium* species and *R. acris*, seeds were collected when they were dark brown or black with a tegument hard enough to resist some nail pressure. We collected seeds approximately every 50 m in elevation, according to our GPS coordinates (see sampling frequency, Figure 2). If multiple plants were present within 50 m, only the seeds of one plant were collected. Each plant had between 5 and 50 seeds. Density of nonnative plants along the elevational gradient was not evaluated.

The six collected species are common along hiking trails in the GNP, but only *P. annua* has progressed into the alpine level of Mont Albert and Mont Sainte-Anne. We only found two individuals of *P. annua* in the alpine level of Mont Albert, and about a dozen on the alpine level of Mont Sainte-Anne, implying that the species is able to tolerate the alpine conditions, but has yet to heavily invade. *P. annua* has only reached the subalpine level of Mont Jacques Cartier.

Seeds were kept in paper bags at room temperature until the dormancy breaking treatment, which was conducted in an environmental chamber from 13 September to 13 November 2017. Seeds of *P. annua* were subjected to warm stratification for 60 d at 20 °C and 90% humidity in a growth chamber, as recommended by Standifer and Wilson (1988) and Baskin and Baskin (1998). Lemmas and paleas were not re-

moved. Seeds of *R. acris*, *H. pilosella*, *H. vulgatum*, *H. caespitosum*, and *P. major* were subjected to cold stratification for 60 d at 5 °C and 90% humidity in a growth chamber, as recommended by Baskin and Baskin (1998).

Seeds were sown in 10-cm petri dishes on humidified Whatman no. 1 filter paper. After the dormancy breaking treatments, the seeds were subjected to a 30-d germination test. Seeds of *P. annua* were germinated at 10 °C for 12 hr of light and 12 hr of dark at 90% humidity in a growth chamber (Frenot and Gloaguen 1994; Kellman-Sopyla and Gielwanoska 2015). Cold stratified seeds were germinated at 20 °C/30 °C for 8 hr light and 16 hr dark, at 90% humidity in a growth chamber (Baskin and Baskin 1998). Germinated seeds were counted and removed daily over a period of 30 d. Water was replenished every 3 d in petri dishes. Seeds were regarded as germinated upon the emergence of the radicle. Except for *P. annua*, seeds of other collected species did not germinate during this test, and were subjected to a second cold stratification, for 90 d. These seeds failed to germinate at a subsequent test and were not included further in the analysis. Therefore, this study focuses on *P. annua* seeds.

Data Analysis

Total germination was determined by calculating the number of germinated seeds over the total number of tested seeds. Germination rate (S) was calculated using the following formula (Kovar et al. 2013):

$$S = N_1 + \frac{(N_2 - N_1)}{2} + \frac{(N_3 - N_2)}{3} + \dots + \frac{(N_n - N_{n-1})}{n}$$

N = number of germinated seeds after n days

The effect of the elevation of maternal plants as well as the date of collection on total seed germinability and rate of germination were determined by multiple regressions. Variances were checked by plotting residual versus fitted values to confirm homogeneity and normality was checked by quantile–quantile comparison plots. These conditions were respected for both regression models. Statistical

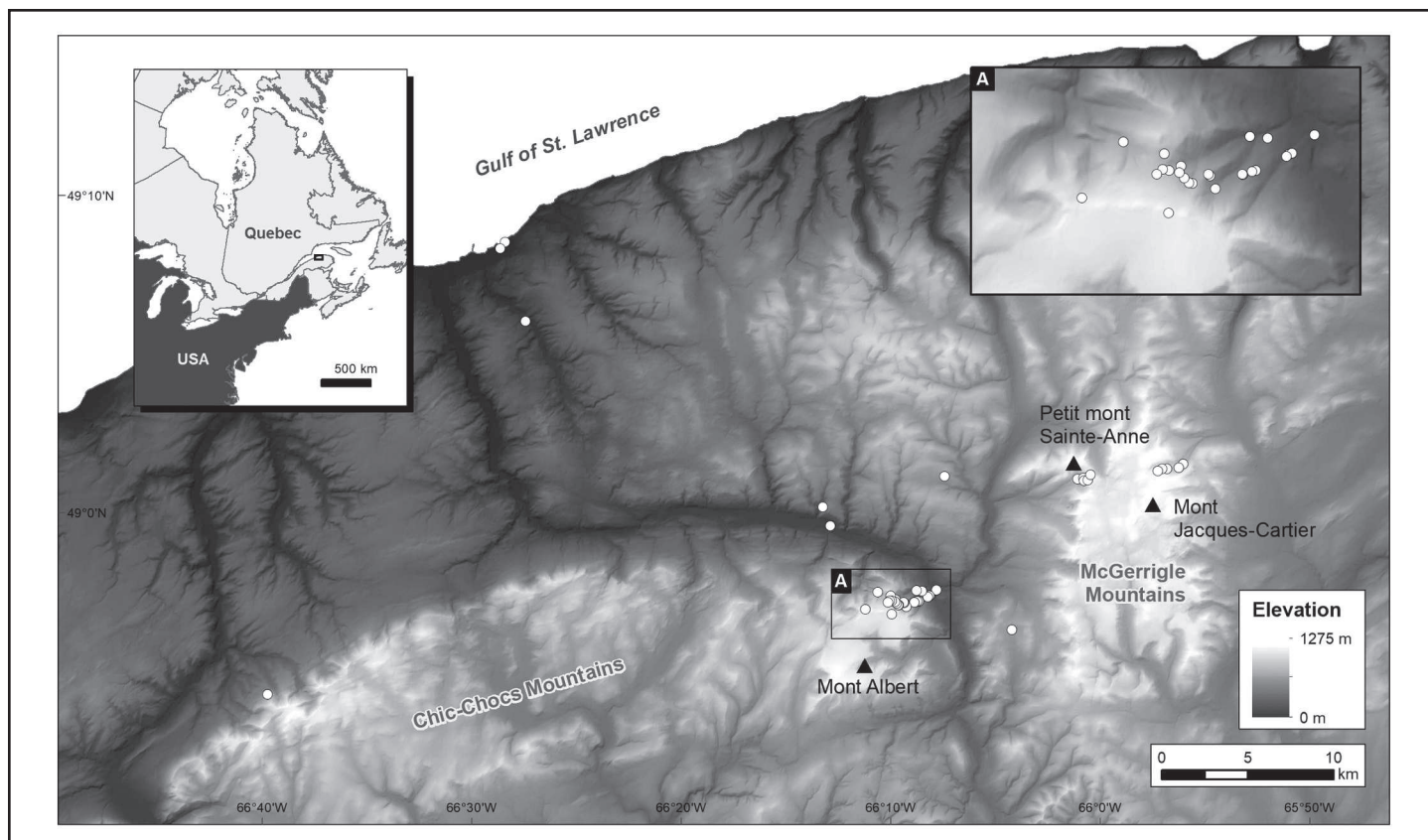


Figure 1. Map of sampling points.

analyses were carried out using R 3.4.3, using the package *olsrr* (Hebbali 2018; R Core Team 2018).

RESULTS

The model “Germination = Date + Elevation + Date × Elevation” was not significant ($P = 0.873$). We did not observe an effect of the date ($P = 0.393$), elevation ($P = 0.196$), or their interaction ($P = 0.216$) on total seed germinability percentage (Figure 3a, 3b). The model “Rate = Date + Elevation + Date × Elevation” was not significant ($P = 0.464$). We did not observe an effect of the date ($P = 0.758$), elevation ($P = 0.739$), or their interaction ($P = 0.729$) on the rate of germination (Figure 3c, 3d). Germination percentages were quite variable, ranging from 0% to 100% with an average of 55%, with 42% of petri dishes germinating at more than 70%, independently of elevation or period of collection (Figure 4a). Germination rates were quite variable, with an average of 0.1274 seeds/d (Figure 4b).

DISCUSSION

Our study determined that elevation of the mother plant did not significantly affect germinability and germination rate of mature *P. annua* seeds in the study area, nor does the date of collection affect these two variables. Generally, elevation drives vegetation composition by limiting plant growth and development due to harsh conditions and low human-mediated propagation (Parks et al. 2005). Temperature

has been shown to be the strongest environmental factor influencing germination (Penfield and MacGregor 2016) because the reduction in dormancy brought by warmer conditions during seed maturation is a very general phenomenon in many species (Fenner 1991). In this sense, higher elevations are generally associated with lower germination potential, due to lower temperatures, although this relationship has been studied in very few species. Furthermore, the effect of elevation on germina-

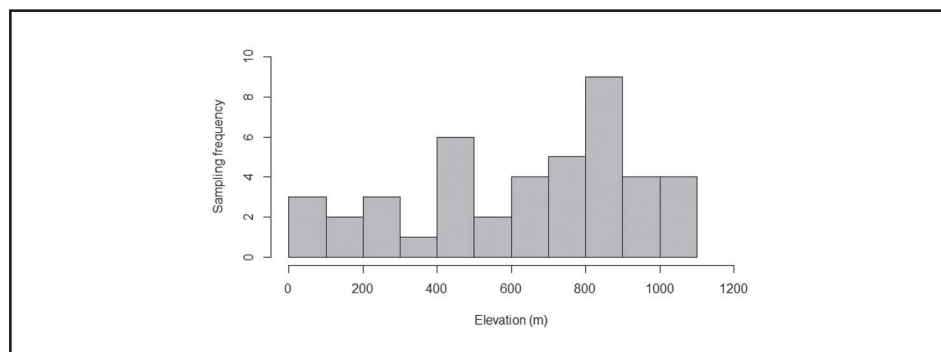


Figure 2. Sampling frequency according to elevation classes.

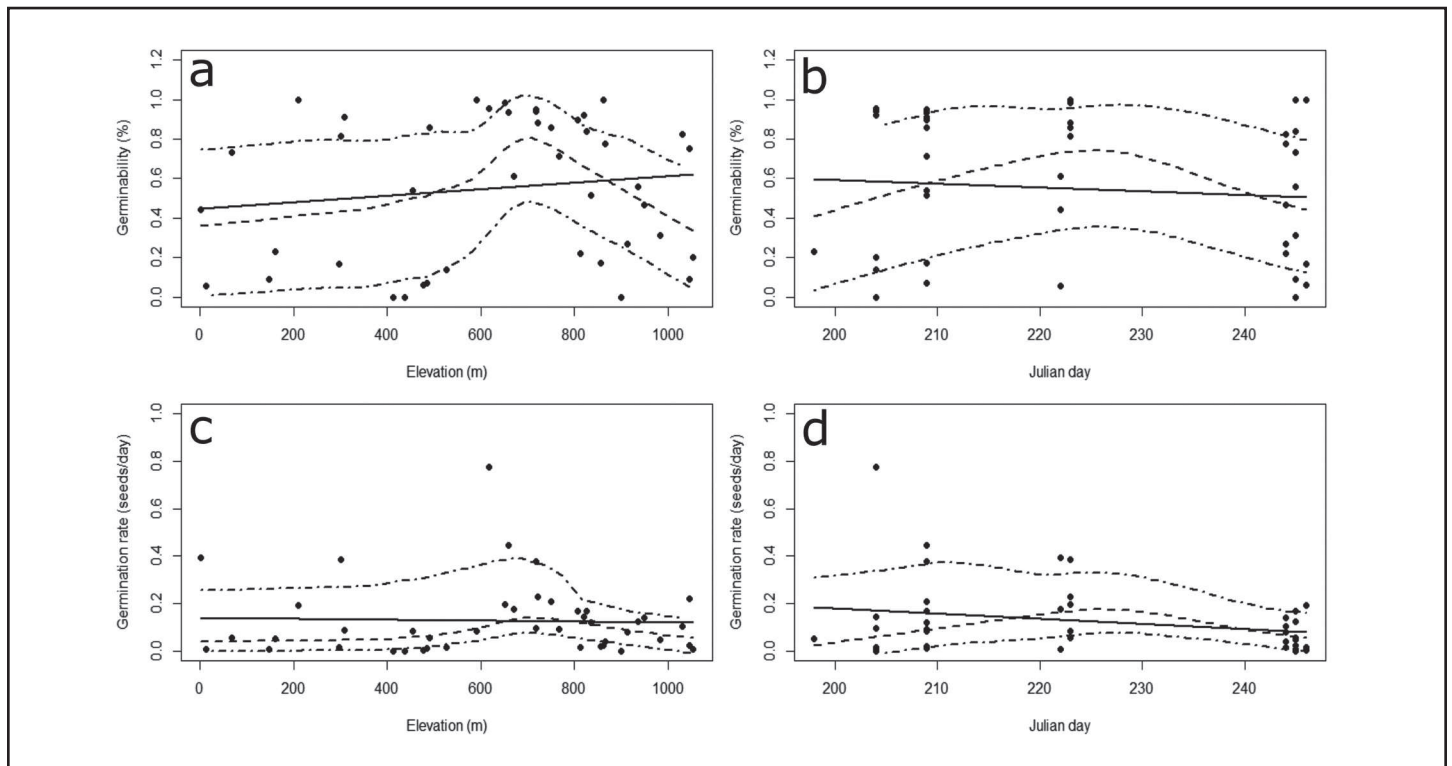


Figure 3: Effect of maternal environment elevation (m) and date of collection (Julian day) on total germinability (a and b, respectively) and germination rate (c and d, respectively) for seeds of *Poa annua* L. collected in the GNP, Québec, Canada.

tion is not consistent for all species, and species-specific studies are necessary (Vera 1997; Giménez-Benavides et al. 2005).

Our study showed that elevation did not affect seed formation and germination in *P. annua*. Mother plants can produce seeds that reach maturity and have full germination potential regardless of the elevation at which they grew, although the species may be limited at elevations higher than those considered in our study. In this sense, elevation itself would not limit the maturation of at least some seeds; once a plant is established, it may produce viable seeds, which favors its proliferation into higher elevations. Furthermore, germination percentages remain quite high at higher elevations (Figure 1), which was quite unexpected, as higher elevations are generally associated with lower temperatures and lower germination potential (Fenner 1991). Many germination percentages higher than 80% are seen at alpine elevations, further proving that the plant's capacity to produce germinable seeds is not affected by mother plant elevation. This is further proof of *P. annua*'s high propagation potential,

because it has a low or easily breakable dormancy. As elevation does not limit the capacity of the plant to produce germinable seeds, we expect further propagation and an increase in density of the species into other disturbed sites in alpine areas, which would be facilitated by the regular presence of hikers along the paths (Parks et al. 2005). In fact, occurrence of nonnative species increases with the number of visitors in a protected area (Lonsdale 1999). Very few plants of this species have been found in alpine areas, but our results highlight the possible expansion of *P. annua* into other disturbed sites.

P. annua generally exhibits greater germination percent at temperatures around 12 °C (Frenot and Gloaguen 1994; Kellman-Soplya and Gielwanowska 2015). This could explain its adaptation to mountainous Arctic and Antarctic ecosystems, where summer temperatures are low. In Antarctica, *P. annua* has adapted to the temperatures of this region, to the point that plants that invaded areas have been recognized as a new ecotype (Kellmann-Soplya and Gielwanowska 2015). *P.*

annua is the most problematic invader in the Antarctic due to its high fecundity, wide tolerance, and high plasticity, which also make it one of the most successful invaders worldwide (Frenot et al. 2005; Williams et al. 2016). Nevertheless, elevation did limit the density of seeds in the seed bank in Antarctica, implicating elevation in limiting *P. annua* invasion velocity (Williams et al. 2016). As such, *P. annua* is able to tolerate conditions in alpine levels along disturbed hiking paths, although its potential to invade non-disturbed vegetation is unknown, as nonnative plants often require different traits to invade natural vegetation rather than disturbed sites (McDougall et al. 2018).

As for date of collection, we assumed that later collection dates would be correlated with higher germination, as germinability is promoted by short-day regimes (Fenner 1991). Considering seeds were collected from July to September, germination should increase through the summer as day length decreased and seeds had more time to mature. The lack of significant effect attributable to collection date could

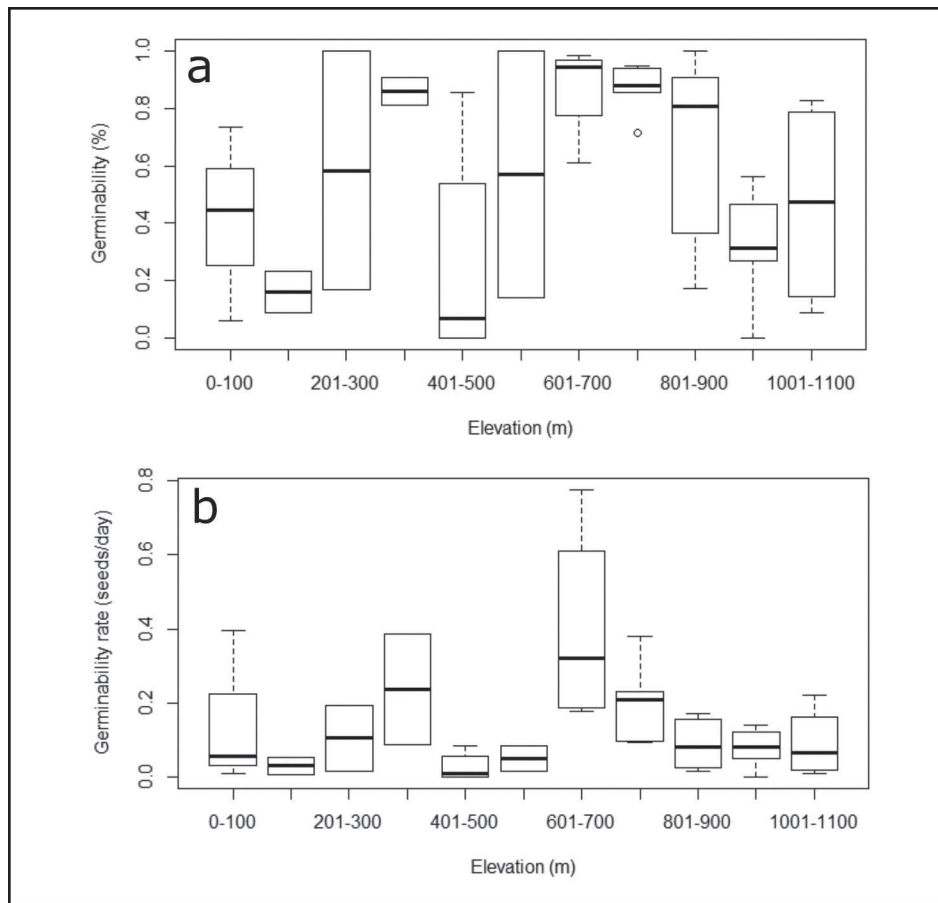


Figure 4. Box and whisker plot of germinability (a) and germination rate (b) according to elevation classes.

be due to the fact that seeds were collected when phenological traits (stramineous color of culms or floral parts, seed color, and hardness) indicated maturity; if seeds were not yet mature, they were not collected. Furthermore, *P. annua* produces many inflorescences per season, peaking in early summer and autumn, with the greatest amount of seeds produced in autumn. This would allow the production of more seedlings, which would imply that mature seeds are available during a large portion of the summer, regardless of light regime (Law 1981).

In this study we did not capture the effect of elevation on the whole process of invasion by *P. annua*. Such investigation would require considering the amount of viable seeds produced and the density of plants, as well as other factors that could affect germination and fecundity, such as the slope, exposure, and snowfall (Xu et al. 2017). It may also be relevant to study the

demographic processes of these invasions to better evaluate the success of nonnative species in harsh ecosystems as well as their potential to invade natural vegetation. In this connection our study reveals that *P. annua* is a very successful invader that has already reached disturbed alpine zones but its potential to invade the natural ecosystem remains unknown.

ACKNOWLEDGMENTS

We would like to thank Isabelle Glazer and Alany Blanchette for their help during the fieldwork, as well as Virginie Labrecque for her help during the germination tests. We thank the GNP for allowing us to conduct this study. We thank Marie-Andrée Roy for her help creating a map of sampling points. We thank both of the anonymous reviewers. This study was supported by UQAR special research fund allocated to LS.

Elise Deschenes is an undergraduate student at the University of Québec in Rimouski.

Eloise Caubel was an exchange student at the University of Québec in Rimouski and has now started a masters at the University of Vandoeuvre-lès-Nancy.

Luc Sirois received his PhD in plant biology of the University Laval in Québec, Québec. He is currently a Professor of Biology at the University of Québec in Rimouski.

LITERATURE CITED

- Arevalo, R.J., J.D. Dalgado, R. Otto, A. Naranjo, M. Salas, and J.M. Fernandez-Palacios. 2005. Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). *Perspectives in Plant Ecology, Evolution and Systematics* 7:185-202.
- Barros, A., and C.M. Pickering. 2013. Non-native plant invasion in relation to tourism use of Aconcagua Park, Argentina, the highest protected area in the southern hemisphere. *Mountain Research and Development* 34:13-26.
- Baskin, C., and J. Baskin. 1998. *Seeds: Ecology, Biogeography and Evolution of Dormancy and Germination*. 2nd edition. Academic Press, San Diego, CA.
- Becker, T., H. Dietz, R. Billeter, H. Buschmann, and P.J. Edwards. 2005. Altitudinal distribution of alien plant species in the Swiss Alps. *Perspectives in Plant Ecology, Evolution and Systematics* 7:173-183.
- Boudreau, F. 1981. *Écologie des étages alpin et subalpin du Mont Jacques-Cartier, Parc de la Gaspésie, Québec*. Master's thesis, University of Laval, Québec.
- Colautti, R.I., I.A. Grigorovich, and H.J. MacIsaac. 2006. Propagule pressure: A null model for biological invasions. *Biological Invasions* 8:1023-1037.
- Daehler, C.C. 2005. Upper-montane plant invasions in the Hawaiian Islands: Patterns and opportunities. *Perspectives in Plant Ecology, Evolution and Systematics* 7:203-216.
- Davidson, A.M., M. Jennions, and A.B. Nicotra. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecological Letters* 14:419-431.
- Environment Canada. 2018. Climate normals and averages 1981–2010. Ste Anne des Monts. Accessed 15 May 2018 from <http://

- climate.weather.gc.ca/climate_normals>.
- Fenner, M. 1991. The effects of the parent environment on seed germinability. *Seed Science Research* 1:75-84.
- Fernald, M.L. 1925. Persistence of plants in unglaciated areas of boreal America. *Memoirs of the American Academy of Arts and Sciences* 15(3):239-342.
- Foxcroft, L.C., P. Pysek, D.M. Richardson, P. Genovesi, and S. MacFadyen. 2017. Plant invasion science in protected areas: Progress and priorities. *Biological Invasions* 19:1353-1378.
- Frenot, Y., and J.C. Gloaguen. 1994. Reproductive performances of native and alien colonizing phanerogams on a glacier foreland, Ile Kerguelen. *Polar Biology* 14:473-481.
- Frenot, Y., S.L. Chown, J. Whinam, P.M. Selkirk, P. Convey, M. Skotnicki, and D.M. Bergstrom. 2005. Biological invasions in the Antarctic: Extent, impacts and implications. *Biological Reviews* 80:45-72.
- Gallagher, R.V., R.P. Randall, and M.R. Leishman. 2014. Trait differences between naturalized and invasive plant species independent of residence time and phylogeny. *Conservation Biology* 29:360-369.
- Giménez-Benavides, L., A. Escudero, and F. Pérez-García. 2005. Seed germination of high mountain Mediterranean species: Altitudinal, interpopulation and interannual variability. *Ecological Research* 20:433-444.
- Hebbali, A. 2018. *olsrr: Tools for building OLS regression models*. R package version 0.5.1. Accessed 5 May 2018 from <<https://CRAN.R-project.org/package=olsrr>>.
- Kellmann-Sopyla, W., and I. Gielwanowska. 2015. Germination capacity of five polar Caryophyllaceae and Poaceae species under different temperature conditions. *Polar Biology* 37:1753-1765.
- Kollmaier, M., G.S. Gurung, K. Hurni, and D. Maselli. 2005. Mountains: Special places to be protected? An analysis of worldwide nature conservation efforts in mountains. *International Journal of Biodiversity Science and Management* 1:181-189.
- Kovar, P., L. Vozar, and J. Jancovic. 2013. The influence of water extracts of selected turfgrass species on germination and initial growth of *Poa annua* L. *Acta Universitatis Agriculturae et Silviculturae Mendelianae Brunensis* 61:677-681.
- Law, R. 1981. The dynamics of a colonizing population of *Poa annua*. *Ecology* 62:1267-1277.
- Lembrechts, J.J., A. Pauchard, J. Lenoir, M.A. Nunez, C. Geron, A. Ven, P. Bravo-Monasterio, E. Teneb, I. Nijs, and A. Milbau. 2016. Disturbance is the key to plant invasions in cold environments. *Proceedings of the National Academy of Sciences* 113(49):14061-14066.
- Levine, J.M., P.B. Adler, and S.G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecological Letters* 7:975-989.
- Lockwood, J.L., P. Cassey, and T. Blackburn. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20:223-228.
- Lonsdale, W.M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522-1536.
- McDougall, K.L., J. Lembrechts, L.J. Rew, S. Haider, L.A. Cavieres, C. Kueffer, A. Milbau, B.J. Naylor, M.A. Nunez, A. Pauchard, et al. 2018. Running off the road: Roadside non-native plants invading mountain vegetation. *Biological Invasions* 20:3461-3473.
- [MDELCC] Ministère du développement durable et de la lutte contre les changements climatiques. 2018. La serpentine du mont Albert. Accessed 15 May 2018 from <<http://www.mdelcc.gouv.qc.ca/biodiversite/habitats/serpentine-mont-albert/index.htm>>.
- Molina-Montenegro, M.A., J. Peñuelas, S. Munné-Bosch, and J. Sardans. 2012. Higher plasticity in ecophysiological traits enhances the performance and invasion success of *Taraxacum officinale* (dandelion) in alpine environments. *Biological Invasions* 14:21-33.
- Parks, C.G., S.R. Radoosevich, B.A. Endress, B.J. Naylor, D. Anzinger, L.J. Rew, B.D. Maxwell, and K.A. Dwire. 2005. Natural and land-use history of the Northwest mountain ecoregions (USA) in relation to patterns of plant invasions. *Perspectives in Plant Ecology, Evolution and Systematics* 7:137-158.
- Pauchard, A., C. Kueffer, H. Dietz, C. Daehler, J. Alexander, P. Edwards, J. Arévalo, L. Cavieres, A. Guisan, S. Haider, et al. 2009. Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment* 7(9):479-486.
- Peña, E., M. Hidalgo, B. Langdon, and A. Pauchard. 2008. Patterns of spread of *Pinus contorta* Dougl. ex Loud. invasion in a natural reserve in southern South America. *Forest Ecology and Management* 256:1049-1054.
- Penfield, S., and D.R. MacGregor. 2016. Effects of environmental variation during seed production on seed dormancy and germination. *Journal of Experimental Botany* 68(4):819-825.
- Powell, K.I., J.M. Chase, and T.M. Knight. 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. *American Journal of Botany* 98:539-548.
- Pysek, P., V. Jarosik, J. Pergl, and J. Wild. 2011. Colonization of high altitudes by alien plants over the last two centuries. *Proceedings of the National Academy of Sciences* 108(2):439-440.
- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Standifer, L.C., and P.W. Wilson. 1988. A high temperature requirement for after ripening of imbibed dormant *Poa annua* L. seeds. *Weed Research* 28:365-371.
- Vera, M.L. 1997. Effects of altitude and seed size on germination and seedling survival of heathland plants in north Spain. *Plant Ecology* 133:101-106.
- Vila, M., J.L. Espinar, M. Hejda, P.E. Hulme, V. Jarosik, J.L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pysek. 2011. Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecological Letters* 14:702-708.
- Williams, L.K., P. Kristiansen, B.M. Sindel, S.C. Wilson, and J.D. Shaw. 2016. Quantifying the seed bank of an invasive grass in the sub-Antarctic: Seed density, depth, persistence and viability. *Biological Invasions* 18:2093-2106.
- Xu, J., W. Li, C. Zhang, W. Liu, and G. Du. 2017. The determinants of seed germination in an alpine/subalpine community on the Eastern Qinghai-Tibetan Plateau. *Ecological Engineering* 98:114-122.