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Plastic biomass allocation as a trait increasing the invasiveness of annual bluegrass (*Poa annua* L.) in Antarctica

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Abstract
The plasticity of functional traits promotes invasiveness of a species. Biomass allocation, as one of these traits, is responsible for resource acquisition, and its plastic modifications can be of adaptive value in new environments before any genetic adaptations may occur. Our aim was to compare in situ biomass allocation in aboveground and belowground organs in an Antarctic and a Polish population of annual bluegrass (*Poa annua*), the only alien plant species successfully invading Antarctica. The Antarctic population was characterised by three times lower aboveground biomass, more compact plant growth habit and higher fraction of biomass allocated into belowground organs than in the Polish population. The differences between populations are probably a result of adaptation to local conditions. The modifications of the studied traits in the Antarctic population are most likely a response to extreme atmospheric and edaphic conditions and enable the species to survive and spread in this hostile environment. Our results are in accordance with the balanced growth hypothesis. At the same time, these trait values enhance species performance under Antarctic conditions making *P. annua* a potential threat to local plant communities under altering climate changes and growing human impact scenario.

Keywords Biomass allocation · Invasive species · Plant morphology · Phenotypic plasticity

Introduction

Plastic resource allocation in plants is a response to varying growing conditions affecting dispersal, distribution, resilience, and speciation (Harper and Ogden 1970; Hickman 1975; Reekie and Bazzaz 1987; Dong and de Kroon 1994). Hence, it has a substantial effect on plant's competitiveness (Berendse and Elberse 1990). Functional traits related to physiology, biomass allocation, growth rate, size, and fitness affect invasiveness (Alpert et al. 2000; van Kleunen et al. 2010; Espeland 2013; Colautti et al. 2017). Invasive species

are often physiologically plastic, which allows them to take advantage of a variety of habitats and different ecological niches (Baker 1974; Meekins and McCarthy 2001; Richards et al. 2006). In consequence, a species can be well adapted to the conditions of the colonised area without genetic changes (Alpert et al. 2000; Chwedorzewska and Bednarek 2012). The plastic response enables the survival of a population even before any favourable genetic changes may take place. Therefore, species plasticity has been suggested as one of the key traits important for predicting species invasiveness (Rejmanek and Richardson 1996).

Many authors point to resource allocation as one of the traits important for species invasiveness. This is because plastic biomass allocation enables the control of resource absorption from the environment. Greater root biomass allows for better acquisition of nutrients and water from soil, and greater photosynthetically active biomass enables a more efficient collection of solar energy (Sultan 1995, 2000; Ryser and Eek 2000). Plastic biomass allocation is therefore an important parameter during species invasion, because it directly affects adaptation to the conditions prevailing in the new environment. This results in a broadening of the tolerance to environmental conditions, whereby species can

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survive in different ecological niches (Sexton et al. 2002; Richards et al. 2006; Geng et al. 2016).

Theoretically if the source and invaded habitats share similar environmental conditions, there is no need for plastic response of a species conquering new sites. Phenotypic plasticity of the invasive species is most evident and often necessary when conditions differ between the source and target habitats. In such a case, plasticity can be the main factor that determines establishing of the species in a new environment and further invasion success (Hulme 2007; Espeland 2013; Colautti et al. 2017). In particular, harsh conditions, differing from the majority of potential source habitats and being on the border of endurance for most vascular plant species, are met in Maritime Antarctica (e.g. Robinson et al. 2003; Galera et al. 2015).

The only invasive plant species successfully conquering the harsh Maritime Antarctic environment and establishing a self-sustaining population in the region is annual bluegrass (*Poa annua* L.), one of the most common grass species in the world. The species is of Eurasian origin with the centre of its range in temperate climates (Grime et al. 1988; Mitich 1998; Vargas and Turgeon 2003). It grows in a variety of climatic zones from the equator to the polar regions (Vargas and Turgeon 2003). The species has been noted for over 30 years in Point Thomas Oasis on King George Island, Maritime Antarctica (Galera et al. 2017). Due to harsh environmental factors, this Antarctic population exhibits specific morphological traits (Galera et al. 2015).

The aim of our work was to compare biomass allocation in aboveground and belowground organs of annual bluegrass in two populations of the species occurring under different environmental conditions in Maritime Antarctica and Poland. We were interested in finding out how these traits may vary to exploit the local environment and to what extent the biomass allocation of the studied species is shaped by different climatic and/or edaphic factors. This is an initial study of biomass allocation of the species in situ. This research reports differences in the studied populations under local conditions and precedes a common garden study in which climatic factors and soil properties will be controlled.

Methods

Data collection

For our study, we chose two locations where *P. annua* populations are found. One of the sampling sites was situated in the vicinity of the Polish Antarctic Station H. Arctowski (62°09′36″S, 58°28′16″W), King George Island, South Shetlands, Maritime Antarctica. The other sampling site was situated in the Botanic Garden of the Polish Academy of Sciences (52°06′19″N, 21°05′43″E), Warsaw, Poland—representing one of the core native range populations (Tutin 1952). The two locations differ in climatic characteristics (Table 1). The King George Island site has polar climate (Galera et al. 2015, 2018) with sub-zero temperatures even during the short Antarctic "summer" (annually 143 days with mean daily temperature above 0 °C, Kejna 1992). There is no growing season defined as a period with mean daily temperature above 5 °C (Table 1). The site is characterised by strong desiccating wind (Wierzbicki 2009), soil of initial type (Bölter et al. 1997; Nędzarek 2008; Łachacz et al. 2018), low competition, and no herbivory (Galera et al. 2018). Contrastingly the Warsaw site receives a temperate climate with sufficient rainfall and optimal temperature during the growing season (Galera et al. 2015) that lasts over 200 days a year (Table 1). In this

Table 1 Comparison of climatic characteristics between study sites

Climate characteristics	Warsaw	King George Island
Mean annual temperature (°C)	9.2[a]	− 1.9[b]
Mean temperature during the coldest month (°C)	− 1.7 (January)[a]	− 6.3 (July)[b]
Mean temperature during the warmest month (°C)	10.5 (July)[a]	2.2 (January)[b]
Mean annual precipitation (mm)	553.9[a]	429.7[b]
Mean annual wind speed (km/h)	12.6[a]	32.8[b]
Mean annual number of days with snowfall (days)	125[a]	210[b]
Mean length of the thermal winter season (days)	89[c]	222[d]
Mean length of the growing season (days)	214[c]	0[d]

Length of the growing season calculated according to Frich et al. (2002) definition (period with mean daily temperature above 5 °C)

[a]WeatherOnline (2016)—data from Warsaw-Okęcie Meteorological Station, means based on 2005–2015 time span

[b]WeatherOnline (2016)—data from Argentinian Carlini Station, means based on 2005–2015 time span

[c]Czernecki and Miętus (2017)—data from meteorological stations located in Eastern Lowlands in Poland, means based on 1951–2010 time span

[d]Kejna (1992)—data from Arctowski Polish Antarctic Station, means based on 1978–1989 time span

site, the dry podzolic soil (Puchalski and Gawryś 2002) is relatively more fertile than in our Antarctic study site, but there is pressure from competitors as well as herbivores.

In each site, we sampled 60 randomly selected *P. annua* tussocks. The sampling was performed at the end of *P. annua* growth cycle in February/March 2015 in the Antarctic site and in October 2015 in the Warsaw site. We measured the height of each tussock (0.5 cm accuracy) and carefully dug them without disturb the roots. Our goal was to assess the differences in biomass of aboveground and belowground organs of annual bluegrass in both studied populations. During our study, we observed that tussocks from the Antarctic population were not large enough to measure the dry weight of their organs and failed to be detected by our scale. We therefore had to employ a procedure to extrapolate their mass from photographs of individuals (Fig. 1).

Tussocks were transported to the laboratory, washed to dispose of any remaining soil, separated into individuals in order to minimise the overlapping of leaves and photographed (Fig. 1). The images were used to calculate the area of the above- and belowground parts of the plant (0.01 cm^2 accuracy) as a proxy of biomass, as well as to measure the maximum length of the root within the tussock (0.01 cm accuracy). The measurements were taken with ImageJ software (Rasband 1997–2018). All annual bluegrass individuals were subsequently fractioned into aboveground organs and roots and dried at 40 °C for 24 h. We weighed the aboveground and belowground organs of each tussock on a laboratory scale (0.0001 g accuracy). For the Arctowski population, we were able to collect biomass information for only 27 tussocks as the remaining 33 tussocks were too small to be detected by the scale.

Statistical analysis

Our dataset included a direct biomass measure of the aboveground and belowground organs, as well as an indirect biomass estimate based on photographs. We compared the assessment of biomass using these two methods by correlation analysis. We estimated Pearson correlation coefficients and least-squares linear regression coefficients between the biomass and organ area on the photographs. We compared the regression slopes between direct measurement of biomass and its estimate from photographs separately for aboveground and belowground organs between populations with pairwise comparisons of least-squares means using the Tukey method (Piepho 2004). As the regression coefficients differed between populations, we used them in subsequent analyses to estimate the biomass of organs based on the photographs according to the formula: $B = A \times R$ (B–biomass of plant organs, A—area of plant organs on photographs, R—regression coefficient). Based on our method comparison results, further analyses of biomass were performed not on the direct measurements of biomass, but on their regression-based estimate.

We compared the studied populations in regard to the number of individuals per tussock, tussock height, the length of the longest root in a tussock and aboveground, belowground and total tussock biomass. Furthermore, we calculated shoot-to-root length ratio per tussock and percentage of the belowground biomass in total biomass. The

Fig. 1 All (4) separated and washed individuals of *Poa annua* comprising one of the tussocks collected in Poland. The scale is visible below the plants. Phot. A. Rudak
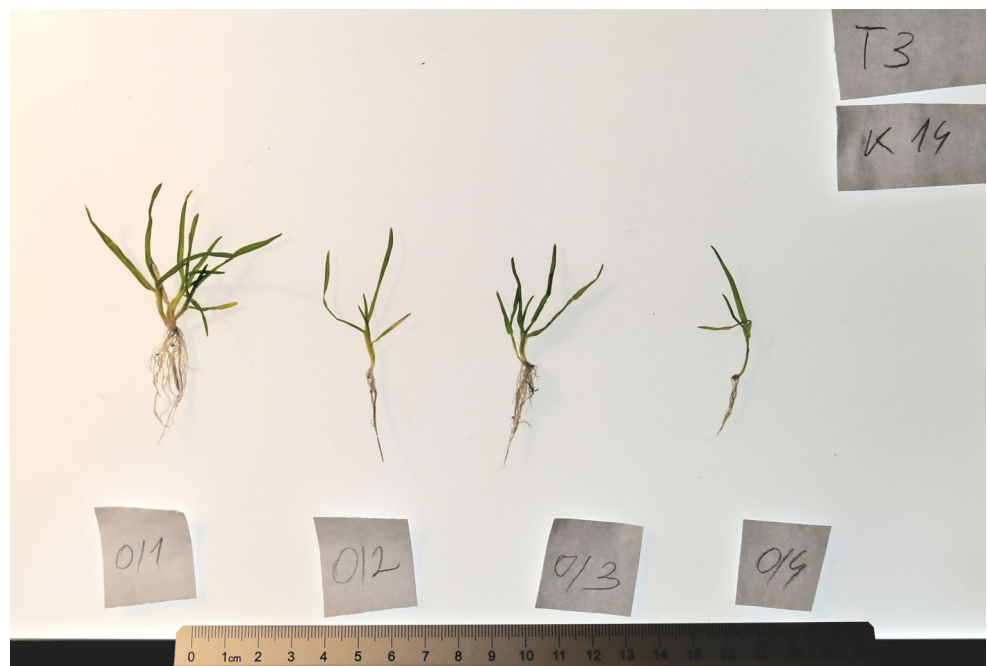
Shapiro–Wilk test showed that the distribution of the measured parameters deviated from the normal distribution; therefore, the Kruskal–Wallis test was used to compare data from analysed populations. All statistical analyses were carried out in the R program with the use of base (R Core Team 2018), lsmeans (Lenth 2016) and multcompView (Graves et al. 2015) packages.

Results

We recorded 233 individuals in 60 tussocks from Poland and 209 individuals in the same number of tussocks from Antarctica. The median tussock height was three times greater in the Polish population than in the Antarctic, but plant roots were shorter (Table 2). In both populations, shoot-to-root length ratio was lower than 1, indicating that roots were longer than shoots, but there were large differences between the populations (Table 2).

We found a strong linear correlation between the biomass and the area of the plant organs on photographs for tussock from both studied populations (Figs. 2, 3). Comparison of the regression slopes between biomass and plant organ area on photographs indicated two groups (Fig. 4). We did not

find significant differences between linear regression slopes for biomass and area of photographed organs within each population, but the slopes differed between populations. The average regression coefficients were 0.0117 for the Antarctic and 0.0079 for the Polish population.

The total biomass of tussocks from Poland was about 2 times higher than from the Antarctic (Table 2). Aboveground tussock biomass was significantly higher in the Polish than in the Antarctic population. The only studied trait that is not significantly different between studied populations was root biomass (Table 2). Biomass allocation expressed as the percent of the belowground biomass in the biomass of the entire tussock also differed between populations with 26.6% for the Polish population and 60.1% for the Antarctic one (Table 2).

Discussion

Estimating biomass based on the photograph area of plant organs

Due to small size of the plants studied, especially from the Antarctic population we had to develop another means of assessing plant biomass. Therefore, we used linear

Table 2 Comparison of studied traits between the Polish and Antarctic *P. annua* tussocks

Median value of trait of the tussock	Location		K–W test	
	Poland	Antarctic	*H*1 statistics	*p value*
Number of individuals	3	1	4.274	*
Tussock height (cm)	4.5	1.5	56.191	**
The length of the longest root (cm)	5.93	8.87	7.650	*
Shoot to root length ratio	0.74	0.16	77.660	**
Total biomass (g)	0.1025	0.0509	6.347	*
Biomass of aboveground organs (g)	0.0728	0.0213	17.675	**
Biomass of belowground organs (g)	0.0248	0.0290	0.080	ns
The percent of the belowground organs in the total biomass (%)	26.6	60.1	65.503	**

$*p < 0.05$, $**p < 0.005$, $^{ns}p > 0.05$
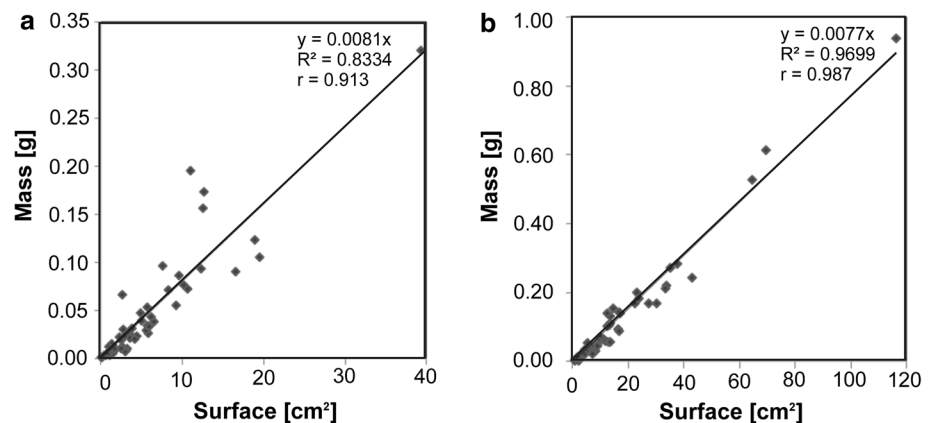
Fig. 2 The relation between the surface of the belowground (**a**) and aboveground (**b**) plant organs on photographs, and the dry mass of *Poa annua* tussocks from Poland

Fig. 3 The relation between the surface of the belowground (**a**) and aboveground (**b**) plant organs on photographs, and the dry mass of *Poa annua* tussocks from Antarctica

a

$y = 0.0117x$
$R^2 = 0.7673$
$r = 0.880$

b

$y = 0.0117x$
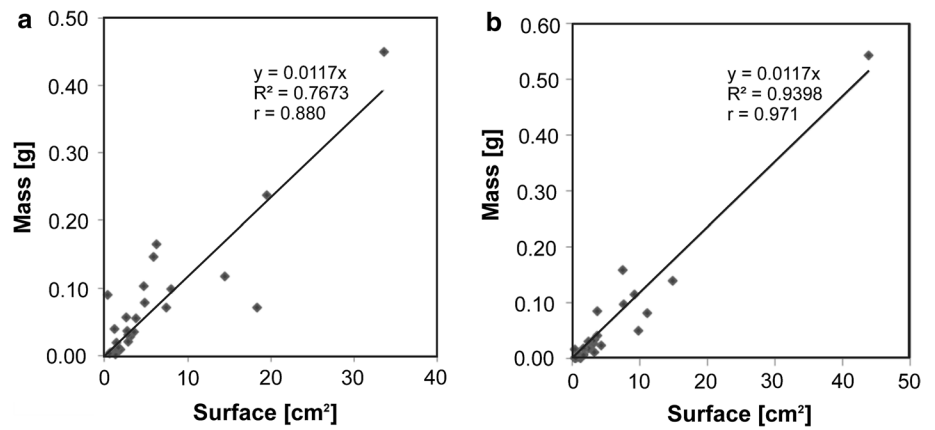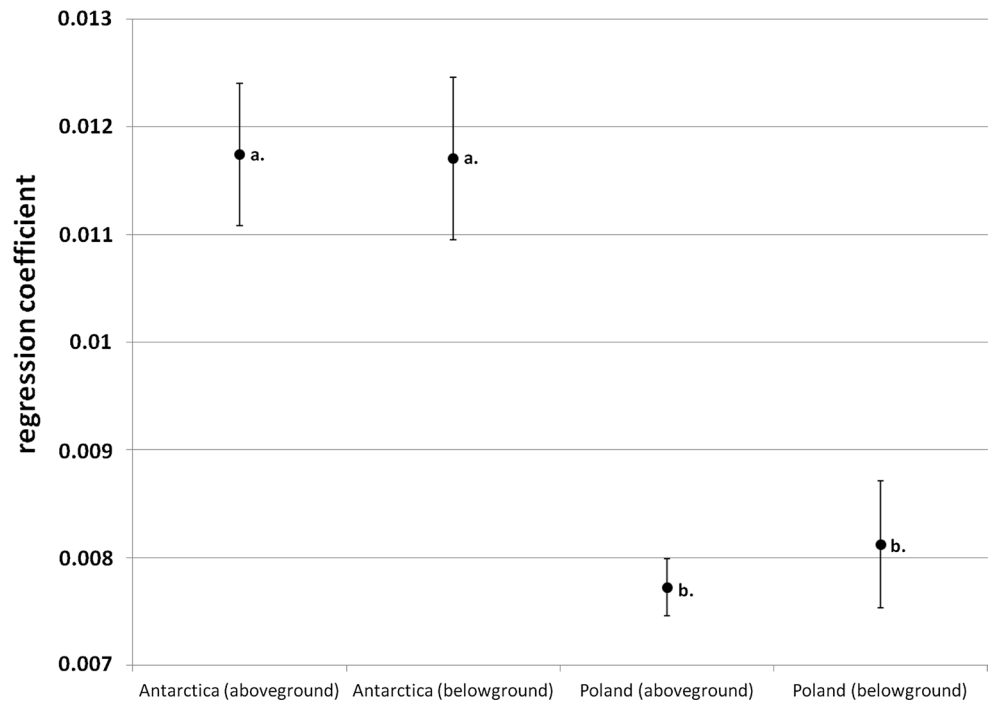$R^2 = 0.9398$
$r = 0.971$

Fig. 4 Regression coefficients with 95% confidence intervals for relation between biomass and surface for aboveground and belowground plant organs from Poland and Antarctica. Lowercase letters indicate Tukey grouping at $p < 0.05$

regression to estimate the biomass of organs from photographs. The regression method is indirect, but gave satisfactory results. The interlacing of roots and leaves induces an error in the estimate, but the error is similar over all measured objects. Our results indicated strong correlation between photographed area and biomass, which may suggest that measuring the photographed area of plant organs is a good proxy of biomass for comparison purposes. This technique may be helpful in biomass allocation estimation, as it requires less time or resources to perform and can help measure specimens otherwise not eligible for examination.

Similar methods are used widely for difficult measurements, like large-area estimations of forest biomass (Brown et al. 1989), commonly using existing regression equations for this purpose. Generalised equations may cause

significant errors and every usage of regression estimates should be thoroughly checked before being applied (Wang et al. 2002). We found significant differences in population-specific regression equations confirming their cross-inapplicability. Also extrapolating the regression line beyond the range of both measured variables can be questioned, but in our opinion it is a better estimate than not having any results at all, especially from unique sites, like Antarctica.

Factors shaping studied tussock traits

Environmental conditions considerably differ between South Shetlands and Poland (Table 1). This demands plastic changes from the invading plant species. Apart from such factors as temperature and soil properties, which may be

studied under controlled environment, biomass allocation may be influenced by an interlacing complex of other factors, which are hard to simulate. One of them is water availability restricting plant growth in the Antarctic. Despite a large supply of water on King George Island in the form of glacial caps, it is periodically inaccessible to plants inducing physiological drought due to low temperature and salinity (Mahajan and Tuteja 2005). Very strong wind often exceeding 40 m/s is another important factor affecting plant growth in Maritime Antarctica (Kowalski 1985; Wierzbicki 2009). Wind acts both as a stressor, causing plant desiccation, and as disturbance factor (Berjak 1979; Gardiner et al. 2016). Differences in these environmental factors may induce multiple responses in plants, which determine the ultimate trait values, depending on their magnitude and potentially interactive effects (Bradshaw 1965).

Response of local populations to contrasting environmental conditions

Our results unequivocally indicate differences in tussock traits and biomass allocation in populations from the two study sites. In the Antarctic population, *P. annua* had lower aboveground biomass than in the Polish population. We did not detect differences in belowground biomass, but plants from the Antarctic had longer roots. Differences in biomass allocation detected by us between the study sites are in accordance with the balanced growth hypothesis (Shipley and Meziane 2002), which states that plant organs responsible for acquisition of the limiting resource should develop better than others. Under harsh conditions, pioneer plants exhibit a similar scheme of biomass allocation which is driven by abiotic factors (Jumpponen et al. 1999). Lower total biomass is often detected in plants growing in sites prone to drought (Enquist and Niklas 2002). In polar regions, members of the Poaceae (grass family) exhibit a xerophytic character, including a lower biomass of the aboveground organs, longer root system and higher root biomass (Giełwanowska et al. 2011).

Low aboveground biomass of plants in the polar regions was found to be driven by low temperature and strong wind (Giełwanowska et al. 2011). Lower biomass of the aboveground organs and lower tussock height detected by us in the Antarctic in comparison with the Polish population may be a result of the differences in temperature and wind conditions between the studied sites. Under suboptimal low temperature, plant growth may be much slower than under optimal climatic conditions. The temperature on the soil surface can be even 10 °C higher than temperature recorded by meteorological stations (Kellman-Sopyła and Giełwanowska 2015). In the Antarctic, a compact plant growth habit may allow aboveground organs to be confined to more favourable conditions present just above the soil surface as well as reduce

transpiration caused by desiccating wind. *Deschampsia antarctica* Desv. (Antarctic hair grass) was shown to have a different growth habit depending on the wind speed, with more erect plants under lower wind speed and more procumbent plants under high wind (Parnikoza et al. 2015). In contrast, plants from a temperate climate may be taller to win competition for light (McCarthy and Enquist 2007).

Species more resistant to drought and harsh climatic conditions were found to have higher biomass allocation in roots (Fort et al. 2012). In comparison with plants cultivated under optimal conditions, the root system of plants experiencing harsh conditions was even twice as large (Gleeson and Tillman 1990). The impact of low nitrogen and phosphorus availability in soil was experimentally shown to impact biomass allocation in many species (Aerts et al. 1991; Müller et al. 2000). The study of nutrient deficiency on the development of *Arabidopsis thaliana* (L.) Hynh. (thale cress) indicated that increased root growth is a consequence of nitrogen and phosphorus deficiency, while other nutrient deficiency does not enhance root growth (Hermans et al. 2006). Although we did not find differences in root biomass between the Antarctic and Polish population, the roots in the Antarctic plants were significantly longer. The larger rhizosphere in the Antarctic population may aid in nutrient and water acquisition. A similar root biomass allocation pattern was found for annual bluegrass occurring in a sub-Antarctic site (Williams et al. 2018). Longer root system may also better anchor the plants against strong wind (Reubens et al. 2009; Gardiner et al. 2016).

The role of phenotypic plasticity in the invasion of *P. annua*

Our results confirm that *P. annua* is a highly plastic species. The differences in biomass allocation observed in this study between two populations of the same species, but from climatic zones highly differing in environment severity (Table 1), show the species high adjustment capability. Also, our previous findings regarding differences in morphological traits between individuals confirm the highly adaptive nature of this species. Modifications of morphological traits make the tussocks (this study) as well as individual specimens (Galera et al. 2015) more compact under harsh conditions, and differences in biomass allocation help with the acquisition of scarce resources. While individuals in the Antarctic population tended to be composed of more shoots (Galera et al. 2015), they still have lower aboveground biomass than individuals from the Polish population. Also their sexual organs are smaller, more compact enabling lower seed set under Antarctic conditions, despite the higher number of panicles per individual (Galera et al. 2015). This may indicate high influence of harsh conditions on plant performance. Nevertheless, these traits can be modified in such a

way that although fecundity is lowered in comparison with optimal growing conditions, the species is able to adapt and set viable seeds in the Antarctic. Together these traits facilitate the ongoing invasion of the species in this hostile environment.

Annual bluegrass has also been reported to show plastic physiological response to different environmental conditions (Giełwanowska et al. 2011). High plasticity in all of these traits, rather than genetic diversity, makes the species highly invasive. This adaptability allows alien species to "set foot" in novel environments before any genetic adaptations may have time to take place (Frenot et al. 2005; Richards et al. 2006). The species has been reported as invasive in sub-Antarctic islands (e.g. Scott and Kirkpatrick 2005; Whinam 2009; Williams et al. 2016; Greve et al. 2017). The species successfully penetrated the Antarctic geographical barrier (Chwedorzewska et al. 2015; Hughes and Pertierra 2016) and established a breeding population on King George Island (Galera et al. 2017). This confirms the pivotal role of high phenotypic plasticity of this species in the invasion success in the broad Antarctic region.

Phenotypic plasticity has been observed to determine the ability of species to succeed in a broad range of habitats (Pigliucci 2001; Leger and Rice 2003; Richards et al. 2006). Modifications of developmental, physiological and life-history traits observed in natural populations exposed to novel environments can be driven by plastic response (Chevin et al. 2013). We found such response in our study species. Besides promoting species persistence, adaptive plasticity can facilitate the rapid spread of invasive species across diverse new habitats (breaking the survival barrier, Blackburn et al. 2011). The start of expansion of *P. annua* in Point Thomas Oasis (Wódkiewicz et al. 2018) may be an effect of this facilitation. The invasion of *P. annua* at Point Thomas Oasis, possible due to the species plasticity, is a most pronounced invasion in the region. It enabled us to study the invasion process in harsh environments and species traits facilitating this invasion. Nevertheless, we started the eradication process to protect this unique ecosystem (Galera et al. 2017). The plasticity of *P. annua* may pose a risk of local tundra communities under a changing climate scenario. Hopefully this invasion can be stopped with the use of proper eradication methods.

Conclusions

Biomass allocation is an important adaptive trait, and its variation can be a response to variable environmental factors like wind speed, availability of nutrients and water conditions. The Antarctic population of *P. annua* in comparison with the Polish one shows significant differences in biomass allocation. The plasticity of this trait as well as other morphological, developmental and physiological traits may greatly facilitate the species invasibility in polar regions. Higher biomass allocation in the belowground organs in the Antarctic population may allow plants to better exploit nutrients and water resources, as well as more efficiently anchor the plant to the ground. Smaller and compact aboveground organs restrict transpiration and reduce surface resistance, making plants less vulnerable to the adverse influence of wind abrasion. Plants are therefore better adapted to survive and set seed under local Antarctic conditions. To what extent these differences are population specific or remain flexible to changing environmental conditions will be a focus of our further studies involving transplant experiments under simulated environmental conditions.

Compliance with ethical standards

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

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