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ORIGINAL PAPER

Spatial structure of the soil seed bank of *Poa annua* L.—alien species in the Antarctica

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Abstract *Poa annua* L. (annual bluegrass) is the only non–native flowering plant species that has successfully established a breeding population in the maritime Antarctic and has been shown to maintain a soil seed bank. The characteristic of the spatial structure of the Antarctic population of this species is the formation of distinct dense clumps—tussocks. In the temperate zone the species is only loosely tufted. We focused on the characteristics of seed deposition associated with the tussocks and some aspects of the spatial heterogeneity of the soil seed bank of *P. annua* in the Antarctic. We wanted to assess the microspatial structure of the soil seed bank of annual bluegrass at Arctowski Station. Therefore we compared the number of seeds deposited underneath and in the vicinity of *P. annua* clumps. Our results indicate that *P. annua* in the Antarctic maintains a soil seed bank comparable to species typical for the polar tundra. The microspatial structure of *P. annua* soil seed bank in the Antarctic is highly associated with the presence of tussocks. Seeds are deposited underneath the tussock rather than in the vicinity of the clump. Our results also indicate that seeds are able to survive the Antarctic winter and readily germinate under optimal conditions.

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Introduction

In polar conditions, where temperature stress, water availability and snow cover are unpredictable, the strategy of soil seed bank formation may be of an adaptative value. Due to prolonged viability of seeds stored in the soil and their ability to germinate over time, the risk associated with their germination under unfavorable conditions may be reduced (Venable and Brown 1988). At least some seeds, instead of germinating while environmental conditions remain unfavorable, are able to stay dormant until conditions improve. Therefore many Arctic tundra species have developed different degree of seed dormancy, enabling them to postpone seed germination to optimal conditions (Baskin and Baskin 2001).

The Antarctic tundra consists mostly of cryptogams and has two native flowering plant species *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv. (Komárkowá et al.1985). Only one alien angiosperm, *Poa annua* L. has survived, bred and dispersed in the maritime Antarctic. While at Cierva Point (Antarctic Peninsula) a small patch of *Poa pratensis* has been noted (Pertierra et al. 2013), this species does not produce seeds, and therefore does not form a soil seed bank. *P. annua* was introduced accidentally to the vicinity of Polish Antarctic Station Arctowski over 28 years ago (Olech and Chwedorzewska 2011; Chwedorzewska and Bednarek 2012). The local Antarctic population of this species forms tussocks (Wódkiewicz et al. 2013), while in the temperate zone the species is only loosely tufted (Grime et al. 1986). *P. annua* forms a soil seed bank in temperate regions (Lush 1988), as well as in the Antarctic (Wódkiewicz et al. 2013).

We focused our research on the characteristics of seed deposition and some aspects of the spatial heterogeneity of the soil seed bank of *P. annua* in the Antarctic. Our objective was to investigate if *P. annua* caryopses are deposited mainly in the soil under or outside the tussocks. This is connected with safe sites for seed persistence, seed dispersal, the expansion mechanism and the possible further spread of the species. Our question was whether tussock enlargement may be mediated through seed deposition and new individual recruitment in the immediate vicinity of mother plants enabling the tussocks to expand by the means of seed dispersal. We were also interested in the deposition of seeds influenced by strong local winds and a preliminary assessment of seed dispersal outside the tussock.

Materials and methods

Soil samples were collected from the vicinity of Arctowski Station (62°10′S, 58°28′W) occupied by a population of *P. annua* during the austral summer season 2011/2012. Twenty randomly selected tussocks with a diameter of 5–40 cm were investigated. We noted the diameter and height of each tussock and designated four sampling points for the soil seed bank assessment: one was situated directly underneath the tussock and the other 10 cm from the tussock edge (Fig. 1). We chose this spatial scale because we wanted to assess if seeds are deposited within the mother clump or if they are displaced away from their source. Furthermore, we assumed that the selected clump is the major source of seeds in the surrounding soil. In the area occupied by the studied population the distance between clumps is rather short (around 30–40 cm, see Fig. 2). Therefore, if we had extended the spatial scale of our sampling, other *P. annua* clumps might have interfered with the

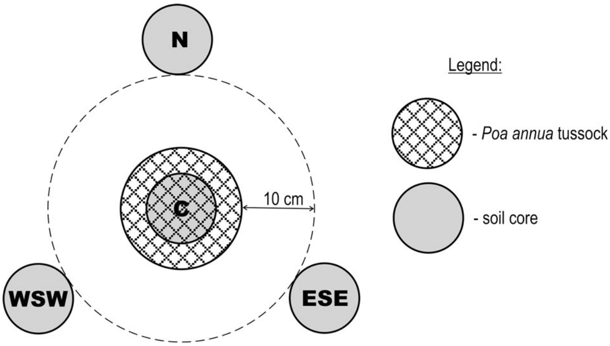

Fig. 1 Sampling scheme. C, N, WSW, ESE—soil sample location in relation to tussock position

Fig. 2 *Poa annua* in the vicinity of Arctowski Station

assumed seed rain and our interpretation of results might have been biased. The selected scheme potentially allowed to minimize the interference of seed rain of plants growing in the vicinity. At each sampling point we collected 100 cm^3 of soil from the 0–5 cm layer. We collected 80 soil samples amounting to 8 liters and 0.157 m^2 soil surface area. The collected samples were air dried at room temperature at the Station and transported to our laboratory in Poland at 4 °C.

We sieved the samples through 0.5 and 1.5 mm sieves and extracted caryopses from the 0.5–1.5 mm soil fraction under a stereoscopic microscope. Extracted caryopses and the remaining soil were placed in a germination chamber for 3 months under 12 h photoperiod, 10/23 °C. These optimal germination conditions were used to promote germination in all seeds with potential germination capability and therefore to assess the size of the soil seed bank of living diaspores. Under Antarctic conditions these seeds would have remained a part of a living soil seed bank with the potential ability to germinate when conditions become adequate. Thus we assessed the size of the soil seed bank with the extraction method and the germination method. At the same time we estimated the germination capacity of seeds by germination tests of seeds extracted from soil samples. We assumed that seeds which failed to germinate were not viable.

To calculate seed densities per square meter we divided the seed count in a sample by the area of the sample (Baskin and Baskin 2001). We used nonparametric statistics, as the distribution of seeds in samples was not normal. We used the sign test to compare the seed bank size assessed with the extraction and germination methods for samples from the center point. With Spearman correlation we checked the relation between the tussock diameter and height and the size of the seed bank, as well as the relation between the size of the seed bank estimated with the extraction and germination methods. We performed Friedman's ANOVA to check for differences between sampling points around the clump. The analysis was performed with SAS 9.2 (SAS Institute Inc. 2007) and Statistica 9.0 (StatSoft and 2009).

Results

Altogether we extracted 520 *P. annua* caryopses. This corresponds to 3,312 seeds m^{-2}. Out of all extracted seeds, 426 germinated, which is nearly 82 %. Additionally, 43 seeds germinated from samples left after the propagule extraction, therefore altogether 469 seeds germinated from the collected soil samples. Thus, the size of *P. annua* seed bank surrounding the tussocks assessed with the germination method corresponded to 2,986 seeds m^{-2}. For the analysis of differences in the seed bank size assessment between the extraction and germination methods we used only the central sampling points and excluded sampling points surrounding the tussock from the analysis, as in most of them we detected single seeds (Table 1). We found a difference in the seed bank size assessment with the extraction and germination methods for sampling points situated underneath the tussocks (sign test $M = 6.5$, $p = 0.0002$, $N = 20$). The median difference in the seed bank size assessed with both methods was 2 seeds. Therefore this difference in the assessment corresponds to around 10 % of the mean seed bank size assessed with either the germination or the extraction method (Table 1). Further analysis was restricted to the germination data, as it summarizes information about living diaspores.

We found significant differences in the seed bank size from different sampling points (Friedman's ANOVA $Q = 35.7162$, $p < 0.0001$). A comparison of mean ranks for all sampling points indicated that the majority of seeds were deposited underneath the tussocks (Fig. 3). The seed bank under the tussocks was relatively rich (10466 ± 9636 (mean ± SD) seeds m^{-2}, median 6,621 seeds m^{-2}). The sizes of the soil seed bank did not differ between sampling points surrounding the tussocks (399 ± 1345 (mean ± SD) seeds m^{-2}, median 0 seeds m^{-2}).

Table 1 Mean and standard deviation of number of *Poa annua* seeds in samples located underneath (C), and around (N, WSW, ESE) the tussocks in the vicinity of Arctowski Polar Station

Soil sample location	Extraction method		Germination method	
	Mean	SD	Mean	SD
C	24.85	21.68	21.10	19.09
N	0.40	0.80	0.20	0.40
WSW	0.35	0.79	1.05	3.47
ESE	0.40	0.74	1.10	2.86
All samples	26.00	21.69	23.45	20.04

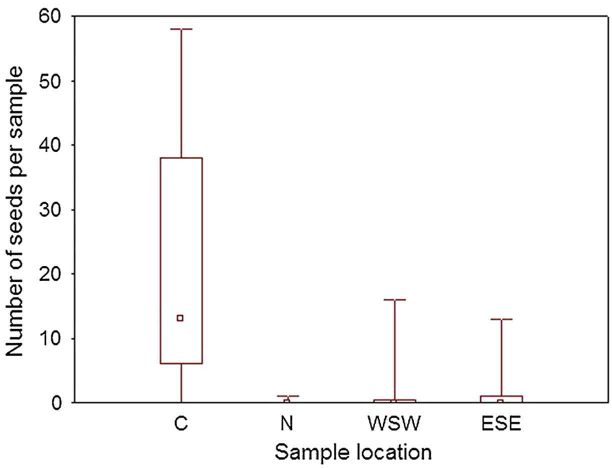

Fig. 3 Differences in the size of *P. annua* soil seed bank between different sampling points relative to tussock position. C, N, WSW, ESE—soil sample location in relation to tussock position, *square box* - median, box: 25–75 %, whiskers: min–max

We did not find any significant correlation between the seed bank size and *P. annua* clump size (diameter, height). There was, however, a negative correlation between clump size and percent of seeds germinating from soil samples (R = −0.72165, $p = 0.0007$, $n = 18$ for clump diameter and R = −0.63247, $p = 0.0049$, $n = 18$ for clump height).

Discussion

Soil seed bank size in Antarctic conditions

The average size of *P. annua* soil seed bank reported in our study was around 3,000 seeds m^{-2}. The discrepancies between the seed bank size of *P. annua* evaluated with two methods were relatively small, only 10 %. Our estimation of *P. annua* seed bank size, especially in the soil underneath the tussocks (over 10,000 seeds m^{-2}) may be associated with the sampling strategy targeted on functional plant units in the population. Significant differences in the size of the soil seed bank underneath the clump and in the area outside the clump, even 10 cm from the edge of the clump, indicate a high spatial variability of the soil seed bank, which was associated with the presence of the clump. Soil between tussocks, even only 10 cm away, may completely lack deposited seeds (median = 0; Table 1).

The size of the soil seed bank of *P. annua* is within the limits reported for the Arctic (3,400 seeds m^{-2} in undisturbed sites; McGraw and Vavrek 1989) and alpine (6,000 seeds m^{-2} in a disturbed site; Chambers 1993) tundra. The seed bank of sub-Antarctic regions has received less attention and seems to be smaller—about 1,000 seeds m^{-2} (Arroyo et al.1999). Both *C. quitensis* and *D. antarctica* form in Antarctica a persistent soil seed bank of around 1,650 and 5,645 seeds m^{-2} respectively (McGraw and Day 1997, Ruhland and Day 2001). The abundance of *P. annua* soil seed bank is intermediate in relation to both native vascular plant species. *Poa annua* soil seed bank size underneath the tussocks, however large in comparison with other tundra plants, is just a fraction of the species' seed bank as reported from temperate regions (30,000–210,000 seeds m^{-2}; Lush 1988).

In our preliminary research we found that around 45 % of seeds from the previous year's infructescences are capable of germination (Wódkiewicz et al. 2013). This time we found that over 80 % of seeds extracted from the soil were viable, as revealed by germination experiments. Lower germination capacity of freshly collected seeds than of seeds recovered from soil samples may also indicate that part of seeds are dormant upon collection and over time this dormancy is broken, thus enabling the seeds to form a soil seed bank instead of germinating under sub-optimal conditions. This difference may also be associated with a seasonal variation in germination ability of *P. annua* in the Antarctic caused by huge differences between years in meteorological conditions (temperature, liquid water aviability, snow cover etc.) during the vegetation season (Kejna et al. 2013).

Spatial structure of P. annua seed bank in the Antarctic population

Our sampling allowed the comparison of *P. annua* soil seed bank characteristics at Arctowski Station between points situated underneath the tussock and in the vicinity of the clump. Soil around clumps in either direction showed a minimal seed bank size in comparison with the center of the clump. The distance of 10 cm from the edge of a clump represented the space between clumps, as the clumps are spaced approximately at 30–40 cm distance (Fig. 2). The increased number of seeds in the soil beneath the clump might suggest that seeds are deposited mainly within the mother clump, and only a small fraction may be transported at a larger distance.

The tussock may be an efficient seed trap in contrast with bare soil and act for seed accumulation similarly to larger shrubs (Bullock and Moy 2004). Artificial turf, similar to grass, has been shown to efficiently trap seeds blown by the wind in the Arctic tundra (e.g. Molau and Larsson 2000). Beside seed production, *P. annua* clumps may present safe sites for seed persistence (Jumpponen et al. 1999). Therefore we might speculate that the local spread of *P. annua* in the future might largely depend on clump expansion rather than on the formation of new distinct clumps. The formation of new clumps is probably a stochastic phenomenon dependent on long distance seed dispersal, topography and surface soil characteristics favorable for seed entrapment and subsequent germination (Chambers et al. 1991). Also human dependent seed transport may play a role in the species spread, similarly to the way in which seeds get transported to Antarctic research stations (see e.g. Lee and Chown 2009; Lityńska-Zając et al. 2012).

Similar aggregated spatial characteristics of the soil seed bank was observed in arid regions (Wang et al. 2005). This similarity may depend on strong winds, specific plant architecture and environmental factors. However, factors driving spatial distribution of the soil seed bank in arid environments differ from the Antarctic tundra in the presence of animal activity reshaping the spatial distribution of seeds (Hulme 1998), and in the existence of more species with different growth habit, which might interact with the distribution of the shed seeds.

Seed deposition underneath the mother plant is not an unusual means of seed dispersal (Wang et al. 2005), especially in the case of seeds without any specific adaptations aiding their dispersal. The following seedling development is usually limited by intraspecific competition. In the case of the Antarctic population of *P. annua* high concentration of plants within the tussock may confirm this rule—at least some of the tussocks consist of many individuals (unpublished data). Moreover, high density of plants within the tussock may be of an adaptative value for the persistence of plants in extreme polar conditions.

Our earlier observations suggest that the tussocks are rather stable in time (unpubl. data). *Poa annua* is capable of forming perrenial ecotypes (Gibeault 1971). Therefore at least some of the clumps may be capable of surviving over several vegetation periods. Diaspores deposited in the soil can accumulate underneath the tussocks for an extended period of time. An interesting finding of our study was that the percent of germinating seeds of *P. annua* in Antarctica was negatively correlated with the clump size. A possible explanation might be that larger clumps may be older and have accumulated seeds through a longer period of time. With time some of the seeds deposited in the soil may lose their viability and yet be distinguishable due to slow decomposition rates in cold climates. Therefore in larger clumps the germinability of seeds may be lower than in small, young clumps, where all seeds are relatively young and have not lost their viability yet.

The tussock may not only be the source of diaspores in the underlying soil, but also present safe sites for the accumulation of soil seed bank. The clumps might function as seed traps for propagules transported by wind. Mechanisms associated with clump formation will be the focus of our further research.

Conclusions

Poa annua maintains in the Antarctic a soil seed bank comparable to plants typical for the polar tundra. The species' seed bank in the vicinity of Arctowski is linked spatially with the extant population, as in other environments (Wódkiewicz and Kwiatkowska-Falińska 2010). The microspatial structure of the soil seed bank in the Antarctic is highly associated with the presence of tussocks. Over 80 % of seeds extracted from soil were viable and readily germinated under optimal conditions. A large number of seedlings germinating from soil samples indicates that they are able to survive the Antarctic winter. A still open question remains if the tussocks present a safe site for the accumulation of seeds transported by wind.

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