Poa annua L. in the maritime Antarctic: an overview

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ABSTRACT. *Poa annua* is the only flowering plant species that has established a breeding population in the maritime Antarctic, through repeated anthropogenic introduction. The first appearance of this species in the Antarctic was observed in 1953. Annual bluegrass inhabits mainly anthropogenic sites, but recently has entered tundra communities. The functioning of *P. annua* in the Antarctic could not have been possible without adaptations that enable the plants to persist in the specific climatic conditions typical for this zone. *Poa annua* is highly adaptable to environmental stress and unstable habitats: huge phenotypic and genotypic variability, small size, plastic life cycle (life-history types ranging from annual to perennial forms). The spreading of *P. annua* in the Antarctic Peninsula region is a classic example of the expansion process following anthropogenic introduction of an invasive species, and illustrates the dangers to Antarctic terrestrial ecosystems that are associated with increasing human traffic.

Introduction

The annual bluegrass *Poa annua* L. (Poaceae) is the only non-indigenous flowering plant species that has established a breeding population in the Antarctic. Other alien plant species recorded in Antarctic terrestrial communities for example *Nassauvia magellanica* J.F. Gmel., *Gamochaeta nivalis* Cabrera (Smith and Richardson 2011) have only reached the status of ephemerophytes. A small patch of *Poa pratensis* L. has been observed since 1954–1955 austral summer season until today at Cierva Point, Antarctic Peninsula (Smith 1996; Pertierra and others 2013). In Antarctica this patch is maintained only by clonal spread, there has been no seed production and only incomplete development of the sexual structures (Pertierra and others 2013). The diaspores of *Juncus bufonius* L. from soil samples collected on King George Island have been found germinating under laboratory conditions in Chile, however the species has not been physically observed in Antarctica (Cuba-Díaz and others 2013), as well as a fern, *Elaphoglossum hybridum* (Bory) Brack. cultured from mineral sediment in cryoconite holes in the ice cap of Signy Island, South Orkney Islands (Smith 2013).

With the increase of tourist traffic from Tierra del Fuego to the Antarctic Peninsula region (IAATO 2001–2014) as well as the rise in research activities connected with many scientific programmes (for example Chwedorzewska and Korczak 2010; Greenslade and others 2012; Hughes and others 2011; Hughes and Convey 2014; Tin and others 2009, 2013), it may be only a matter of time until more plant species are dispersed into west Antarctica. A similar phenomenon has already been observed on sub-Antarctic islands (for example Frenot and others 1999, 2001, 2005; Gremmen and Smith 1999). Harsh conditions prevailing in Antarctica together with other constrains have protected the region from natural colonisation and from invasions of exotic species in the past (Chwedorzewska and Bednarek 2008, 2011). Growing intensity of tourism and governmental activities coupled with climate change can break this isolation. The area has recently been warming up rapidly (Turner and others 2013). These newcomers are potentially imported every year by human vectors (Chwedorzewska and Korczak 2010; Chown and others 2012a, 2012b; Lityńska-Zając and others 2012; Augustyniuk-Kram and others 2013; Chwedorzewska and others 2013; Huiskes and

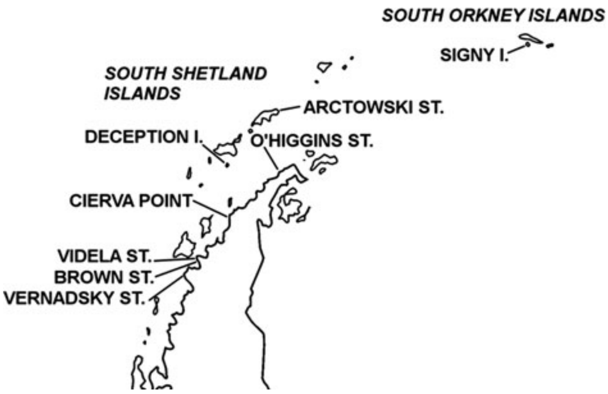

Fig. 1. Sites in the maritime Antarctic at which *Poa annua* was recorded.

others 2014) and/or already are deposited in the soil seed bank (Wódkiewicz and others 2013, 2014; Cuba-Díaz and others 2013). They may await for favorable conditions and establish in the vegetation when environmental conditions ameliorate.

History of expansions in Antarctica

Poa annua was recorded for the first time in Antarctica in 1953 near the ruined whaling station on Deception Island, South Shetland Islands (Skottsberg 1954: Fig. 1). According to Longton's (1966) observations conducted during the austral summer season of 1964–1965 the species flowered and produced scattered seedlings. Collected seeds also germinated successfully. This population was destroyed during a volcanic eruption in November 1967 (Collins 1969).

In 1967 *P. annua* together with 38 other alien species (34 angiosperms and four pteridophytes) was experimentally introduced at Factory Cove 60°43′S, 45°36′W (Signy Island, South Orkney Islands, Fig. 1) from Falkland Islands (Edwards and Greene 1973). *Poa annua* was the most successful among them. During successive austral summers every year plants have flowered and developed fertile seeds. After three seasons' research the experiment was destroyed (Edwards and Greene 1973; Edwards 1980).

In a similar experiment concerning the introduction of *Nothofagus pumilio* (Poepp. et Endl.) Kasser and *N. antarctica* (G. Forster) Oerst. in the summer of 1954–1955 *Poa pratensis* was accidently introduced to Cierva Point, Antarctic Peninsula (Corte 1961 after Pertierra and others 2013). In 1981 a single well-established flowering *P. annua* clump was observed by Smith (1984) close to Faraday Station 65°15′S, 64°14′W (at present Vernadsky Station, Fig. 1) on Galindez Island (Argentine Islands, Antarctic Peninsula) and was destroyed before 1985 (Smith 1996).

The expansion of *P. annua* in the vicinity of Polish Antarctic Station H. Arctowski 62°09′S, 58°28′W (King George Island, South Shetland Islands, Fig. 1) is very well documented (Olech 1996; Olech and Chwedorzewska 2011). This permits the estimation of the rate and range of this process during the last 28 years. In the austral summer of 1985–1986 single individuals of annual bluegrass were observed for the first time next to the station living quarters. During next seasons the population of *P. annua* increased in density and abundance within the original area and expanded into new areas (Olech 1996). In the summer season of 2005–2006 *P. annua* was observed for the first time in tundra communities. In summer 2006–2007 the number of individuals in tundra communities as well as the total number of localities further increased (Olech and Chwedorzewska 2008). In summer 2008–2009 an extensive population of *P. annua* was recorded in a new locality on the deglaciated moraines of the Ecology Glacier, approximately 1.5 km from Arctowski at the area of ASPA (Antarctic Specially Protected Area) 128. This new population was not very numerous and consisted of about 70 individuals occupying about 100 m^2 (Olech and Chwedorzewska 2011).

During the two Chilean expeditions in 2007–2008 and 2009–2010 individual specimens of *P. annua* were found further south in new localities situated on the Antarctic Peninsula near the Chilean and Argentinean bases: General Bernardo O'Higgins (63°19′S, 57°54′W), Gabriel González Videla (64°49′S, 62°51′W) and Almirante Brown (64°52′S, 62°54′W). During the second Chilean expedition in February 2010 a single flowering turf was found approximately half a kilometer from Whaler's Bay (62º58′S, 60º33′W), Deception Island. The individual was eradicated from the area (Molina-Montenegro and others 2012, Fig. 1). The spreading of *P. annua* and other alien species (see for example Hughes and Worland 2010; Hughes and others 2012) in the Antarctic Peninsula region are examples of the expansion process following anthropogenic introduction, discovery, and operator failure to attempt or achieve rapid eradication, illustrating the dangers to Antarctic terrestrial ecosystems and highlighting the necessity to monitor their spread and gather information on their ecology which might be vital to the control and removal of organisms introduced by human agency.

Origin of *Poa annua* in the Antarctic

The history of human influence in the Antarctic Peninsula region goes back to the beginning of the 19th century. Excessive commercial exploitation took place during the 19th and early 20th century, initially through hunting for seal and, then, whaling. After this period field bases and scientific stations have begun to be established (for example Chwedorzewska 2009; Tin and others 2009). There is no accurate data concerning when the population of *P. annua* was observed at Deception Island for the first time. Annual bluegrass could have been introduced to this locality by whalers working in the on-shore station, built in 1912 and abandoned in 1931 or/and by the British (first observation is dated to 1953) running a permanent base from 1944 (Skottsberg 1954) to 1967 when volcanic eruption forced their withdrawal (Collins 1969). Again in February 2010 a single flowering turf was found on Deception Island. It is unlikely that seeds of *P. annua* survived the volcanic eruption in 1967, so the most probable vector of this new introduction is human. Presently, on the South Shetland Islands, especially on King George Island, there are several all-year stations with developed infrastructure and a couple of summer field bases. Similarly to Deception Island those stations are often visited by tourists. According to IAATO (data collected regularly from 1991) Arctowski is one of the most frequently visited research stations in the whole Antarctic Peninsula region (Chwedorzewska and Korczak 2010). The number of tourist visits during the last seven austral summer seasons ranged from 350 to 5700 of landing persons per season according to the Arctowski station logbook. As well as the tourist visits, at the same time the number of expedition members working at Arctowski ranged from 13 to 39 bringing more than 50 tons of cargo per year (Arctowski Station logbook). Despite the high tourist traffic in some Antarctic stations, the main introduction routes seems to be associated with the provisioning of the stations by cargo and personnel (Frenot and others 2005; Chwedorzewska and Korczak 2010; Chown and others 2012a, 2012b; Lityńska-Zając and others 2012; Augustyniuk-Kram and others 2013; Chwedorzewska and others 2013; Huiskes and others 2014) and earlier by industrial activity in the sub-Antarctic as well as in the Antarctic (Frenot and others 2005).

According to available historical data one can make the hypothesis that at Arctowski station the diaspores of *P. annua* probably originated from Poland, most likely from unsterilised soil for the greenhouse transported to the station in 1978. This is supported by observations conducted during 2000–2001 Polish Antarctic Expedition when emergence of *P. annua* seedlings was observed in the greenhouse building in a box containing soil destined for incineration (Chwedorzewska personal observation). This hypothesis was also supported by investigations conducted during three austral summer seasons (2007–2008, 2008–2009, 2009–2010). In a subsequent study the cargo, clothes and equipment of the Polish Antarctic Expeditions to Arctowski were examined for the presence of alien propagules. This study showed that a substantial number of non-indigenous propagules enters Arctowski every year (Lityńska-Zając and others 2012; Augustyniuk-Kram and others 2013; Chwedorzewska and others 2013). Among them were caryopses and remains of spikelets of P. *annua*. Diaspores are probably most effectively transported in the crannies of field footwear. The majority of cargo and station personnel came directly from Poland. This seems to point out that annual bluegrass originated from that country and was probably introduced to Antarctica not once but through multiple events (Lityńska-Zając and others 2012). However, some cargo, mainly fresh products, were brought from Argentina or Chile, therefore the introduction from different sources could not be excluded (Chwedorzewska and others 2013). This evidence supports the hypothesis of constant flow of fresh genetic material of this species to the vicinity of the station, which is reflected by an astonishingly high genetic variability in the introduced population in comparison with Polish populations (Chwedorzewska 2008; Chwedorzewska and Bednarek 2012). Thus new more restrict phytosanitary regulations were introduced to Arctowski in 2013 in order to protect this area from further invasions of species whose potential vector can be the human and/or their activities (*Non-native Species Manual* 2011).

During the 2009–2010 growing season *P. annua* was recorded for the first time on the Antarctic Peninsula near Chilean and Argentine bases, and these findings were also attributed to the presence of tourists or national operator staff (Molina-Montenegro and others 2014). The Argentine base Almirante Brown is one of the most visited stations in the Antarctic with ca. 11,000 landed visits during the season of 2009–2010. Similarly, Chilean base Gabriel González Videla received ca. 2,000 landed visits (IAATO 2001–2014). On the other hand, scientific and logistic activities in these places have increased considerably in the last time. For example, the number of Chilean scientific projects concerning Antarctica and scientists' visits to the region have increased over twofold in the last 10 years, with a consequent expansion and construction of the bases. Thus, tourists as well as scientists, and logistic operators could be responsible for the introduction, establishment and spread of *P. annua* in the Antarctic (Molina-Montenegro and others 2014).

Supply for the Antarctic stations is loaded mainly from disturbed areas, like farms and holding areas in ports, where both the abundance and diversity of invasive species from elsewhere in the world is huge (Slabber and Chown 2002; Lee and Chown 2009a, 2009b). Thus the sources of introduction of *P. annua* to those localities may be very diverse but most likely the main points of origin are Central Europe and South America.

Habitats

Poa annua occurs in the Antarctic Peninsula region, where the climate is the least extreme in the Antarctic (Chwedorzewska 2009). The species favours mainly areas with the mildest conditions, such as on Deception Island, where it grew on unstable volcanic ash, where substrate temperature was consistently, above air temperature and in some extent sheltered from the wind (Longton 1966), or locations which are humid and sheltered from the wind as at the vicinity of Arctowski (Olech 1996). At that station *P. annua* occurred firstly in habitats disturbed by human activities (for example by earthworks or vehicles; or in the cracks of concrete structures filled with soil, Olech 1996) and in pioneer zones, for example on the forefield of a retreating glacier, where the species has been observed on the leeward slope in the humid hollows (Olech and Chwedorzewska 2011). Annual bluegrass also inhabits anthropogenic sites at the vicinity of the Chilean and Argentine bases. Survival of *P. annua* was higher in sites with soil disturbed by anthropogenic activities, suggesting that some human activities could be a significant factor related to the abundance and potential spread of *P. annua* in the Antarctica (Molina-Montenegro and others 2012, 2014).

Presently, *P. annua* also enters tundra communities associated with two native vascular plants, *Deschampsia antarctica* Desv., *Colobanthus quitensis* (Kunth) Bartl., and mosses such as *Bryum pseudotriquetrum* (Hedw.) P. Gaertn., B. Mey. & Scherb. and *Ceratodon purpureus* (Hedw.) Brid. (Olech and Chwedorzewska 2008). Recent laboratory evidence has shown that *P. annua* begun to compete with the native vascular plants, exerting a negative impact on their physiology and biomass (Molina-Montenegro and others 2012).

Fig. 2. A perennial tussocks which has been observed in the vicinity of Arctowski during several consecutive years (photo K. J. Chwedorzewska).

Adaptations to polar conditions

Numerous characteristics make *P. annua* highly adaptable to environmental stress and unstable habitats: huge phenotypic and genotypic variability, small size, plastic life cycle: life-history types ranging from annual to perennial forms (for example Law 1981, Grime and others 1986; Frenot and others 1999, 2001; Holm and others 1997; Mitich 1998). The functioning of *P. annua* in the Antarctic could not be possible without specific adaptations, which enable the plants to persist the climatic conditions typical for this zone. *Poa annua* shows both 'r' (rapid development, a high rate of population growth, early reproduction, compact form and a single reproductive cycle, usually annual plant life cycle) and 'K' (slower development, a greater competitive ability, delayed reproduction, greater biomass per individual, continued reproduction, usually perennial plant life cycle) life strategies depending on environmental variables (Law and others 1977). Under stress conditions annual bluegrass shows more likely the 'K' strategy (McNeilly 1981, Chen and others 2003). Under the sub-Antarctic (Walton and Smith 1973; Walton 1975) as well as the Antarctic (Chwedorzewska and Bednarek 2012) polar conditions, where the unstable environment does not guarantee seedling survival, selection seems to favour perennial individuals with greater biomass (Fig. 2).

The development of substantial freezing tolerance enables the survival of individuals at low temperatures, with LT_{50} (median lethal temperature) as low as −31,6°C for some ecotypes (Dionne and others 2001). This freezing tolerance is probably connected with high accumulation of water soluble sugars (mainly sucrose) in response to low temperature. In some ecotypes there is even more than 20% of sucrose in dry matter (Dionne and others 2010).

Annual bluegrass can produce a huge number of seeds in very short time, even thousands per individual (Law 1981). Seeds can germinate even two days after fertilisation over a wide range of environmental conditions. They may retain viability for several years in the soil seed bank (Hutchinson and Seymour 1982). As shown by Wódkiewicz and others (2013), *P. annua* at Arctowski successfully reproduces sexually with more than 50% of fully developed, viable caryopses that can survive the maritime Antarctic winter not only in the soil, but also directly on the previous year's inflorescence. Furthermore, germination tests of freshly collected seeds showed that *P. annua* did not differ significantly in mean germination success from *Colobanthus quitensis*, while the germination success of this introduced species was significantly higher than of *Deschampsia antarctica* (Wódkiewicz and others 2013; Molina-Montenegro and others 2014). However the germination success of native plants might be different after stratification (for example Hennion and others 2006). It has also been shown that annual bluegrass maintains a soil seed bank comparable to species typical for the polar tundra (Wódkiewicz and others 2013, 2014). That way seeds are able to survive the Antarctic winter and readily germinate under optimal conditions. This species also often reproduces vegetatively (Vargas and Turgeon 2004).

The characteristic spatial structure of the Antarctic population of *P. annua* is distinct dense clumps or tussoks (Wódkiewicz and others 2014). At least some of the tussocks consist of many individuals (Fig. 3). In the temperate zone the species is only loosely tufted (Grime and others 1986). The microspatial structure of *P. annua* soil seed banks in Antarctica is highly associated with the presence of tussocks. Seeds are deposited underneath the tussock rather than in the vicinity of the clump. High density of plants within the tussock may be of an adaptive value for the persistence of plants in extreme polar conditions (Wódkiewicz and others 2014). Earlier observations suggest that the tussocks are rather stable in time (Fig. 2). This finding is in agreement with earlier data underlining the capability of *P. annua* to form

Fig. 3. Individuals isolated from one clump (photo A. Gasek).

perennial ecotypes (Gibeault 1971). Therefore at least some of the clumps may be capable of surviving at least over several vegetation periods.

The response of *P. annua* to polar conditions is also evident in morphometric traits. Work is continuing on this phenomenon. Populations thriving in the Antarctic, which is the latitudinal extreme of the species distribution, differ from populations from the centre of the species distribution (European lowland). Plants from the altitudinal extreme (mountain localities) of the species range exhibit morphological characteristics intermediate between lowland and Antarctic populations. This indicates that environmental factors seem to be the main driving force for morphological differentiation of this species. Populations for the morphometric analysis were chosen after genetic analysis, which pointed out that most likely the population of *P. annua* from Arctowski originated from Poland. Genetic analyses indicated significant decrease of variability (Chwedorzewska and Bednarek 2012). Despite the genetic relationship of the Antarctic and Polish populations, some of observed differences in morphological features may have adaptive value. The phenomenon of epigenetic 'transgeneration memory' in plants (Molinier and others 2006), may underlie those significant morphological differences. This is a reaction of plants to stress factors resulting in changes of DNA methylation patterns, very often manifested in changes at the phenotype level. Stress conditions not only led to transformation but also played a role in the stabilisation of the 'new phenotype'. The results obtained with the metAFLP technique also point out a similar mechanism in the *P. annua* population from the Antarctic as compared to the population from the centre of the species range. Significantly higher methylation variability was observed in the Antarctic population than in the Polish one, despite a contrary trend in genetic variability. This is probably a reaction to stress conditions prevailing in polar environment (subzero temperatures, specific light regime, short vegetation season, salinity, desiccating winds etc.). Such reaction to stress manifested by a significant increase in frequency of epigenetic changes can lead to phenotypic changes accelerating the adaptation processes (Chwedorzewska and Bednarek 2012). In this way an acquired feature could potentially be fixed, as it is forced by the environment, which was already observed in *P. annua* by La Mantia (2009). The relation between morphological variability and genetic/epigenetic variation and the fixation of morphological traits should be the focus of further studies.

Conclusions

The spreading of *P. annua* in the Antarctic Peninsula region is an example of expansion process and could serve as a model, on the basis of which the course and consequences of further invasions may be predicted and monitored. This process also highlights the dangers to Antarctic terrestrial ecosystems that are resulting from increasing human traffic in this region. The results on the functioning of this species in Antarctica collected in various study fields may shed light on the alien species spread in this region in association with regional warming; it may also play an important role in the prediction of the course and outcome of subsequent invasions. Understanding the history of *P. annua* will allow the application of different policies and actions in protection against other invasive species and develop effective methods of their eradication.

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