Accepted Manuscript

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PII: S1439-1791(17)30284-0
DOI: https://doi.org/doi:10.1016/j.baae.2018.02.003
Reference: BAAE 51083

To appear in:

Received date: 3-9-2017
Revised date: 9-2-2018
Accepted date: 9-2-2018

Please cite this article as: Williams, L. K., Shaw, J. D., Sindel, B. M., Wilson, S. C., and Kristiansen, P.,Longevity, growth and community ecology of invasive *Poa annua* across environmental gradients in the subantarctic, *Basic and Applied Ecology* (2018), https://doi.org/10.1016/j.baae.2018.02.003

Longevity, growth and community ecology of invasive *Poa annua* across environmental gradients in the subantarctic

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Abstract

Poa annua is a cosmopolitan weed in turf grass. It is a widespread non-native species in the subantarctic and also occurs in the Antarctic Peninsula. It has highly variable morphology, longevity and reproductive capacity across both its invaded and native range. Little is known about the ecology of *P. annua* in the subantarctic, particularly its longevity, morphological variation across small spatial scales and competitive ability. We monitored individual *P. annua* plants on subantarctic Macquarie Island to assess their longevity; quantified morphology and biomass allocation across environmental gradients; and assessed community diversity indices in areas of varying *P. annua* density. We show that *P. annua* plants on Macquarie Island are perennial, and their morphology varies with elevation, animal disturbance and soil properties. At low altitude, coastal sites with high animal disturbance and deep, sandy soils, *P. annua* plants are larger and native plant diversity is low. Conversely, at high altitude sites *P. annua* plants are smaller and the diversity of native species is not reduced. This new information informs why *P. annua* is the most successful plant invader in the subantarctic and quantifies some key characteristics enabling an invasive species to function well beyond its natural range. Community ecology theory can also explain patterns in the ecology of *P. annua* on Macquarie Island.

Highlights

* *Poa annua* populations on Macquarie Island are commonly perennial
* morphology is highly variable, even with fine-scale soil and environmental changes
* successful at low altitude disturbed sites with deep, sandy soils
* biomass predominantly allocated to persistence, but high reproductive output can be achieved
* traits likely to increase competitiveness, especially under climate change

Keywords: alien, Antarctic region, wintergrass, weed, perenniality

Introduction

Poa annua L. is a cosmopolitan weed (Heide 2001). Its introduced range extends to the Arctic (Warwick 1979), Antarctic Peninsula (Chwedorzewska et al. 2015) and subantarctic (Frenot et al. 2005; Williams et al. 2013, McGeoch et al. 2015) (Fig. 1). It is the only introduced plant with an established, reproducing population in the Antarctic (Chwedorzewska et al. 2015), and is the most widespread non-native plant in the subantarctic (McGeoch et al. 2015). The longevity, morphology and reproductive capacity of *P. annua* varies greatly across its secondary and native range, largely in response to environmental conditions (Warwick 1979, Soreng & Peterson 2012). *Poa annua* plants in the Antarctic and subantarctic differ in their ecology from populations elsewhere (Galera et al. 2015). On subantarctic Macquarie Island, *P. annua* was accidentally introduced by seal hunters nearly 150 years ago. It is now widespread on the island, found from coastal tussock vegetation to the wind-swept feldmark (Selkirk et al. 1990), and appears to differ considerably in its morphology and reproductive output.

The ecology and population dynamics of *P. annua* have been well studied in temperate turf grass where the species is a particular management problem (Beard et al. 1978, Wu et al. 1987, Mitich 1998, Heide 2001). In turf grass systems, *P. annua* tolerates disturbance and nutrient enrichment (Beard 1978, Heide 2001), has very high seed bank densities (e.g. 210 000 seeds m^{-2}) (Lush 1988) and competes with sown turf grass species (Beard et al. 1978). Some research on the ecology and population dynamics of *P. annua* has been undertaken in the subantarctic. *Poa annua* is widespread in the subantarctic, occurring on all the major island groups and is highly tolerant of grazing by introduced herbivores, wildlife disturbance, nutrient enrichment and trampling (Copson 1984, Bergstrom & Smith 1990, Scott & Kirkpatrick 1994, 2013, Hausmann et al. 2013, Whinam et al. 2014). It is also an early coloniser of bare ground, deglaciated areas and landslips (Frenot et al. 1997, 1998). Other aspects of the ecology of *P. annua*, such as longevity, morphology and competitive ability are less well understood. Given the variability seen in *P. annua* elsewhere, aspects of its ecology are likely to differ both between the subantarctic islands and within islands in response to differing environmental variables.

Longevity is an important and variable plant trait influencing population dynamics, often closely aligned with a plant's morphology. Field observations suggest there are annual and perennial populations of *P. annua* in the subantarctic (Frenot et al. 2005). Tussocks in the Antarctic have been observed to be perennial (Chwedorzewska et al. 2015), and the Macquarie Island populations have been suggested to be perennial (Ellis et al. 1971, Selkirk et al.

1990). However, to the best of our knowledge, the longevity of individual *P. annua* plants in the subantarctic has never been quantified *in situ*.

The morphology of *P. annua* plants can vary both within the Antarctic and subantarctic region and is largely attributed to environmental factors. *Poa annua* plants growing in the Antarctic (South Shetlands) and subantarctic Kerguelen and Crozet Islands are smaller and more compact due to the lower growing temperatures and wind and snow damage than those from Poland, a likely source location of the Antarctic *P. annua* population (Frenot & Gloaguen 1994; Galera et al. 2015). When *P. annua* plants sourced from different populations around the world (including subantarctic Macquarie Island) were grown under common garden conditions, plants maintained morphological differences in response to provenance, albeit for an unspecified time period (Ellis et al. 1971). Frenot et al. (1999) observed distinct morphological differences in *P. annua* between populations on subantarctic Kerguelen and Crozet. Although plants were similar in size, those from Kerguelen had higher reproductive fertility, possibly due to vertebrate enrichment (higher nitrogen and phosphorus) at the Kerguelen sites. Plants also differed in morphology within each archipelago in response to environmental factors such as soil particle size (Frenot et al. 1999). Whilst the aforementioned research shows there is variability in the morphology of *P. annua* across the Antarctic region, the variability in *P. annua* morphology across smaller spatial scales (i.e. between populations within an island) and the drivers of this variation (environmental correlates) requires more research.

The competitive ability of *P. annua* and its impacts on native plant communities in the subantarctic appear to vary between sites. Some studies show that while *P. annua* is an early coloniser of bare ground, it does not directly compete with native species but is outcompeted over time in established native vegetation (Scott & Kirkpatrick 2008, 2013; Whinam et al. 2014). Other studies report that in the highly disturbed, nutrient-enriched areas around seal haul outs, *P. annua* forms low grasslands and dominates the native vegetation (Frenot et al. 2001, Haussmann et al. 2013). Pot trials with *P. annua* collected from the Antarctic Peninsula, however, showed the species competes directly with native plants (Molina-Montenegro et al. 2012, 2016). Competitive ability therefore depends on specific environmental factors.

As the most widespread invasive plant species in the subantarctic region, it is important to understand the ecology of *P. annua* as this has implications for management, conservation and invasion biology in the region and informs invasive plant biology more broadly. Given these knowledge gaps we aimed to better understand the ecology, and competitive ability and impact of *P. annua* on native species by: 1) quantifying the longevity of *P. annua* on subantarctic Macquarie Island, 2) assessing its morphological variation in response to fine-scale environmental variables, and 3) quantifying the community dynamics of *P. annua*. We hypothesised that: 1) *P. annua* would have a perennial lifecycle on Macquarie Island in response to the colder, harsher conditions, 2) the variability in the morphology of *P. annua* across the island would be explained by differences in environmental variables and 3) dense infestations of *P. annua* may suppress the diversity and growth of native species.

The explanation, prediction and management of biological invasions remains difficult and satisfactory explanations and predictions of invasive species is required Heger et al. 2013). Thus our study contributes to the explanation of why and how *P. annua* is an effective weed on Macquarie Island, within the framework of community ecology theory.

Materials and methods

Study sites

Macquarie Island (54°30’ S, 158°57’ E) has a mean annual temperature of 4 °C, precipitation of 980 mm and wind speed of 30 km h^{-1} with little variation throughout the year (Australian Bureaeu of Meteorology 2016). The island consists of an undulating plateau with an average elevation of 200-300 m above sea level (a.s.l.) surrounded by escarpment or steep coastal slopes and thus has a highly variable altitudinal range and topography that determines vegetation and plant growth (Selkirk et al. 1990). Megaherbs and tussock grasses dominate tall coastal and slope vegetation at low altitudes; short grasses, herbs and sedges predominate in mid-altitude vegetation; and bryophytes and cushion plants dominate high altitudes (Terauds et al. 2014).

Six sites were established in the austral summer of 2013 (Jan/Feb) in different plant communities across topographic, altitudinal and *P. annua* density gradients:

Bauer Bay and Tractor Rock - low altitude (< 50 m a.s.l.) and high *P. annua* cover (> 60%); Bauer Bay Slope and Doctor’s Track - mid altitude (100-150 m a.s.l.), medium *P. annua* cover (15-50%); Lower Boot Hill and Upper Boot Hill - high altitude (> 250 m a.s.l.), low *P. annua* cover (< 10%). An additional three sites were established in December 2013: The Nuggets – low altitude, high *P. annua* cover; Sawyer Creek - mid-altitude, medium *P. annua* cover; Mount Power – high altitude, low *P. annua* cover.

At each site location, elevation and aspect (of the slope face) were determined by handheld GPS. Soil depth was measured at ten randomly selected points across each site by inserting a graduated steel rod to a maximum depth of 85 cm. Animal disturbance (i.e. old rabbit burrows, wildlife trampling) was visually estimated: as low – soil and vegetation intact (value of 1); medium – some disturbance (2) or high – much of the soil and vegetation disturbed (3). Exposure was inferred based on prevailing winds and topography: low – sheltered from prevailing winds (1); medium – some exposure (2) or high – exposure to much of the prevailing winds (3). Two soil cores of 70 mm diameter and 200 mm depth were collected from a single representative location at each site and stored in plastic bags under refrigerated conditions until transported back to Australia for analysis. Cores from each site were homogenised, oven dried (40 °C) and sieved to 2 mm prior to analysis. Soil pH and electrical conductivity were determined according to Rayment and Higginson (1992); soil particle analysis using the pipette method (Day 1965), soluble sulphur using the method adopted from Blair et al. (1991) and absorbance using an inductively coupled plasma optical emission spectrometer (ICP-OES). Exchangeable calcium (Ca), potassium (K), magnesium (Mg) and sodium (Na) (measured in ammonium chloride at pH 7 with ICP-OES) (Rayment & Lyons 2011) and phosphorus (P) (Colwell P method) (Rayment & Higginson 1992) were determined. Samples were also ground to < 0.5 mm for % total nitrogen (N) and % total soil organic carbon (SOC) analysis (TruSpec Series Carbon and Nitrogen Analyser – LECO). Soil water content was determined by drying five replicates of 10 g of soil overnight at 105 °C. Soil particle analysis was not possible for The Nuggets and Sawyer Creek due to high organic matter content. The environmental and soil characteristics of each site are shown in Appendix 1 and were used to explain variation of plant morphological traits and species diversity indices in the principle components analysis.

Longevity

In February 2013, 20 *P. annua* plants (where we define plant as a single ramet) of various vegetative and reproductive stages were randomly tagged at each of the original six sites, resulting in 120 tagged plants. Only plants that could be determined to be a single ramet were tagged. Plants were marked and the number of tillers, maximum tiller length (to tip of the longest leaf), number of generative tillers and plant stage (vegetative/flowering/seeding) were recorded. Plants were photographed to document frost heave, erosion and sand deposition. In December 2013, March 2014 and April 2015 plants were re-measured.

Morphology

In February 2013, twenty 1 x 1m quadrats were randomly selected within a 20 x 20 m area at each of the original six sites. One *P. annua* plant (or a 5 x 5 cm clump of *P. annua* when cover was dense) was collected from each quadrat (20 plants/site), except at Upper Boot Hill (some quadrats contained no *P. annua* plants, so multiple plants were collected from quadrats which did contain plants). Plants (including roots) were extracted to a depth of 15 cm and rinsed of soil using a pressurised hose. The number of tillers, maximum tiller length, maximum root length, plant stage and number of generative tillers were recorded. Plants were sectioned into reproductive parts; roots and tillers, dried at 80 °C for 48 hours and weighed to give an indication of reproductive and vegetative biomass.

Community structure

Vegetation was assessed within twenty 1 x 1 m quadrats at all 9 study sites in Jan/Feb 2014. The species present (richness) and percentage canopy cover of each species were recorded. Species diversity of each site was estimated using Simpson diversity (calculated as 1-D) (Lande 1990) to capture both species abundance and the variance of the species' abundance distribution. Simpson diversity was not calculated at Upper Boot Hill due to most quadrats having no or little plant cover.

Data analysis

All statistical analyses were conducted in R version 3.1.3 (R Core Team 2014). Longevity data, plant traits, biomass allocation, diversity indices and *P. annua* cover were analysed using mixed models ('lme' function in the lme4 package) with site as a fixed effect and samples as a random effect. Where P values were significant (< 0.05), means were separated using 95% confidence intervals using the 'effect' function in the effects package. Linear regression ('lm' function with F tests) was used to assess correlations between plant traits and diversity indices, and environmental and soil characteristics.

PCA was used to evaluate the combined interactions between plant traits/diversity indices and environmental and soil characteristics. Non-significant variables from the linear regressions were not included as loadings. Environmental variables that were strongly correlated with plant traits or diversity indices ($R^2 > 0.25$) were selected as loadings. Strongly correlated soil variables (e.g. cations) were included as a single variable. PCA was carried out using the 'princomp' function in the stats package (Venables & Ripley 2002).

Results

Longevity

Most of the tagged *P. annua* plants at each site (50-100%) survived for at least 11 months (Fig. 2). At least 20% of the tagged plants persisted at each site for 27 months, showing the population exhibits perenniality. Only five plants (of 120) were recorded as dead. Plant losses were attributed to dynamic landscape processes such as landslips (Bauer Bay Slope, Tractor Rock – early 2015), sand movement (Bauer Bay Beach), frost heave (Lower and Upper Boot Hill – winter 2013/14) or abundant growth of neighbouring plants (Bauer Bay Beach, Tractor Rock – 2014/15).

Morphology

The morphological traits of *P. annua* plants varied between sites (Table 1). Plants at high altitude Lower Boot Hill and Upper Boot Hill were smallest (mean of 1.8 and 1.1 g respectively), with the fewest tillers (15.3 and 12.5, respectively). Plants at Upper Boot Hill had the shortest (3.7 cm) and lowest number of generative tillers (3.2) while plants at Lower Boot Hill had the shortest roots (11.0 cm). Conversely, the largest plants were found at the low altitude Tractor Rock and Bauer Bay Beach. Tractor Rock had the largest plants (19.2 g, 85.4 tillers, 28.0 generative sems and root length of 21.8 cm). Plants at Bauer Bay Beach had the longest tillers (28.7 cm). Plants at the mid altitude sites of Doctor's Track and Bauer Bay Slope were intermediate in size. Most biomass was allocated to roots (60.8-80.0%), followed by tillers (18.3-31.6%), with little allocated to reproductive material (1.6-7.6%) (Table 1). Morphological variation was greater within the low altitude populations of Tractor Rock and Bauer Bay Beach than the higher altitude populations (as indicated by the spread of points, Fig. 3).

Environmental variables were strong drivers of the differences in plant morphological traits between sites (indicated by the proximity of the arrow loadings in the PCA, Fig. 3). Elevation, animal disturbance, soil depth and sand content were the strongest drivers as indicated by regression analysis (Table 2). In general, large plants (greater dry weight, numerous tillers, long tillers, many generative tillers, long roots) occurred at low elevation sites which had high *P. annua* cover, deep, sandy soils and high animal disturbance (Bauer Bay Beach, Tractor Rock). Medium-sized plants were located at sites with high soil water content and low pH, low animal disturbance and low sand content (Bauer Bay Slope, Doctor's Track). Small plants (low dry weight, few tillers, short tillers, few generative tillers, short roots) were associated with high elevation, high soil magnesium content, low *P. annua* cover, low animal disturbance, shallow slope, low sand content, low pH and shallow soil (Lower Boot Hill, Upper Boot Hill) (Fig. 3, Table 2).

Community structure

Species richness and Simpson diversity varied between the sites (Table 3). The three low altitude sites (Bauer Bay Beach, Tractor Rock, The Nuggets) had the lowest mean species richness per sample (< 3.2). The high altitude site Upper Boot Hill had similar species richness (3.9) while Lower Boot Hill, also at high altitude, had the greatest species richness (8.0). The other sites showed intermediate species richness. Two of the low altitude sites, Tractor Rock and The Nuggets, had the lowest mean Simpson index (< 0.4) whilst the high altitude sites Lower Boot Hill and Mount Power had the greatest Simpson index (0.9). Bauer Bay Beach and the mid altitude sites had an intermediate Simpson index.

In general, sites which had the lowest species richness and lowest Simpson index (Bauer Bay Beach, Tractor Rock, The Nuggets) were very strongly associated with high animal disturbance and high *P. annua* cover. They were also associated, but less strongly, with low soil water content, low potassium and low exposure (indicated by the closeness of the arrow loadings in the PCA, Fig. 4. Conversely, sites with increased species richness and Simpson index (all other sites) were found at higher elevations with increased exposure, greater soil water content and soil potassium, low animal disturbance and low *P. annua* cover. Regression analysis revealed that *P. annua* cover was the strongest driver of the variation in species richness ($P < 0.01$, $R^2 = 0.61$) and Simpson index ($P < 0.01$, $R^2 = 0.89$), with high *P. annua* cover associated with lower species richness and Simpson index (Table 4).

Discussion

Longevity

Previous researchers have suggested that *P. annua* populations can be annual in the subantarctic (Walton 1975, Bergstrom et al. 1997, Frenot et al. 2005) but we found *P. annua* plants to be perennial on Macquarie Island. Most plants in the subantarctic, both native and non-natives, are perennial (Convey et al. 2006a). Perennial plants are better suited to the harsh Antarctic climate due to greater investment in survival mechanisms allowing them to withstand the harsh winter and quickly regrow tillers and roots when the short growing season begins (Ellis et al. 1971, Frenot et al. 2001, Convey et al. 2006b). This provides an advantage over annual species which need to quickly germinate, emerge and grow to avoid competition from established perennial species (Billings & Mooney 1968, Billings 1974), particularly if the level of disturbance is not maintained. The perennial nature of *P. annua* enables it to compete with other plant species on Macquarie Island. It would be difficult for *P. annua* to establish each season without continuous disturbance as it would be outcompeted by the longer-lived, taller native species.

Morphology

Here we show that *P. annua* morphology is highly variable across very small spatial scales on Macquarie Island. Variability within a population can be attributed to both phenotypic plasticity and genetic variation. Given few individuals of *P. annua* were introduced to Macquarie Island, it has been present for only 140 years, it is widely distributed, it is wind-pollinated and Macquarie Island is one of the windiest environments in the world, it is unlikely that population partitioning is occurring and genetic variance is responsible for the variability. Indeed phenotypic plasticity is responsible for the morphological variability of *P. annua* elsewhere in temperate regions (Beard 1996, Vargas & Turgeon 2004) as well as the subantarctic and Antarctic (Galera et al. 2015, Molina-Montenegro et al. 2016). We attributed the morphological variability of *P. annua* across Macquarie Island to environmental gradients, with greater intra-population variability at low altitude sites.

Altitude is the most important driver of morphological variation of *P. annua* on Macquarie Island. At the low altitude coastal sites, the warmer, more protected conditions enhance plant growth. Conversely, at high altitude sites plant growth is restricted by the strong winds and colder temperatures (Hautier et al. 2009). Animal-derived disturbance and associated nutrient enrichment are important drivers of *P. annua* abundance in the subantarctic (Walton 1975, Ryan et al. 2003, Haussmann et al. 2013). Here we have identified that animal-derived disturbance is also a key correlate of *P. annua* morphological variation on Macquarie Island. Animal-derived nutrient enrichment occurs at coastal sites but is largely absent at high altitude sites. We did not identify nutrients as a key driver of growth, despite the presence of large plants at sites with high animal-derived distrubance and high nutrient inputs. Most likely, nutrients are leached to deeper soil depths than those sampled yet the constant supply of nutrients allows accessibility by plants (Lehmann & Schroth 2003). Elsewhere on subantarctic Kerguelen, variation of *P. annua* plants between sites was attributed to differences in soils, with a more vigorous form growing at a site with greater fine particle content which was associated with higher nutrients (Frenot et al. 1999). Here we show that on Macquarie Island soil characteristics such as depth, pH and water content are also associated with morphological variation of *P. annua*.

Previous research shows that *P. annua* on Macquarie Island can produce very dense soil seed banks up to 100 000 seeds m^{-2} which can persist for several years (Williams et al. 2016) and that this process is driven by *P. annua* cover and soil wetness and to a lesser degree, elevation, animal disturbance and soil depth. These dense seed banks are likely to enhance the persistence of the species on the island. Here we show that for *P. annua* plants biomass allocation was consistent across all sites, despite environmental differences. Plants allocated considerably more to root biomass than to reproductive structures as has been found on Kerguelen (Frenot et al. 1997). This is a common survival strategy for plants growing in colder, harsher conditions (Hautier et al. 2009) and it may also enable them to quickly recover from the winter (Scott & Billings 1964). On Kerguelen, *P. annua* also had very little reproductive biomass (8%), with the majority of the biomass composed of tillers (53%) rather than roots (such as on Macquarie). This may be due to the contrast in soils between the two islands with shallow, infertile glacial soils restricting root growth on Kerguelen (Frenot et al. 1997). On Macquarie Island, *P. annua*'s high biomass allocation to roots is likely to aid persistence in established perennial native flora and may enable plants to access nutrients at greater depths (Ericsson 1995).

Community structure

Vegetation assemblages throughout the subantarctic are driven by environmental variables such as moisture, exposure, soil material, salt spray, altitude, slope, rock cover, and particularly nutrient enrichment and disturbance by wildlife (Smith & Steenkamp 2001; Ryan et al. 2003; Frenot et al. 2005; Scott & Kirkpatrick 2005). On Macquarie Island, environmental and soil characteristics also drive plant community diversity. However, where *P. annua* occurs at high densities, the diversity and abundance of native species is lower compared to areas with lower *P. annua* cover. This contrasts with much of the previous research regarding the competitive ability of *P. annua* in the subantarctic. Long term monitoring studies from Macquarie Island suggest that in established native vegetation, with no on-going disturbance, native species outcompete *P. annua* over time (Scott & Kirkpatrick 2008, 2013; Whinam et al. 2014). Other authors suggest that *P. annua* does not directly compete with native species, but rather colonises the open ground created by disturbance before other species can establish (Frenot et al. 2001; Scott & Kirkpatrick 2005; Olech & Chwedorzewska 2011). With the eradication of invasive rabbits from Macquarie Island in 2014 and the cessation of the associated vegetation grazing, community structure will greatly change. We show that on Macquarie Island at low altitiudes where there is high animal disturbance, *P. annua* occurs at very high densities and may be supressing the diversity of native vegetation.

Application to ecological theory

Community ecology theory is an important framework that can be used to understand biological invasions. The concept of niches and niche opportunity presented in Shea and Chesson (2002) can be applied to this study of *P.*

annua on Macquarie Island. The two defining aspects of an organism's niche are 1) how a species responds to resources, natural enemies and the physical environment (which determines its ability to invade) and 2) the effects of the species on the invaded locality (Chesson 2000). The effects and responses of the native species in the invaded community determines whether the community provides opportunities for invasion ('niche opportunities') (Shea & Chesson 2002). On Macquarie Island, resource opportunities exist for *P. annua*. At coastal sites, nitrogen is in abundance and disturbed ground is plentiful. *Poa annua* has a high tolerance of elevated nutrient levels and requires disturbed ground to establish (Scott & Kirkpatrick 1994, 2013, Frenot et al. 1997, 1998, Hausmann et al. 2013), providing the species with a distinct advantage over native species that do not tolerate these conditions as well. Following the eradication of rabbits on Macquarie Island and the release of grazing pressure on *P. annua* (Terauds et al. 2014), *P. annua* no longer has any natural enemies on the island, allowing it to grow and flourish unrestrictedly. In response to the physical environment on Macquarie Island, *P. annua* has a perennial lifespan, providing a greater advantage in the cold, harsh conditions than if it was an annual as elsewhere in the world. *Poa annua* also responds differently to the physical environment across small scales on Macquarie Island. The largest plants grow at low altitudes where there is high wildlife disturbance and deep, sandy soils. At these sites, diversity of native species is low. At the more exposed high altitude sites with no animal disturbance and shallow, gravelly soils, *P. annua* plants are small and the diversity of native species is greater. Thus at low altitudes on Macquarie Island, the community provides greater opportunities for invasion than at high altitude, helping to explain the variation in morphology of *P. annua* across environmental gradients on Macquarie Island.

Conclusion

Poa annua has many traits which make it a successful invader within the subantarctic – a high tolerance of animal-derived disturbance, grazing by introduced mammals and a high reproductive output. Here we quantified the ecological drivers of *P. annua* and its persistence on Macquarie Island. We now know it is perennial and highly plastic in its morphology, and this variability appears to be in response to fine-scale changes in soil and environmental factors. The species allocates most of its biomass to persistence, but is also able to maintain high reproductive output on a per area basis, as indicated by high seed bank density at certain sites. These traits are likely to lead to increased competition with the perennial native flora of Macquarie Island. These newly quantified traits give us a better understanding of *P. annua* as the most widespread and abundant non-native species on Macquarie Island and help explain how it is a successful invader in the subantarctic. The niche opportunity theory helps to explain the distribution and morphological variation of *P. annua* on Macquarie Island, whereby the specific environmental variables and vegetation communities at low elevations provides a greater opportunity for invasion compared to high elevation areas.

Acknowledgements

We thank the Tasmanian Parks and Wildlife Service for granting us access to Macquarie Island, the Australian Antarctic Division for logistical support and Luis Rodriguez Pertierra for field support.

Funding: This work was supported by the Australian Antarctic Science Foundation (project AAS 4158) and the University of New England (Australian Postgraduate Award).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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Figure captions

Fig. 1. Distribution of *Poa annua* on the main sub-Antarctic islands and the Antarctic Peninsula, as indicated by grey circles. Modified from Australian Antarctic Data Centre 2005.

Fig. 2. Number of tagged *Poa annua* plants remaining at Tractor Rock (◇); Bauer Bay Beach (○); Bauer Bay Slope (△); Doctor's Track (□); Lower Boot Hill (×) and Upper Boot Hill (+) after 0 (February 2013), 11 (December 2013), 14 (March 2014) and 27 (April 2015) months.

Fig. 3. Principal component analysis of *Poa annua* cover (Poa); plant morphological traits (dry weight -Wei; number of tillers - Til; Tiller length - Til.l; Number of reproductive tillers - R.til; Root length - R.len) and environmental characteristics (Animal disturbance - Dis; Elevation - Ele; Soil magnesium - Mag; Slope - Slo; Soil depth - S.Dep; Soil pH - pH; Soil sand content - San; and Water content – Whc) according to the first two components. Study sites: low elevation - Tractor Rock (◇), Bauer Bay Beach (○); mid elevation - Doctor's Track (□), Bauer Bay Slope (△); high elevation - Lower Boot Hill (×);and Upper Boot Hill (+).

Fig. 4. Principal component analysis of *Poa annua* cover (Poa), community indices (species richness - Ric; Simpson's diversity – SiD) and various environmental characteristics (Animal disturbance - Dis; Elevation - Ele; Exposure - Exp; Potassium - Pot; Sulphur - Sul; Water content – Whc) according to the first two components. Study sites: low elevation - Tractor Rock (◇), The Nuggets (▲), Bauer Bay Beach (○); mid elevation - Sawyer Creek (■), Doctor's Track (□), Bauer Bay Slope (△); high elevation - Lower Boot Hill (×); Mt Power (●);and Upper Boot Hill (+).

Tables

Table 1. Morphological characteristics (mean ± 95% confidence intervals) of plants at study sites; significant differences (*P* < 0.05) are between sites and shown by different letters, * Galera et al. (2015).

Site	Tractor Rock	Bauer Bay Beach	Doctor's Track	Bauer Bay Slope	Lower Boot Hill	Upper Boot Hill	Antarctica*
Total dry weight (g)	19.2 ± 2.8^{a}	10.9 ± 2.8^{b}	12.1 ± 2.8^{b}	4.9 ± 2.8^{c}	1.8 ± 2.8^{c}	1.1 ± 2.8^{c}	3.0 ± 1.0
% shoots	22.5 ± 6.3^{bc}	31.6 ± 6.3^{ab}	18.3 ± 6.3^{c}	31.2 ± 6.3^{ab}	20.3 ± 6.3^{bc}	23.6 ± 6.3^{bc}	
% roots	75.8 ± 7.0^{ab}	60.8 ± 7.0^{abc}	80.0 ± 7.0^{a}	65.7 ± 7.0^{abc}	74.3 ± 7.0^{abc}	74.0 ± 7.0^{c}	
% reproductive	1.7 ± 3.3^{a}	7.6 ± 3.3^{a}	1.6 ± 3.3^{a}	3.1 ± 3.3^{a}	5.4 ± 3.3^{a}	2.4 ± 3.3^{a}	
No. tillers	85.4 ± 9.8^{a}	58.0 ± 9.8^{b}	46.6 ± 9.8^{b}	42.3 ± 9.8^{b}	15.3 ± 9.8^{c}	12.5 ± 9.8^{c}	7.6 ± 6.7
Tiller length (cm)	21.4 ± 4.1^{ab}	28.7 ± 4.1^{a}	14.7 ± 4.1^{bc}	19.2 ± 4.1^{b}	9.1 ± 4.1^{cd}	3.7 ± 4.1^{d}	
No. reproductive tillers	28.0 ± 4.0^{a}	23.9 ± 4.0^{a}	12.2 ± 4.0^{b}	8.6 ± 4.0^{bc}	5.1 ± 4.0^{bc}	3.2 ± 4.0^{c}	4.0 ± 3.3
% of total tillers	32.8	41.2	26.0	20.3	32.9	25.2	
Root length (cm)	21.8 ± 1.7^{a}	15.1 ± 1.7^{b}	14.8 ± 1.7^{b}	13.0 ± 1.7^{bc}	11.0 ± 1.7^{c}	13.0 ± 1.7^{bc}	

Table 2. *P* and R^2 values of linear regressions of *Poa annua* morphological traits against *P. annua* cover and environmental and soil characteristics; symbols in brackets indicate the direction of the relationship.

Statistic	Degrees of freedom	*Poa annua* cover		Total dry weight		No. tillers		Tiller length		No. reproductive tillers		Root length	
				P	R^2	P	R^2	P	R^2	P	R^2	P	R^2
Poa annua cover				ns	-	0.028 (+)	0.68	0.015 (+)	0.75	0.002 (+)	0.92	ns	-
Animal disturbance	1, 118	0.002 (+)	0.92	ns	-	ns	-	ns	-	0.004	0.87	ns	-
Aspect	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Elevation	1, 110	0.011 (-)	0.80	0.020 (-)	0.72	0.004 (-)	0.87	0.007 (-)	0.83	0.007 (-)	0.83	ns	-
Exposure	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Soil													
Calcium	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Carbon	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Depth	1, 117	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Electrical conductivity	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Magnesium	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Nitrogen	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
pH	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Phosphorus	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Potassium	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Sand content	1, 118	0.019 (+)	0.731	ns	-	ns	-	ns	-	0.023 (+)	0.70	ns	-
Sodium	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Sulphur	1, 118	ns	-	ns	-	ns	-	ns	-	ns	-	ns	-
Water content	1, 118	ns	-	0.010 (-)	0.80	0.003 (-)	0.90	ns	-	0.030 (-)	0.66	0.028 (-)	0.67

Table 3. Mean species richness per sample and mean Simpson index (± 95% confidence intervals) for each site. Different letters indicate significant differences between sites ($P \leq 0.05$), determined by separating means using 95% confidence intervals using the 'effect' function in the effects package of R.

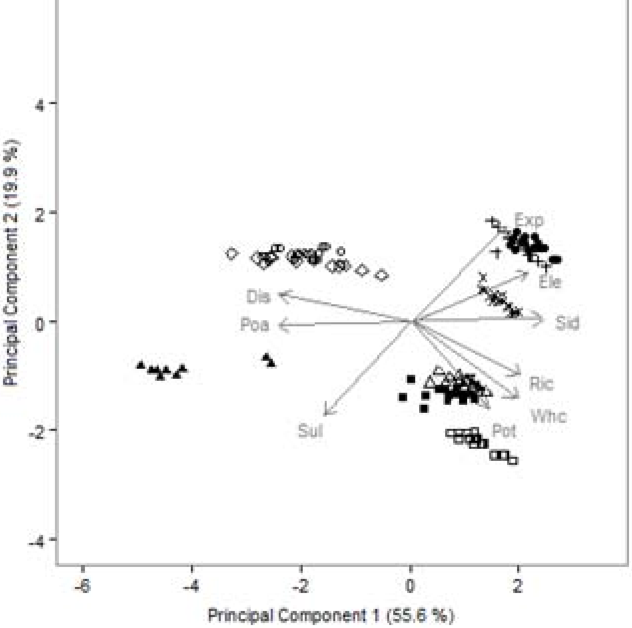
Site	**S**	**1-D**
Tractor Rock	2.5 ± 0.6^{de}	0.3 ± 0.1^{c}
The Nuggets	1.5 ± 0.6^{e}	0.2 ± 0.1^{d}
Bauer Bay Beach	3.2 ± 0.6^{cd}	0.6 ± 0.1^{b}
Sawyer Creek	6.0 ± 0.6^{b}	0.7 ± 0.1^{b}
Doctor's Track	7.9 ± 0.6^{a}	0.8 ± 0.1^{a}
Bauer Bay Slope	6.3 ± 0.6^{b}	0.8 ± 0.1^{a}
Lower Boot Hill	8.0 ± 0.6^{a}	0.9 ± 0.1^{a}
Upper Boot Hill	3.9 ± 0.6^{c}	Not calculated
Mount Power	6.4 ± 0.6^{b}	0.9 ± 0.1^{a}

Table 4. Linear regressions of community indices against *Poa annua* cover and environmental and soil characteristics; symbols indicate the direction of the relationship.

Variables	Degrees of Freedom	Species richness		Simpson's diversity	
		P	R^2	*P*	R^2
Poa annua cover	1, 149	< 0.01	0.61 (-)	< 0.01	0.89 (-)
Animal disturbance	1, 149	< 0.01	0.47 (-)	< 0.01	0.48 (-)
Aspect	1, 149	ns	-	ns	-
Elevation	1, 149	< 0.01	0.08 (+)	< 0.01	0.44 (+)
Exposure	1, 149	< 0.05	0.03 (+)	< 0.01	0.32 (+)
Slope	1, 149	< 0.01	0.23 (-)	ns	-
Soil					
Calcium	1, 149	ns	-	< 0.01	0.07 (+)
Carbon	1, 149	ns	-	< 0.01	0.09 (+)
Depth		ns	-	< 0.01	0.20 (-)
Electrical conductivity	1, 149	< 0.01	0.09 (+)	< 0.05	0.03 (+)
Magnesium	1, 149	ns	-	< 0.01	0.11 (+)
Nitrogen	1, 149	ns	-	< 0.01	0.09 (-)
pH	1, 149	< 0.01	0.05 (-)	ns	-
Phosphorus	1, 149	< 0.01	0.15 (+)	< 0.05	0.03 (+)
Potassium	1, 149	< 0.01	0.20 (+)	< 0.01	0.24 (+)
Sand content	1, 109	< 0.01	0.32 (-)	< 0.01	0.39 (-)
Sodium	1, 149	ns	-	ns	-
Sulphur	1, 149	< 0.01	0.08 (-)	< 0.01	0.29 (-)
Water content	1, 149	< 0.01	0.54 (+)	< 0.01	0.28 (+)

Appendix 1: Environmental and soil characteristics of study sites on Macquarie Island, DL = detection limit.

Characteristic	Tractor Rock	The Nuggets	Bauer Bay Beach	Sawyer Creek	Doctor's Track	Bauer Bay Slope	Lower Boot Hill	Upper Boot Hill	Mount Power
Latitude °	-54.5106	-54.5281	-54.5548	-54.6417	-54.5061	-54.5481	-54.5192	-54.5204	-54.5428
Longitude °	158.9326	158.9313	158.8786	158.9003	158.9278	158.8803	158.9152	158.9151	158.9108
Elevation (m)	2	23	24	109	115	136	258	278	338
Aspect (°)	90 (E)	45 (NE)	225 (SW)	260 (W)	45 (NE)	135 (SE)	45 (NE)	90 (E)	45 (NE)
Animal disturbance	2	3	3	1	1	1	1	1	1
Exposure	2	1	2	2	1.5	2	2.5	3	3
Average soil depth (cm)	> 85	> 85	83	> 85	> 85	63	56	9	> 85
SOIL									
Carbon (%)	0.2 ± 0.0	61.2 ± 0.8	0.3 ± 0.1	48.2 ± 0.1	44.0 ± 1.0	13.2 ± 0.2	7.6 ± 0.4	0.5 ± 0.0	9.6 ± 0.4
Nitrogen (%)	< DL	5.1 ± 1.5	< DL	4.2 ± 0.0	3.7 ± 1.0	1.2 ± 0.0	0.6 ± 0.0	< DL	0.6 ± 0.0
Phosphorus (μg g^{-1})	45.3 ± 1.5	8.8 ± 0.2	90.7 ± 17.6	154.5 ± 23.7	8151.8 ± 274.5	244.0 ± 10.0	48.1 ± 32.2	24.7 ± 0.6	39.6 ± 25.9
Sulphur (μg g^{-1})	16.2 ± 0.9	123.2 ± 2.1	9.8 ± 0.2	50.5 ± 1.0	43.5 ± 1.1	49.8 ± 1.8	6.5 ± 0.1	2.4 ± 0.1	4.4 ± 0.1
Exchangeable potassium ($cmol^+ kg^{-1}$)	0.3 ± 0.0	0.3	0.4 ± 0.2	0.9 ± 0.2	1.4 ± 0.0	1.0 ± 0.1	0.4 ± 0.1	1.0 ± 0.2	0.4 ± 0.2
Exchangeable calcium ($cmol^+ kg^{-1}$)	2.6 ± 0.0	8.1	1.9 ± 0.1	7.8 ± 0.2	8.7 ± 0.1	18.6 ± 0.3	2.9 ± 0.0	17.9 ± 0.2	2.6 ± 0.1
Exchangeable magnesium ($cmol^+ kg^{-1}$)	1.4 ± 0.0	7.6	16.4 ± 0.1	9.8 ± 0.2	10.6 ± 0.5	16.4 ± 0.3	4.3 ± 0.1	29.1 ± 0.7	2.5 ± 0.1
Exchangeable sodium ($cmol^+ kg^{-1}$)	0.6 ± 0.0	2.7	2.6 ± 0.2	2.9 ± 0.0	3.0 ± 0.0	2.6 ± 0.1	0.8 ± 0.0	2.0 ± 0.2	1.0 ± 0.2
pH (1:5 H_20)	6.9 ± 1.7	4.8 ± 0.3	8.2 ± 0.1	4.9 ± 0.3	5.1 ± 0.1	4.8 ± 0.1	5.5 ± 0.0	6.2 ± 0.0	7.6 ± 0.0
Electrical conductivity $_{(1:5)}$ (μs cm^{-1})	59.5 ± 2.1	356.3 ± 81.3	43.0 ± 1.0	482.7 ± 5.7	379.3 ± 11.8	558.7 ± 8.6	58.4 ± 2.4	55.3 ± 2.8	105.1 ± 1.1
Sand content (%)	99.3	n/a	99.1	n/a	70.5	64.1	77.0	72.5	80.9
Clay content (%)	0.2	n/a	0.3	n/a	14.8	15.8	12.9	14.1	9.8
Silt content (%)	0.5	n/a	0.6	n/a	14.7	20.1	10.1	13.4	9.3
Water content (%)	5.1 ± 0.7	88.9 ± 0.3	7.2 ± 0.5	85.7 ± 0.2	69.7 ± 5.0	64.5 ± 4.8	52.9 ± 9.0	24.7 ± 4.5	66.7 ± 2.3



Principal Component 2 (19.9 %)
Principal Component 1 (55.6 %)
4
2
0
-2
-4
-6
-4
-2
0
2
Exp
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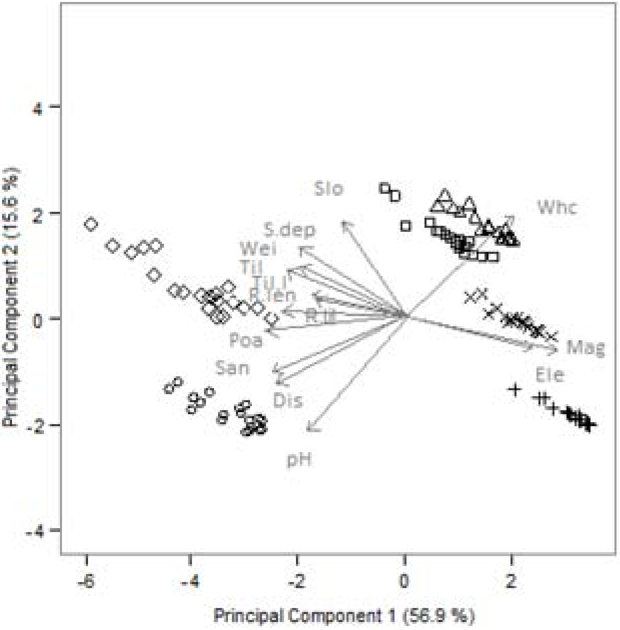

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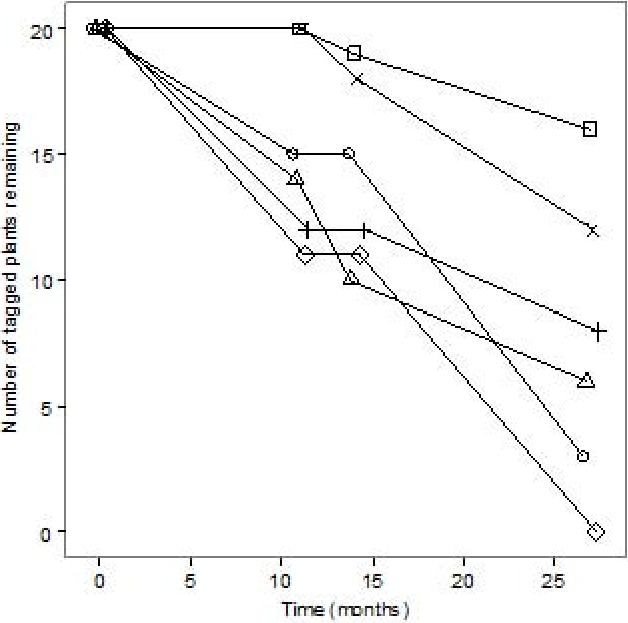
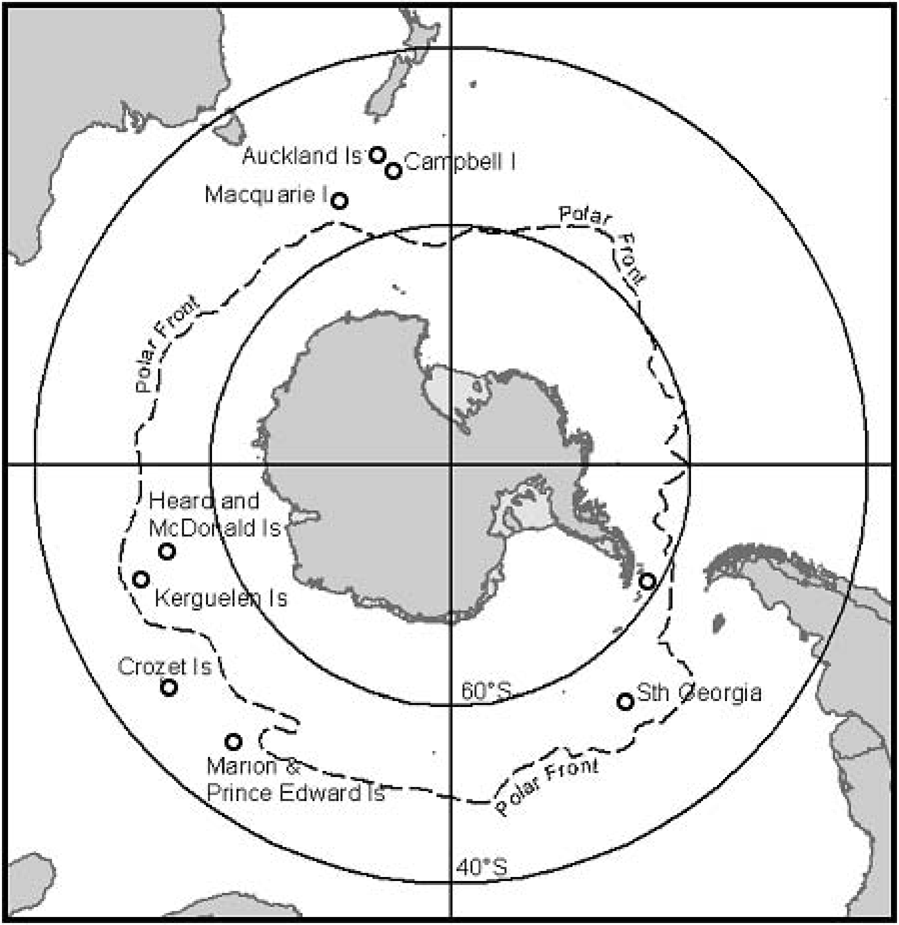
2
Principal Component 2 (15.6 %)
Principal Component 1 (56.9 %)



Number of tagged plants remaining
20
15
10
5
0
0
5
10
15
20
25
Time (months)



Auckland Is
Campbell I
Macquarie I
Polar Front
Polar Front
Heard and McDonald Is
Kerguelen Is
Crozet Is
Marion & Prince Edward Is
60°S
Sth Georgia
Polar Front
40°S