

DOI: 10.5586/asbp.3606

**Publication history**

Received: 2018-06-28

Accepted: 2018-12-05

Published: 2018-12-31

**Handling editor**

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**Authors' contributions**

AR performed the experiments and statistical analysis; KJC, HG, MW, and AZ collected seed material; MW conceived the idea of the study; HG collected the literature; HG, AR, and MW wrote the manuscript

**Funding**

This work was supported by the National Science Center, Poland (grant number 2013/09/B/NZ8/03293). The study was carried out at the Biological and Chemical Research Center, University of Warsaw, established within a project cofinanced by the EU European Regional Development Fund under the Innovative Economy Operational Program, 2007–2013.

**Competing interests**

No competing interests have been declared.

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## ORIGINAL RESEARCH PAPER

Seed germination and invasion success of *Poa annua* L. in AntarcticaAgnieszka Rudak<sup>1</sup>, Halina Galera<sup>1</sup>, Anna Znój<sup>2</sup>, Katarzyna J. Chwedorzewska<sup>2</sup>, Maciej Wódkiewicz<sup>1\*</sup><sup>1</sup> Faculty of Biology, Biological and Chemical Research Center, University of Warsaw, Żwirki i Wigury 101, 02-089 Warsaw, Poland<sup>2</sup> Institute of Biochemistry and Biophysics, Polish Academy of Sciences, Pawińskiego 5a, 02-106 Warsaw, Poland\* Corresponding author. Email: [wodkie@biol.uw.edu.pl](mailto:wodkie@biol.uw.edu.pl)**Abstract**

One of the first steps to successful invasion of plant species that reproduce sexually is seed germination, which may be highly influenced by climatic conditions. We studied *Poa annua*, a cosmopolitan species found across all climatic zones and the only alien species that has successfully colonized the Antarctic. Our research questions were: (i) if harsh polar conditions restrict seed germination of *P. annua* and (ii) if the germination capacity of the Antarctic population of the species is due to high germination aptitude in the source population. We compared germination of seeds collected from eight populations around the world (maritime Antarctica, S Chile, W Argentina and E Argentina, NE USA, SW Croatia, C Poland and S Poland). We followed germination of seeds collected in the field and acquired from plants cultivated under unified optimal conditions. We found significant differences between populations in germination characteristics of seeds collected in the field. These could be associated with seed ripening in different locations. Seeds obtained under favorable conditions differed in stratification requirements. The germination potential of the Antarctic population is lowered by unfavorable polar conditions impacting seed maturation. Thus, the species' invasion in the Antarctic seems highly restricted by the harsh environment. Environmental unsuitability may restrict invasions of other species in the same way potentially. However, this environmental barrier protecting Antarctica from invasions may be broken under a climate warming scenario.

**Keywords**

common garden; genetic diversity; environmental control; invasive species; survival analysis; maritime Antarctica

**Introduction**

Because of strong spatial isolation and harsh environmental conditions [1], only about 10 alien plant species have been recorded in Antarctica up until now. All of them were either eradicated or exterminated due to natural stochastic events [2], except one – annual bluegrass (*Poa annua* L.) [3]. This species was capable of surviving and producing viable caryopses able to germinate under local polar conditions [4] and forming a soil seed bank comparable to native species [5,6]. In the 2014/2015 Antarctic summer season, an invasive population of this species spreading in Point Thomas Oasis (King Georg Island, South Shetlands, maritime Antarctic) consisted of almost 1,500 tussocks [4]. The existence of this population at Point Thomas Oasis for over 30 years [3] together with the ability of the local population to produce viable seeds able to germinate [5] and the spreading of the species in the Oasis [7] indicate the species' invasion success in the region [4].

For a successful invasion, an alien species has to bypass several barriers [8]. One of them is the reproduction barrier, which may be overcome either through vegetative

propagation or sexual reproduction. For invasive plants such as *P. annua* that mainly reproduce sexually [9], factors limiting seed germination may be an important obstacle to the spread and self-sustenance of the alien population [10,11]. This pertains especially to harsh environments where conditions are especially unfavorable for seed ripening and germination. Thus, the invasive population has to possess specific traits enabling sufficient germination potential under these local harsh conditions.

It has been found that species may differ in their invasion ability due to intraspecific differences between populations [12–14]. Therefore, high invasiveness may not be a species trait, but rather a trait of a specific population. It may also be a case that all populations of a species have low invasiveness, but due to intraspecific admixture between distant populations, a population of high invasiveness arises. The underlying mechanism may be associated with a new combination of traits promoting invasiveness of a species and enabling its ability to thrive in and even conquer a new environment [15,16]. One such trait that may enhance species invasiveness is the ability to produce many viable seeds able to germinate under different conditions.

In this context we studied germination characteristics of *P. annua* from distant populations originating in different climatic zones, as different environmental factors may distinctively drive traits associated with species invasiveness, such as seed germination characteristics. Our research questions were if harsh polar conditions restrict seed germination of *P. annua* and if the germination capacity of the invasive Antarctic population is possible due to high germination aptitude of one of the potential source populations in comparison with other populations of the species from different climatic zones. One of the most probable potential sources for the invasion of annual bluegrass at Point Thomas Oasis is the Warsaw population, as soil for the Station greenhouse was brought from there [3]. The first question may be of special significance with regard to the eradication of the species and enhanced seedling emergence from the soil seed bank under possible local climate warming. This is because present cold environmental conditions favor preservation of seeds already deposited in soil, which may readily germinate under warmer conditions [17] reconstituting the eradicated population. While collecting seed material in the Antarctic we observed that many seeds are smaller than normal annual bluegrass seeds and seem to be immature. Therefore, our working hypotheses were: (i) seeds collected in a harsh environment due to their immaturity should germinate slower and have lower germination ability than seeds collected in more favorable conditions; (ii) seeds produced under favorable (temperate climate) common garden conditions should show no differences in germination characteristics regardless of their provenance.

## Material and methods

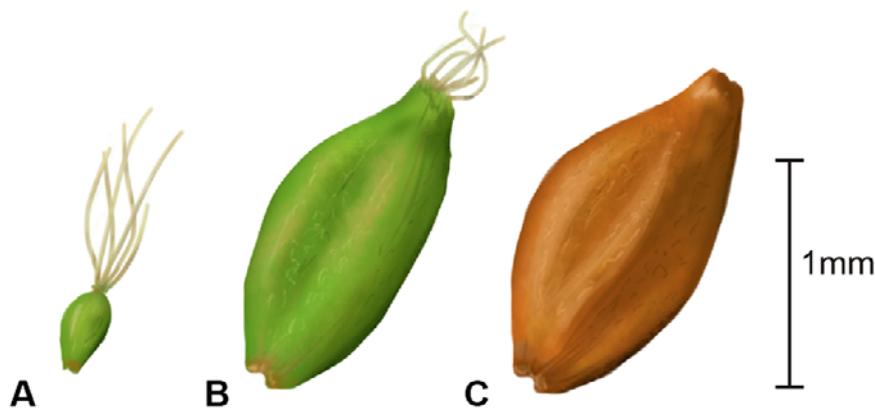
We collected caryopses from eight populations of *P. annua* from different geographic locations representing different climatic zones (Tab. 1). Seed material from all populations was collected in 2015. Additionally, we also included propagules from the same studied Antarctic population, but collected in 2010. The material was air-dried and transported to Warsaw where it was maintained at 4°C until seed germination experiments were performed. To avoid fungal infection, all caryopses were treated before sowing with Sumin's T 75 DS/WS seed dressing according to manufacturer's instructions.

Our initial observations indicated that many caryopses collected in the Antarctic population were immature (smaller than normal and green). Therefore we used 20 panicles collected from the Antarctic population in 2015 to assess seed development. Caryopses were visually inspected and divided into three groups depending on their development after Mitich [18]: fully developed brown caryopses, large immature green caryopses, small and green caryopses with remains of the flower unable to germinate (Fig. 1). For all populations excluding the Antarctic, we used fully developed caryopses (Fig. 1C). Since in the Antarctic population there were many immature caryopses for our experiment on germination of seeds collected in the field, we also used the immature ones from this population (Fig. 1B).

For our first germination experiment (G1) we divided the caryopses into 25-count batches having four replications per population. Fruits were placed on moist filter paper

**Tab. 1** Location and climate types (according to Kottek et al. [43]) of populations from which *P. annua* caryopses were collected.

| Location                       | Köppen–Geiger climate type |               |             |
|--------------------------------|----------------------------|---------------|-------------|
|                                | Main climate               | Precipitation | Temperature |
| Arctowski (maritime Antarctic) | Polar                      | -             | Polar frost |
| Mar del Plata (E Argentina)    | Arid                       | Steppe        | Cold arid   |
| Mendoza (W Argentina)          | Warm temperate             | Summer dry    | Warm summer |
| New York (NE USA)              | Warm temperate             | Fully humid   | Warm summer |
| Warsaw (C Poland)              | Warm temperate             | Fully humid   | Warm summer |
| Punta Arenas (S Chile)         | Warm temperate             | Fully humid   | Cool summer |
| Tatra Mountains (S Poland)     | Snow                       | Fully humid   | Warm summer |
| Trogir (SW Croatia)            | Warm temperate             | Steppe        | Hot arid    |

**Fig. 1** Developmental stages of caryopses collected in the Antarctic population: (A) small caryopses unable to develop (green with remains of the flower); (B) large immature caryopses (green); (C) fully developed caryopses (brown). Graphics by AR.

in Petri dishes in a growth chamber under 12-h photoperiod with 10°C at night and 20°C during the day period. Germination was followed every 2 days, for 54 days. Seeds were noted as germinated when the radicle was visible. This experiment was conducted to control for the maternal effects [19].

For our second germination experiment (G2a) we used caryopses produced by plants grown from seeds in G1 and cultivated in commercially available planting soil in a growth chamber until seed set under the same photoperiod and temperature regime as above. Plants of different provenances were isolated to disable pollen transfer between populations. Caryopses were collected when they started falling out of panicles to ensure their full development and stored subsequently at 4°C for 1 to 3 weeks until sowing. We used 200 caryopses per population divided into eight replications of 25-count batches. The initial treatments and germination conditions were the same as in G1. Seed germination was followed for 54 days and checked daily, due to the need for higher frequency of observations noticed in the first experiment. This experiment was conducted as the second part of a maternal effects [19] experiment and as a control to check for stratification requirements. The third germination experiment (G2b) was performed on the same seed material as G2a, but after 6 months of stratification at 4°C.

To assess differences in seed germination characteristics between populations, in all experiments we used Kaplan–Meyer survival analysis with log-rank test and 95% confidence limits for the survival curves. Differences between populations regarding the first day of germination and logit transformed [20] final germination percent were assessed with a one-way ANOVA with a subsequent Tukey post hoc test at  $p \leq 0.05$ . We

also performed a principal component analysis (PCA) on the first day of germination, final germination percent, and number of days after which 50% of the final germination was reached. All analyses were performed in R [21] with additional multcomp [22], survival [23], and factoextra [24] packages.

## Results

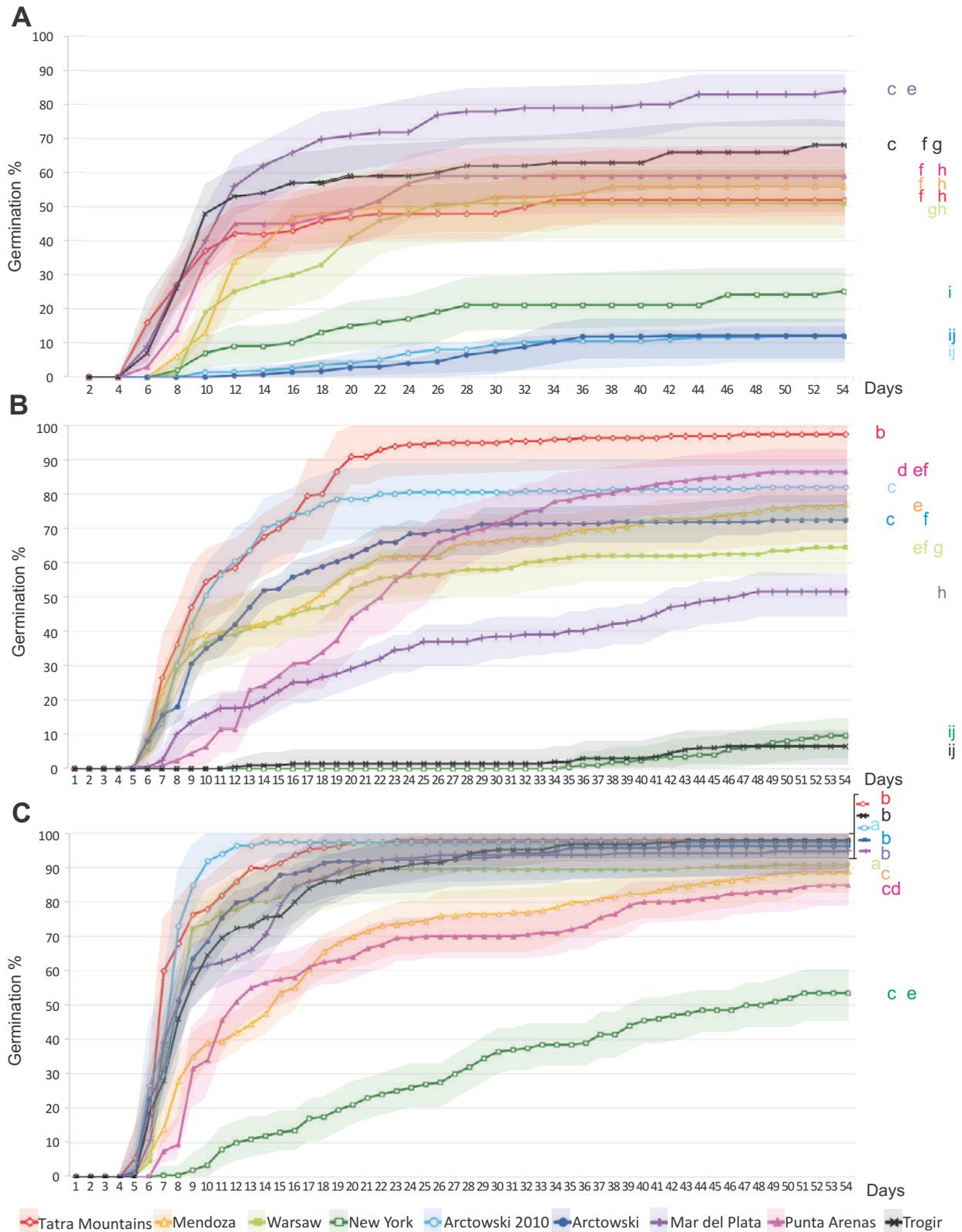
Based on observations of 165 caryopses from 20 panicles collected in Antarctica, prior to the start of the first germination experiment, we classified only 3% of them as fully developed, 53% as immature (the same size as developed seeds, but green color). The remaining 44% of seeds were small and green with remains of the flower and, therefore, were classified as unable to mature (Fig. 1).

We found significant differences between population seed germination curves and performed experiments (logrank test statistics 2,668,  $df = 26$ ,  $p < 0.001$ ). Germination curve analysis for all populations indicated several distinct groups of populations across all experiments (Fig. 2). This grouping was confirmed by ANOVA conducted on the final seed germination percent ( $F = 20$ ,  $df = 26$ , 150,  $p < 0.001$ ) as a similar grouping pattern was observed (Tab. 2). ANOVA on the first day of germination showed differences between populations ( $F = 40.71$ ,  $df = 26$ , 150,  $p < 0.001$ ) and Tukey post hoc grouping at  $p \leq 0.05$  revealed five groups. Four groups with the slowest germination consisted of one population each (in parenthesis we present the first day of germination averaged across replications): New York G2a (38), Trogir G2a (26), Arctowski 2010 G1 (19), and Arctowski 2015 G1 (16). Populations with seed germination later than the fourteenth day after sowing also exhibited low germination percent and germination dynamic (see Fig. 2 and Tab. 2). All other populations formed one group in which seeds began to germinate around the seventh day after sowing.

PCA conducted on three germination characteristics (i.e., final germination percent, first day of germination, and the day when populations reached 50% of their final germination) showed similar differences as previous tests. The first principal component associated with germination speed (both first day of germination and the day of reaching 50% of final germination together contribute 68% to this component) is responsible for more than 80% of differences. The second component is mostly correlated with final germination percent (67% of contribution to this component). Certain populations from G1 (Arctowski 2015 and 2010, New York, Trogir) and G2a (New York, Trogir; see Tab. 1) are grouped together. Additionally, populations from G2a and G2b were generally grouped together having higher final germination percentages and quicker germination speeds than in the G1 experiment and being more concentrated (Fig. 3). Seeds collected in the field (G1) were generally the slowest to germinate and reached lower germination percentage than seeds produced under optimal conditions. Seeds produced under favorable conditions with only short stratification (G2a) showed better germination characteristics. However, they still exhibited poorer performance than seeds stratified for 6 months (G2b), which had the best germination characteristics. Most of the studied populations (except Mar del Plata, New York and Trogir) followed this pattern (Fig. 2 and Fig. 3).

## Discussion

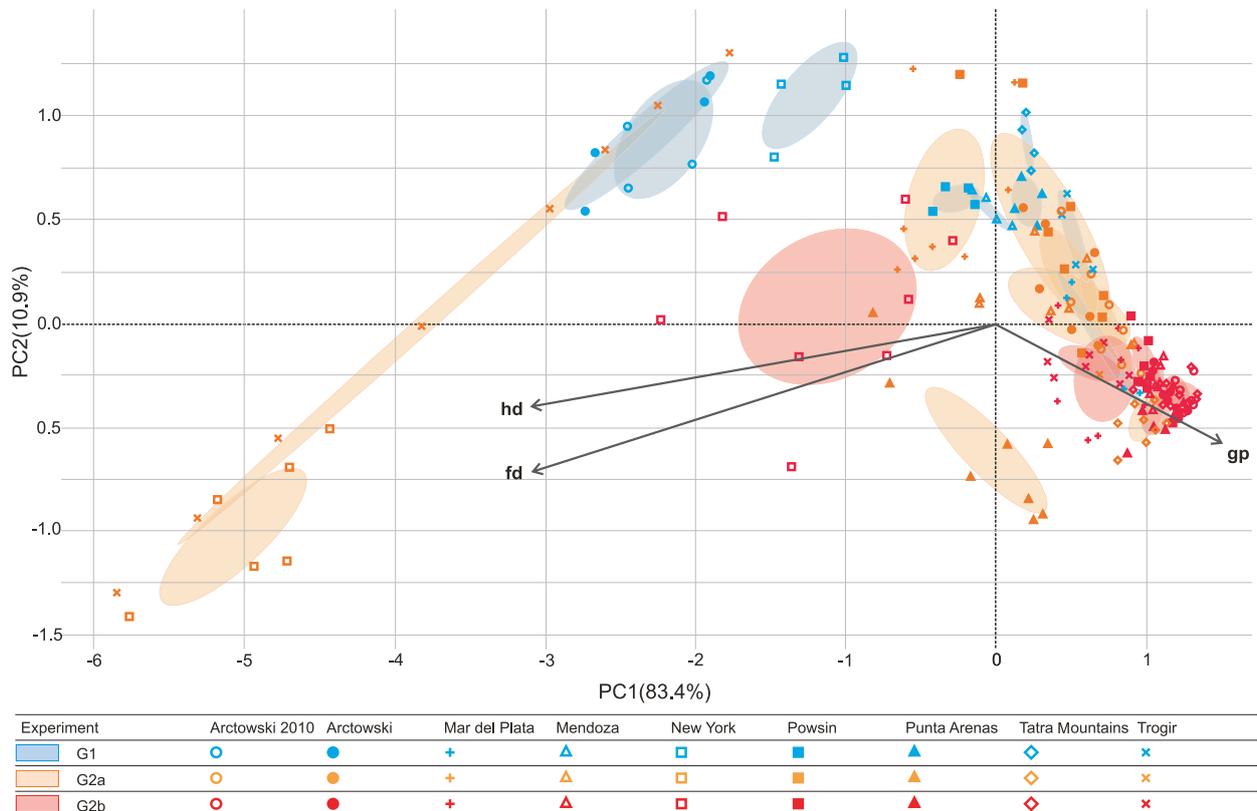
Our research indicated that the germination characteristics of seeds of *P. annua* produced under in-situ conditions and collected in the field (G1) differed under optimal common garden conditions. We observed the lowest germination success and slowest dynamics for the Antarctic population, despite potentially high germination ability of seeds produced under optimal conditions. This indicates the influence of the local environment on germination and seed development, which are part of life history strategy linked with fecundity and successful invasion. As *P. annua* is an autogamous species [25,26], this may be driven by environmentally decreased seed development rather than pollen limitation. The seeds might be immature due to short vegetation



**Fig. 2** Germination curves of seeds from eight examined populations: (A) caryopses collected in situ – G1; (B) caryopses collected from plants precultivated under optimal common garden conditions and stratified at 4°C for 1 to 3 weeks – G2a; (C) caryopses collected from plants precultivated under optimal common garden conditions and stratified at 4°C for over 6 months – G2b. Lighter colored transparent areas indicate 95% confidence intervals for the curves. Letters on the right of each curve indicate the results of grouping conducted on all curves; curves with the same letter are not significantly different ( $p \leq 0.05$ ).

**Tab. 2** Results of Tukey post hoc grouping ( $p \leq 0.05$ ) of all populations from all experiments conducted on their final seed germination percent.

| Experiment | Group number and range of mean germination percentages in corresponding group |  |   |               |   |
|------------|---|--|---|---------------|---|
|            | 1. (0–10%)  | 2. (50–70%)  | 3. (70–80%)                                 | 4. (80–85%)   | 5. (85–100%)  |
| G1         | Arctowski 2015<br>Arctowski 2010<br>New York                                  | Mendoza<br>Warsaw<br>Punta Arenas<br>Tatra Mountains<br>Trogir |   | Mar del Plata |   |
| G2a        | New York<br>Trogir  | Mar del Plata<br>Warsaw  | Arctowski 2015<br>Arctowski 2010<br>Mendoza |               | Punta Arenas<br>Tatra Mountains   |
| G2b        |   | New York   |   |               | Arctowski 2015<br>Arctowski 2010<br>Mar del Plata<br>Mendoza<br>Warsaw<br>Punta Arenas<br>Tatra Mountains<br>Trogir |



**Fig. 3** Results of principal component analysis (PCA) conducted for all populations and experiments using final germination percent (gp), first day of germination (fd), and day when populations reached 50% of their final germination (hd). Ellipses indicate population centroids – color of ellipses indicate different germination experiment variants.

season with suboptimal environmental characteristics [27,28]. This expectation was backed up by our assessment of seed development in the Antarctic population (Fig. 1) and slower germination of seeds collected in the Antarctic population even under optimal conditions (Fig. 2A). We observed that with the exception of the Antarctic population, seeds of all *P. annua* populations germinated around seventh day after sowing, which is in accordance with earlier studies [29]. Slower germination of seeds from the Antarctic population was also observed [5,28] and may be attributed to the time necessary for their after-ripening [9]. We classified only 3% of seeds collected in Antarctica as fully developed (Fig. 1), but the final germination of seeds collected in Antarctica reached around 10% (Fig. 2A). In our earlier research, we found that around 80% of *P. annua* seeds extracted from soil samples from under the tussocks of this species in maritime Antarctica successfully germinated under optimal conditions [6]. This difference between seed germination of seeds extracted from soil [6] and seeds freshly collected from plants (this study) might also confirm that seeds produced under harsh environmental conditions need prolonged after-ripening for their successful germination. These findings are in accordance with our first working hypothesis.

Many authors have stated that invasive species tend to perform better in their invasive range than in the native range [30,31]. However, only several papers focused on seed germination characteristics of an invasive plant species in its natural and secondary (invasive) range [32–36]. The environmental characteristics of the native and invasive range were more or less similar in these studies and the difference between the ranges were mostly in competitor and herbivore assembly. This highlights the diversity of differently operating factors on seed germination. In our study, the invaded habitat conditions differed dramatically from the native range of the studied species. In the case of *P. annua* invasion at Arctowski, harsh climate might be the major invasion-suppressing factor, at least under present environmental conditions [1,37]. Taking into consideration a substantial soil seed bank of the species [5,6], climate warming may induce an “ecological release” effect [17], speeding the invasion process.

Environmental conditions may highly influence many morphological, functional, and phenological traits of a species. This difference in trait state between locations differing in climatic conditions may be driven either by genetic response (fixation of traits especially favorable under specific conditions) or by phenotypic plasticity (tailored reaction of individuals to different conditions despite similar genetic information) and may be passed on to the next generation as maternal effects [19]. In our third germination experiment (G2b), we used seeds produced by plants that were cultivated under common garden conditions and underwent 6 months conditioning at 4°C. All populations exhibited similarly high germination percentage except the one originating from New York. Our second germination experiment (G2a), in which seeds from plants grown under optimal conditions and stratified only for short time period, exposed larger differences between populations. These results suggest differences in seed preconditioning requirements between populations and may be interpreted as genetic differences [30]. This indicates that while *P. annua* is a very plastic species able to tackle different environments, and much of its success can be attributed to phenotypic plasticity [38], the species harbors some genetic differences. On the other hand, differences in seed preconditioning requirements seem not to be enough to preclude the invasion of populations needing seed stratification, as Antarctic climate conditions may seem to indicate favorable seed stratification and storage. The consequently low germination of seeds representing the New York population was surprising and may be also attributed to genetic differences. At this time, we can only speculate that some kind of dormancy disabled them from germinating under optimal conditions. Further studies are needed to confirm this finding.

We could attribute the high differences in seed germination in our first experiment and low differences in the third experiment to maternal effects. However, due to harsh conditions in the Antarctic and problems associated with the right timing of seed collection in other remote populations, it is really hard to disentangle the impact of maternal effects and climate-driven seed immaturity on germination characteristics. Short growing season is an innate characteristic of harsh Antarctic climatic conditions notoriously leading to seed immaturity [39,40]. This immaturity raises the necessity of seed after-ripening before germination, leading to extended germination time. This is a strong selective force which might drive rapid evolution of traits enabling successful

germination. One scenario is shortening the time from seed set to germination. The other is to extend this time making it possible for seeds to mature even over several growing seasons before they are ready to germinate. Indeed, some plant species have been reported to extend their growth under harsh environmental conditions rather than shortening their life cycle. One of them is *P. annua* turning to perennial ecotypes under harsh environments [41,42]. The same might be relevant to seed development and germination. The question if this is an outcome of locally enhanced quick evolution or intraspecific admixture due to repeated introductions remains open.

Higher germination rates of seeds from the Antarctic and Tatra populations after precultivation under optimal conditions (experiments G2a and G2b; Fig. 2B,C) as compared to not precultivated (experiment G1; Fig. 2A) indicates high germination capacity in these populations. This is masked by harsh environmental conditions resulting in low germination of seeds collected in situ. We can speculate that without this high potential germination capacity, no seeds would successfully germinate, especially in Antarctica, as the Tatra population environmental conditions are not as harsh as in the polar region [40]. To protect native Antarctic plant communities from the negative impact of *P. annua* invasion, we already started an eradication process [4]. Nevertheless, seed germination from the soil seed bank may present problems for the control of this species in years to come, especially as this population has already started to form daughter populations [7].

## Conclusion

We found differences in germination characteristics of *P. annua* seeds collected in populations occupying different geographic locations of the species range and climatic zones. We did not observe these differences in germination of stratified seeds obtained from plants grown under unified conditions. We confirmed our hypothesis that seeds collected in harsh environments should germinate slower and have lower germination ability than seeds from optimal conditions due to their immaturity. Our second hypothesis was not fully confirmed as we found differences in germination that may be attributed to genetic differences in seed preconditioning requirements between populations and, especially in the Antarctic population, potentially high germination is drastically lowered by unfavorable polar conditions. Our results highlight the restricting role of invaded environmental conditions on an invasion process operating on the most vulnerable stage in invasive plant development – seed germination. This may be the reason for differences in noted number of successful invasions between the temperate/tropical and polar regions. We conclude that seed germination is definitely an obstacle for many plant invasions in the Antarctic region, presenting a strong environmentally controlled filter for plant invasions and at the same time a strong force potentially influencing rapid evolution of traits enabling persistence of established populations. However, this obstacle may be alleviated by climatic changes, which may result in more cases of invasions in polar environments.

## Acknowledgments

Part of the material used in the paper was collected at Henryk Arctowski Polish Antarctic Station. We thank the editors for their valuable remarks, which helped us improve the manuscript.

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