Influence of the population spatial structure on seed rain distribution of an invasive plant under harsh environment

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Abstract
Distribution of seeds of an invasive species is important for the spread of the invasion and for any directed eradication action. This distribution is driven by seed rain. We studied the influence of tussocks on the spatial pattern of seed rain and resulting population spatial pattern of an invasive Antarctic Poa annua L. population. Our hypothesis was that the tussocks trap wind-dispersed seeds. We set 40 artificial grass seed traps simulating tussocks and 40 soil seed traps (control) in the area occupied by the population. The traps were exposed for a total of 3 years and exchanged periodically. We assessed the seed bank in soil extracted for installation of our control traps. Seed number was determined by the germination method. We did not find any significant difference between the types of traps regarding the number of trapped seeds and the number of traps containing seeds, however trapping events were greater for artificial grass traps. The average size of the seed rain was 13.5 seeds m−2 year−1 and the size of the soil seed bank was 216 seeds m−2. We estimated that accumulation of the soil seed bank required around 16 years. Artificial grass discs may be more efficient than bare soil in accumulating seeds, therefore grass tussocks may influence the spatial population structure not only through local seed deposition, but also by intercepting seeds dispersed by wind. Our research further supports, that directed soil removal from underneath the tussocks is the most efficient eradication method of P. annua in Antarctica.

Keywords Antarctica · Invasive species · Poa annua · Seed dispersal · Seed rain · Astroturf seed traps · Soil seed bank

Introduction
Antarctica is considered the mostly isolated region on Earth, because of the strong spatial isolation and harsh environmental conditions (Galera et al. 2018). However one alien plant species, annual bluegrass (Poa annua L.) has been able to successfully reproduce and disperse in Antarctica. The population of this species, established in the vicinity of Polish Antarctic Station, is dated back to 1985/1986 austral summer (Chwedorzewska et al. 2015; Galera et al. 2019). This species was able to bypass all the invasion barriers and is observed to survive and produce viable caryopses able to germinate under local polar conditions (Galera et al. 2015, 2017; Wódkiewicz et al. 2018). Annual bluegrass also forms a soil seed bank comparable in size to native Antarctic plant species (Wódkiewicz et al. 2013, 2014). Even though this species invasion has been extensively studied (Chwedorzewska et al. 2015; Galera et al. 2019) exact ways of its seed dispersal are not yet known. The determinants and consequences of seed rain of invasive populations are still poorly understood, as there are very little works on this problem (Marchante et al. 2010; Herrera et al. 2011). Additionally these studies have been performed in at least temperate climate leaving the study of seed rain in harsh (Antarctic) conditions a blank spot in our knowledge.

The presence of adult plants is known to shape the species seed rain pattern, because of their architecture and seed dispersal kernels. However the seed distribution pattern is...
also shaped by soil surface characteristics and safe sites for seed persistence and germination. The distribution of seeds influences subsequent population spatial structure (Traveset et al. 2014). It is especially important in polar or alpine environments where seed rain is relatively low and highly depends on favourable wind and surface conditions (Molau and Larsson 2000).

In our earlier research we discovered that the soil seed bank of *P. annua* was mostly concentrated underneath existing tussocks of this species (Wódkiewicz et al. 2014) which is a typical finding for plants in polar climate (Lévesque and Svoboda 1995; Elberling 2000). The basic mechanism responsible for this spatial pattern of the soil seed bank is local production and deposition of seeds underneath the tussocks. We hypothesize that tussocks can additionally trap remote seeds dispersed by wind. This could further promote the tussock spatial pattern of the population rather than turf mat formation. Therefore our goal was to assess the role of standing tussocks in shaping the population spatial pattern. This could be used further to the advantage of eradication actions.

**Methods**

To assess the difference in seed rain distribution between tussocks and bare soil, we prepared two types of seed traps. One type was emulating tussocks and the other bare soil. For tussock traps we used artificial grass (astroturf) circles (11 cm diameter) that were pinned to the ground by metal clamps. Astroturf traps are a common method of simulating plants for seed rain assessment purposes (Wolters et al. 2004; Gough et al. 2015). Bare soil traps were made by preparing 10 cm long PVC tubes (11 cm diameter) with funnel shaped agro-fleece attached with packing tape so they could be filled to the brim with exactly 200 ml of soil. They were filled with local soil sterilised for 2 hours at 150 °C and mounted in the field, in a way that they were levelled with the ground (Fig. 1). Soil extracted during the mounting of soil traps from 0 to 10 cm layer, was collected for subsequent seed bank analysis. The volume of the soil core was 950 ml.

We set 40 traps of each kind in random locations in the area occupied by the population and exchanged the whole set of traps periodically. First set of traps was set on 13.02.2015 and left for 1 month to collect seeds during the vegetation season. On 13.03.2015, the astroturf and soil traps were collected and fresh traps were installed in the same places for the austral winter. In the next austral summer the traps were exchanged on 22.01.2016, 22.02.2016 and 16.03.2016. Due to the lack of possibility of collecting traps in 2017, they were recovered after 22 months (exposition of two austral winters and one austral summer) and collected ultimately on 29.01.2018.

Each time the collected samples were air dried at room temperature and sieved on 2-mm mesh sieve at the Arcticowski Station and transported to Poland at the end of each austral summer. Subsequently the presence of seeds in the traps was determined by the germination method. Samples from soil traps were put in 200 ml containers, watered as required and thoroughly stirred once a month to ensure each seed would have an opportunity to germinate (Ter Heerdt et al. 1996). Samples from astroturf traps were put in 100 ml containers on top of sterilised sand to prevent desiccation. We followed seed germination in a growth chamber under
controlled optimal conditions for the germination of the species (12 h photoperiod, 10 °C during the night and 20 °C during the day) for one growing season (5 months), after which the samples were left in an unheated greenhouse with sub-zero temperatures to overwinter for 3 months. Seed germination was observed for another month in the growth chamber in the same conditions as earlier. Seedlings were counted and the efficiency of seed trapping was measured in number of trapped seeds, number of trap locations from which seeds were recovered regardless of trap exposition periods and number of seed trapping events. We defined a seed trapping event as at least one seed caught in a trap in a given trap exposition period. The difference in seed trapping between different trap types was assessed with a proportion z test. We also used a two proportion z test to check if the proportion of trapping events differed between seed trap types.

Results

After the last exposition, nine of the soil traps and seven astroturf traps were not recovered from the field. Therefore we collected 191 soil traps and 193 astroturf traps. A total of 30 seeds were detected in all recovered traps (Table 1). We did not find statistically significant differences in the number of trapped seeds nor trap locations with seeds between seed trap types (Table 2). However we recorded more seed trapping events for the astroturf than for the soil traps. Based on all 384 installed traps, we estimated that the seed rain in the studied population is 13.5 seeds m\(^{-2}\) year\(^{-1}\). In soil excavated during soil trap installation, we recorded 82 seeds and estimated the soil seed bank size to be 216 seeds m\(^{-2}\). Therefore, taking into account the assessed seed rain we can estimate that it takes approximately 16 years for such soil seed bank to accumulate.

Discussion

Trapping ability of tussocks

It is often observed that because of heavy winds in polar climate seeds are only trapped in sites with favourable conditions, like ground depressions and cavities or other obstacles (Elberling 2000; Alsos et al. 2002). Our expectations were that favourable conditions for trapping seeds could also be provided by tussocks acting as seed traps accumulating seeds blown around by wind, similarly to larger shrubs (Bullock and Moy 2004). We speculated that strong winds during vegetation season in the Antarctic should support long distance dispersal. The presence of grass tussocks may disturb the wind flow close to the soil surface, promoting seed trapping. Although the difference in number of seeds trapped in different seed traps does not confirm this finding, other measures of seed trapping suggest that tussocks may act as functional seed traps, shaping the spatial pattern of the standing population (Table 2). The size of our seed traps was based on tussock size, as tussocks of around 10 cm diameter were observed in the population. We set 40 traps of each type with a total area of 0.38 m\(^{-2}\) for each trap type, yet we were able to record some differences. Lack of differences in the number of trapped seeds between trap types may be a result of small sample size. The sample size might be sufficient in better environmental conditions, but under scarce seed rain may not suffice. This may suggest that seed rain in Antarctica is small and seed dispersal is a rare event leading to the capture of only a small amount of seeds, but tussocks may perform better in that process than bare soil.

In the Arctic, seeds are not dispersed far and tend to accumulate near the parent plant or in specific ground cracks or

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**Table 1** Number of seeds captured in each trap exposition period

| Exposition number | Year of trap exposition | Duration of trap exposition (months) | Number of seeds captured in: | Soil traps | Astroturf traps |
|-------------------|--------------------------|--------------------------------------|-----------------------------|-----------|----------------|
| 1                 | 2015                     | 1                                    | 2                           | 1         | 1              |
| 2                 | 2015–2016                | 10                                   | 2                           | 6         |                |
| 3                 | 2016                     | 1                                    | 0                           | 1         |                |
| 4                 | 2016                     | 1                                    | 0                           | 0         |                |
| 5                 | 2016–2018                | 22                                   | 8                           | 10        |                |

There were 40 traps of each type in each exposition, except for exposition number 5 with 31 soil traps and 33 grass traps recovered.

**Table 2** Comparison of seed trapping by soil and astroturf traps with proportion z test

| Measure of seed trapping          | Soil traps | Astroturf traps | z test statistics | n   | p value  |
|-----------------------------------|------------|-----------------|------------------|-----|----------|
| Number of trapped seeds           | 12         | 18              | 1.095            | 30  | 0.2733   |
| Trap locations with seeds         | 6          | 12              | 1.414            | 18  | 0.1573   |
| Seed trapping events              | 6          | 15              | 1.964            | 21  | 0.0495   |
| Seed trapping events*             | 6          | 15              | 1.995            | 191; 193 | 0.0460 |

The n column represents number of trapped seeds or trapping events.

*Two proportion z test. For two proportion z test the number of samples in the n column represents number of retrieved soil and astroturf traps.
To be quite persistent, with seed viability reaching even 100 years (McGraw and Day 1997). In optimal conditions seed bank of *P. annua* may remain viable for up to 4 years (Warwick 1979) and in the sub-Antarctic up to 2 years (Williams et al. 2016). Therefore we did not expect a 16-year persistency of annual bluegrass seeds in the Antarctic population. However this is an indirect estimate and has to be treated with caution. For annual bluegrass in the Antarctic, the formation of the soil seed bank may proceed similarly as in most polar plants, when produced seeds are immediately added to the persistent seed bank (Lévesque and Svoboda 1995). Seed bank of an invasive plant in Antarctica may be viable longer than expected and with rising temperatures even more stored seeds will be fully mature and able to germinate (Rudak et al. 2018). This can aid the species overcome population collapse (Galera et al. 2019) and should be taken in consideration regarding any eradication programs, as the only method of removing seed bank in this scenario is the removal of plants with the soil underneath them (Galera et al. 2017).

**Conclusions**

Our findings support our hypothesis that existing tussocks may trap *P. annua* seeds better then bare Antarctic soil. We can therefore assume that local distribution plays a major role in the spatial structure of the population through seed production, accumulation and presenting safe germination sites. We also found that *P. annua* seed bank may be viable for longer than it was earlier expected. Further studies are advisable, because understanding this process could help us estimate changes in Antarctic plant cover in case of a rising temperature and improve eradication methods.

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**Author contributions** HG and MW conceived and designed the research. HG, AZ and KJC collected research material. AR and MP conducted ex situ experiment. HG, AR and MW analysed the data and wrote the manuscript.

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**Data availability** All new data were presented in the paper.
Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Consent for publication All authors express their consent to publish the paper.

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