Chapter 1

General Introduction

Plate 1 *Poa annua* growing around a penguin colony on Macquarie Island

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General introduction

The sub-Antarctic environment

Terrestrial Antarctica remains one of the most pristine environments on earth (Chown et al. 2012), less impacted by humans than other parts of the world (Chown & Lee 2009). However, alien species already pose a significant threat to the region and there is concern that climate change and increasing visitation may lead to environmental degradation and increased threat by alien species (Frenot et al. 2005; Chown et al. 2012).

The sub-Antarctic islands are an important component of the Antarctic region along with continental Antarctica and maritime Antarctica. The sub-Antarctic islands form a ring around the Antarctic Polar Frontal Zone between 46 and 54 °S in the Southern Ocean. Island groups include Crozet, Heard, Kerguelen, Macquarie, Prince Edward, McDonald, and South Georgia (Figure 1.1) (Chown & Lee 2009). These islands are distinguished from the more temperate islands of The Falklands, New Zealand Shelf Islands and Tristan de Cunha, Gough, St Paul and Amsterdam which have woody vegetation and a milder climate and are often termed cool temperate (Convey 2007). Together these two groups of islands form the Southern Ocean Islands group (Chown & Lee 2009).

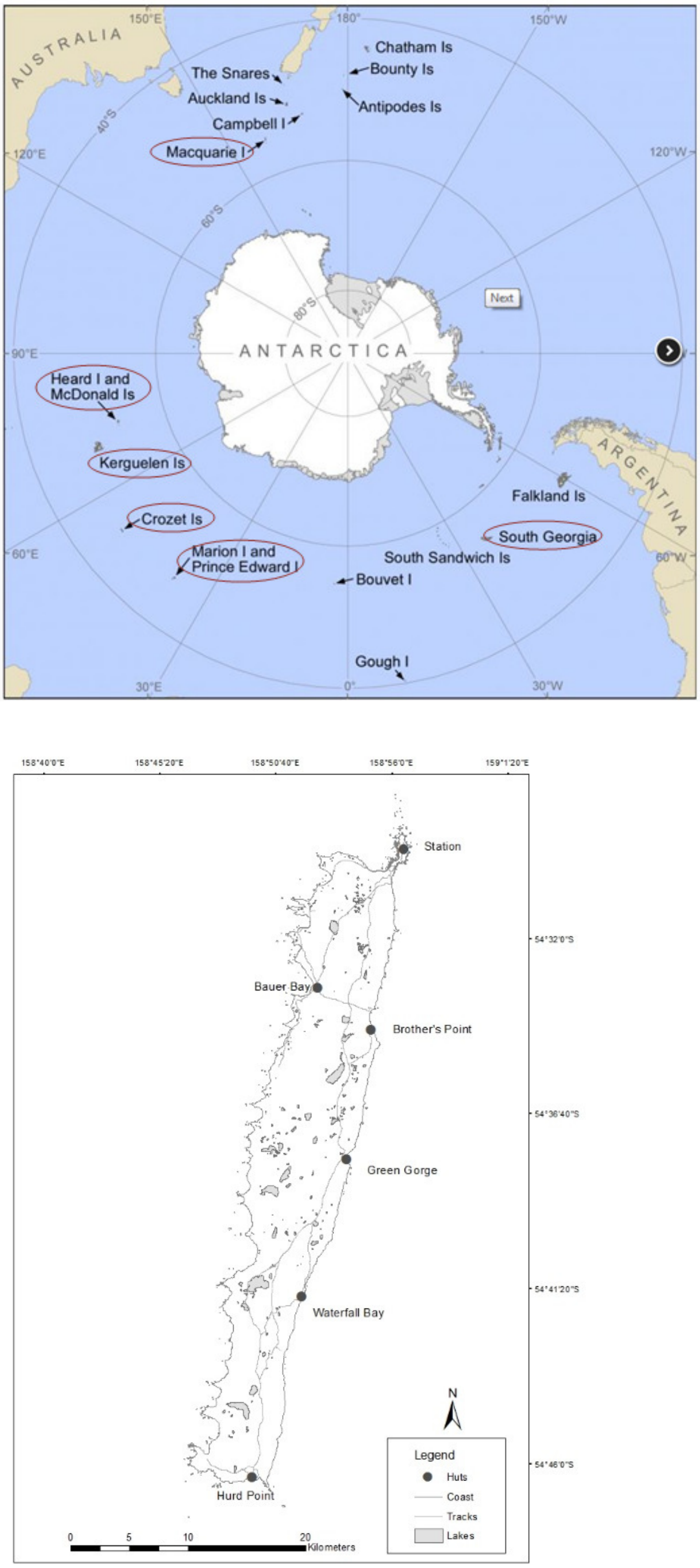

Figure 1.1 (Top) Southern Ocean Islands, including the sub-Antarctic islands ringed in red (Australian Antarctic Data Centre 2011); (bottom) Macquarie Island showing the location of the station and field huts

The sub-Antarctic islands are all strongly influenced by the surrounding ocean and as such have a cool but relatively stable annual temperature (-2°C- 25°C in summer, -10°C-15°C in winter), strong, predominantly westerly winds (>29 km h^{-1}) and high annual precipitation (600-2 400 mm) (Bergstrom & Selkirk 1999; Convey 2007; Pendlebury & Barnes-Keoghan 2007). Temperature is rising across many islands and some are becoming drier (Adamson et al. 1988; Smith et al. 1990; Bergstrom & Selkirk 1999). Mean annual temperatures have increased by up to 1°C on Marion, Macquarie and Kerguelen since the 1940s and annual precipitation has declined by up to 500 mm on Marion and Kerguelen (Bergstrom & Selkirk 1999).

The biota of the sub-Antarctic islands is generally species poor, with representatives from a restricted number of families and low endemism, attributable to the island's remoteness and small size (Smith et al. 1987; Chown et al. 1998; Fountain et al. 1999; Convey et al. 2006). Indigenous land mammals are absent, only a few species of land birds are present and insects are limited to only a few groups (Bergstrom & Selkirk 1999). Trees and shrubs are absent (Selkirk et al. 1990) and the islands are covered in tundra-like vegetation ranging from feldmarks dominated by cushion-forming angiosperms and mosses; to lush closed grassland and herbfield consisting of tussock grasses, graminoids and herbs; and mires of a mix of herbs, sedges and bryophytes (Bergstrom & Selkirk 1999). Across the sub-Antarctic there are 60 species of flowering plants, 16 ferns and club mosses, 250 mosses, 85 liverworts, 250 lichens and 70 macro-fungi (Convey 2007).

The sub-Antarctic islands are some of the least inhabited and most protected ecosystems on the planet and remain as some of the last true wilderness areas in the world (Chown et al. 2001; Whinam et al. 2005; de Villiers et al. 2006). The islands are of considerable biological and conservation value (Smith et al. 1987; Chown et al. 1998, 2001, 2008). They represent unique ecosystems, have a number of endemic or rare species, and support large wildlife concentrations (Dingwall 1995; Chown et al. 1998; Bergstrom & Selkirk 1999). As a result, the conservation value of the sub-Antarctic islands is nationally and internationally recognised (de Villiers et al. 2006; Chown & Lee 2009). Several islands are listed as World Heritage (Chown et al. 2008) and all are managed primarily for natural conservation (Kirkpatrick 2009).

Macquarie Island is an Australian sub-Antarctic island located in the Southern Ocean at 54°30'S, 158°57'E, 1 500 km southeast of Tasmania and just north of the Antarctic Convergence (Shaw et al. 2005). The climate is relatively uniform due to the moderating effects of the ocean (Selkirk et al. 1990). It is cool wet and windy with mean annual temperatures ranging between 4 °C and 6 °C (Australian Bureaeu of Meteorology 2016), mean annual precipitation around 900 mm (Pendlebury & Barnes-Keoghan 2007) generally falling as mist or light rain, (Selkirk et al. 1990) and predominantly westerly winds of 33 km h^{-1} on average and which frequently reach gale force (63-87 km h^{-1}) (Fountain et al. 1999). Light levels are low due to almost constant cloud cover, with a mean daily average of 2.2 hours of sunlight (Copson 1984).

Macquarie island is 35 km long by 5.5 km wide with an area of 12 700 ha (Figure 1.1). It formed 600-700 000 years ago when a portion of the submarine Macquarie Ridge on the boundary of the Pacific and Australasian plates rose above sea level (Adamson et al. 1996). The island comprises an elongated, undulating plateau oriented north-south, dotted with many lakes, tarns and streams and surrounded by escarpment or steep coastal slopes. Average elevation is 200-300 m above sea level with several peaks over 400 m, the highest Mt Hamilton at 433 m. A low lying isthmus, where the research station is located, joins Wireless Hill in the north to the rest of the island (Figure 1.2). The west coast is more rugged than the east coast, receiving the brunt of the westerly winds and ocean swell (Selkirk et al. 1990). The island is totally oceanic in origin, all rocks having formed on or beneath the ocean floor during seafloor spreading (Selkirk et al. 1990). Soils consist of highmoor peat, fen peat, bog peat and dry tundra, with the type formed largely dependent on wind velocities and the absence/presence of a water table and the nature of the ground water (Taylor 1955).

Figure 1.2 Biogeographical features on Macquarie Island. (Left-right): Isthmus and North Head at the northern end of the island; the plateau; east coast of the island; feldmark

The flora of Macquarie Island is relatively species poor as it developed in isolation from other land masses. The geographical location and harsh climate favours development of dense, herbaceous, peat forming vegetation. Trees and shrubs absent (Selkirk et al. 1990). Only 42 indigenous vascular plant species are present, including four endemics (de Salas & Baker 2015). Megaherbs and tussock grasses dominate tall coastal and slope vegetation; short grasses, herbs and sedges predominate mid-altitude; and bryophytes and cushion plants dominate high altitudes (Terauds *et al.* 2014). Non-vascular plants are diverse with over 85 moss, 50 hepatics, 150 lichen, at least 127 algae and over 200 fungi (Selkirk et al. 1990). Six distinct vegetation communities are found: tall tussock grassland, short grassland, herbfield, mire, feldmark, and fernbrake (Figure 1.3, Table 1.1) (Taylor 1955; Selkirk et al. 1990).

Figure 1.3 Major vegetation communities on Macquarie Island. (Left-right): tall tussock grassland; short grassland; herbfield; mire; feldmark; fernbrake

Table 1.1 Vegetation communities on Macquarie Island

Community	Dominant species	Location
Tall tussock grassland	Poa foliosa, megaherb Stilbocarpa polaris, fern Polystichum vestitum	Better drained sections of coastal terraces, most of the coastal slopes, sheltered, well drained valleys
Short grassland	Shorter grasses Agrostis magellanica, Luzula crinita, Uncinia spp, Deschampsia chapmanii, Festuca contracta	Raised beach terraces and plateau where water table and wind exposure is moderate to high
Herbfield	Megaherbs Pleurophyllum hookerii, S. polaris, fern Blechnum penna-marina, herb Aceana magellanica	Raised coastal terraces, flats, valleys, slopes to 380 m, with moderate wind velocity
Mire	Juncus scheuchzerioides, Ranunculus crassipes, Montia fontana, Cardamine corymbosa, many bryophytes	Where water table is at/slightly above ground surface on valley floors, plateau, raised coastal terraces
Feldmark	Cushion plant *Azorella macquariensis,* lichens, bryophytes	Areas subject to high wind velocities
Fernbrake	Fern P. vestitum	Sheltered valleys

Macquarie Island provides important habitat for penguins, albatross, petrels and seals. There are no native land mammals but over 90 species of birds have been recorded and six species of seal are common (Parks and Wildlife Service 2006). Over 300 species of invertebrates are present (Greenslade 2006).

Macquarie Island is of high conservation value due to its outstanding natural values and unique geology. The island, islets and sea stacks are a Nature Reserve managed by Tasmanian Parks and Wildlife, the highest reservation status under state government, and its waters are protected in a Marine Park. It is a Biosphere Reserve, Natural Estate Property and has critical habitat values under the Environmental Protection and Biodiversity Conservation Act 1999. It is inscribed on the International Union for the Conservation of Nature World Heritage List, the highest conservation status possible (Carmichael 2007; Chown et al. 2008). Visitation is highly regulated (de Villiers et al. 2006)

Biological invasions in the sub-Antarctic

Weeds (here after referred to as invasive or non-native species) are defined as plants growing where they are not wanted (Monaco et al. 2002). They are found in almost all environments (Zimdahl 2013) and affect crop and animal production, reduce visibility on roadsides, create a fire hazard; affect waterways, create problems in recreational, industrial and environmental areas (Monaco et al. 2002) and displace native species (Natural Resource Management Ministerial Council 2007). They have certain biological characteristics that allow them to be successful (Sindel 2000; Monaco et al. 2002). These include high fecundity, quick growth, reproduction and spread, dormant wind-blown seed which is easily dispersed, self-compatibility, non-specialised pollination, dual modes of reproduction, environmental plasticity, tolerance of a range of environmental conditions, adaptations to grazing and resistance to control (Rejmánek & Richardson 1996; Sindel 2000; Pyšek & Richardson 2008; Moravcova et al. 2015).

Although the sub-Antarctic islands are some of the last ecosystems in the world to be altered by humans (Bergstrom & Selkirk 1999), they are no longer pristine (Pendlebury & Barnes-Keoghan 2007). Since the 19th Century the uncontrolled exploitation of seals, whales and penguins and past and present fisheries has impacted on the marine environment (Convey 2007). The early sealing, oiling and whaling activities together with scientific and logistical operations have introduced numerous alien species (Smith et al. 1987; Frenot et al. 2005; Whinam et al. 2005; Chown & Lee 2009; Shaw et al. 2010).

A number of non-native plants have established in terrestrial Antarctica (Hughes et al. 2015), however more invasions have occurred in the sub-Antarctic where over 100 non-native vascular plant species have established (Frenot et al. 2005). Most of these have limited impact due to restricted distributions (Frenot et al. 2005, Visser et al. 2010) but some threaten sub-Antarctic ecosystems (Bergstrom & Smith 1990, Gremmen et al. 1998, Frenot et al. 2005, le Roux et al. 2013). The sub-Antarctic islands are particularly at risk from invasive species (Convey et al. 2006; Chown & Lee 2009) as they lack representatives from some biological groups and disturbance leaves niches available to invasion (Smith et al. 1987; Lebouvier et al. 2011). Today most management plans acknowledge the risk of biological invasions and measures have been developed to prevent the introduction of non-native species (Chown et al. 2005, Whinam et al. 2005, de Villiers et al. 2006). However, invasion by alien species remains one of the most significant threats to the Antarctic region and is likely to be exacerbated by climate change and increased human activity (Frenot et al. 2005, de Villiers et al. 2006).

On Macquarie Island, deliberate and accidental introductions have occurred since its discovery (Copson & Whinam 2001). Introduced cats, weka, rabbits, rats and mice all had detrimental impacts on native flora, fauna and landscapes (Copson 1984; Shaw et al. 2005; Bryant & Shaw 2007) but have since been eradicated (Springer 2011; Terauds et al. 2014).

Rabbits in particular had devastating consequences for the island. Rabbit grazing caused changes in species distribution, local and landscape scale damage including changing complex vegetation communities to grazed lawns/bare ground, selective grazing of palatable species and the loss of tall tussock vegetation which provides important habitat for nesting seabirds, invertebrates and mega herb vegetation; and prevents land slippage and erosion (Bergstrom et al. 2009; Shaw et al. 2011; Springer 2011; Scott & Kirkpatrick 2013). In 2007 an integrated rabbit and rodent eradication program was initiated resulting in complete eradication in 2014 (Terauds et al. 2014) and recovery of *P. foliosa* on coastal slopes and shifts in community composition (Shaw et al. 2011; Scott & Kirkpatrick 2013). The reduction in grazing pressure is likely to result in changes in species abundances and distribution, shifts in community composition, short-term fluctuations in the extent of exotic species and discovery of previously undetected alien species (Whinam et al. 2014).

Seven non-native vascular plants have established on Macquarie Island since European discovery (de Salas & Baker 2015). Two small clumps of *Anthroxanthum odoratum* were eradicated in 1989 (Copson & Whinam 2001). A single clump of *Rumex crispus* was recorded in December 1980 and was removed in 1996 (Copson & Whinam 2001). Single individuals of *Agrostis stolonifera* and *Agrostis capilaris* were discovered in 2014 and control initiated (Pertierra *et al.* 2016), although this has not been successful (Tasmanian Parks and Wildlife, unpublished data). Three alien species, *Cerastium fontanum, Poa annua* and

Stellaria media remain (de Salas & Baker 2015) and have been widespread for at least 35 years (Copson 1984).

Poa annua

Of the non-native plant species established in the sub-Antarctic, *P. annua* (L.) is the greatest concern due to its wide distribution and environmental impact (McGeoch et al. 2015). *Poa annua* or wintergrass is a member of the Poaceae (Mallett 2002). Originally from Europe, it is a cosmopolitan weed (Heide 2001) growing from temperate areas to alpine and polar regions, but not arid zones. It is tolerant of shade, trampling, compaction, mowing, poor soil aeration and grazing (Beard 1970; Warwick 1979). The species is highly tolerant of disturbance (Molina-Montenegro et al. 2014) and is spread by animals (Walton 1975; Leader-Williams et al. 1987; Haussmann et al. 2013). It is adapted to all soil textures but prefers fine textured, moist, fertile soils with a pH of 5.5-6.5 (Youngner 1959; Warwick 1979; Klein 2008). It has a low nutrient requirement (Klein 2008) but can also grow in nutrient enriched areas (Walton 1975). *Poa annua* thrives in human-modified habitats (i.e. paths, cultivated land) but is also found in natural disturbed areas (beaches, stream edges) (Warwick 1979; Hutchinson & Seymour 1982; Heide 2001). *Poa annua* is well-known in temperate turf grass throughout the world where its control is a constant battle (Downing et al. 1970, Wu et al. 1987, Lush 1988, Christians 2006).

Whilst *P. annua* can be generally classified as a C_3 bunch grass and winter annual (Figure 1.4) (Christians 2008), its morphology is extremely variable. The species is often classified as an annual with an erect, compact, bunched growth habit, quick flowering, dense seed formation and dormant seed; or a perennial with a prostrate growth habit, slow flowering, spreads by tillering and has no seed dormancy, although there appears to be a spectrum in variation between the two (Youngner 1959; Gibeault 1970; Beard 1996; Vargas & Turgeon 2004).

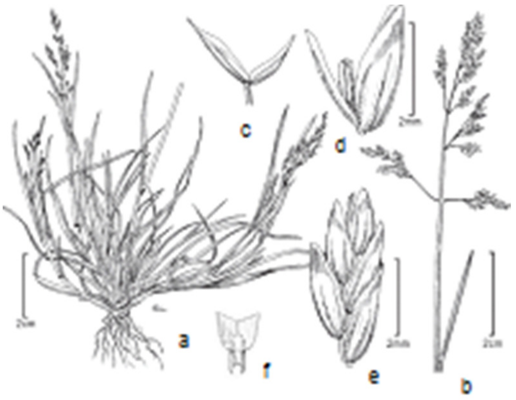

Figure 1.4 ***Poa annua*** **habit (a), inflorescence (b), glumes (c), floret, palea, anthers (d), florets (e), collar region, ligule (f) (Penn State College of Agricultural Sciences 2014)**

The lifespan of *P. annua* is generally 1-5 years depending on whether the plant is annual or perennial (Youngner 1959; Callahan & McDonald 1992; Breuninger 1993), but it can be as short as 21 days (Ryser & Urbas 2000). *Poa annua* primarily propagates by seed (Beard 1970), but can also reproduce asexually by rooting at the nodes (Warwick 1979). The large, heavy pollen and flowers close to the ground are suited to wind pollination, suggesting the species is primarily selfing with some outcrossing (Tutin 1973 in Johnson *et al.* 1993). Pollen viability is as high as 82-99 % (Ellis 1973).

Seed production of *P. annua* is high (Warwick 1979). Each caryopsis produces a single seed and a single inflorescence can produce 62 seeds on average (Law 1981). Individual plants can produce up to 22 500 seeds and seed bank densities can be up to 210 000 seeds m^{-2} in golf course turf (Mengistu 1999). Most seeds fall near the parent plant (Hutchinson & Seymour 1982; Wódkiewicz et al. 2014) with dispersal distances as low as 20 cm (Wódkiewicz et al. 2014). However, the seeds are small and light and can be easily dispersed (Fountain et al. 1999) by wind, rain, birds, shoes, clothing, stock food, bedding, machinery and animal dung (Warwick 1979; Hutchinson & Seymour 1982; Bergstrom & Selkirk 1999; Klein 2008). Humans are a key dispersal agent (Warwick 1979).

Poa annua is a weed worldwide (Warwick et al. 1980; Breuninger 1993; Dionne et al. 2001), most commonly in human modified habitats but also in disturbed natural environments (Beard 1970; Warwick 1979; Mitich 1998). It infests crops (Beard 1970, Holm et al. 1997 in Mitich 1998), contaminates grass seed (Mengistu et al. 2000), is host for a wheat fungus and contributes to hay fever (Breuninger 1993). *Poa annua* is a major problem in turf grass throughout North America, Europe and Australia (Downing et al. 1970; Wu et al. 1987; Lush

1988; Christians 2006) where it thrives in the highly irrigated, fertile, mowed habitats (Callahan & McDonald 1992), is difficult to maintain in summer and causes an unsightly appearance (Downing et al. 1970; Lush 1988). It does present benefits as an economically important forage and turf species when grown in monoculture (Johnson et al. 1993; Mitich 1998). *Poa annua* is a particularly successful weed because it is highly tolerant of grazing and disturbance, survives and reproduces in many different habitats, is extremely variable and has high fecundity (Warwick 1979, Wu et al. 1987, Callahan & McDonald 1992, Breuninger 1993, Christians 2008).

Poa annua is the most common alien species in the sub-Antarctic, found on all of the major sub-Antarctic Islands (Convey et al. 2006b) and on the Antarctic Peninsula (Chwedorzewska 2015). It occurs on South Georgia, Marion, Macquarie, Heard, Prince Edward, Crozet and Kerguelen, and the Southern Ocean Islands Auckland, Campbell, Gough and the Falklands (Du Puy et al. 1993; Frenot et al. 2001). It was unintentionally introduced to multiple sub-Antarctic islands by humans (le Roux et al. 2013) where it is spread by seabirds (Scott 1989; Bergstrom & Smith 1990) and elephant seals (Scott & Kirkpatrick 2005). Its high tolerance of grazing has enabled it to spread significantly on islands with introduced herbivores (Walton 1975, Scott & Kirkpatrick 2013). Rates of spread have been found to be as high as 1.48 km^2 per year on Marion Island (le Roux et al. 2013).

In the sub-Antarctic, *P. annua* thrives in disturbed, nutrient enriched sites around seal and penguin colonies (Walton 1975, Haussmann et al. 2013). In seal affected sites it forms dense stands, dominating the vegetation for areas up to 100 m^2 but occurs singly or in small clumps around seabird colonies, or forms narrow fringe around penguin colonies (Ryan et al. 2003). It is also a coloniser of the open stony ground of glacial moraines (Walton 1975). It spreads into native communities and displaces native species in the sub-Antarctic (Frenot et al. 2001), and competes with vascular plants native to the Antarctic Peninsula (Molina-Montenegro et al. 2012). The distribution of *P. annua* across the sub-Antarctic and Antarctica continues to increase and as with other alien species, it is predicted to further widen its range and have a greater competitive ability with future climate change (Lewis Smith 1996, Chown et al. 2012, le Roux et al. 2013, Molina-Montenegro et al. 2015, 2016). Despite this, very little is known about the biology and ecology of this highly variable plant in the sub-Antarctic.

On Macquarie Island, *P. annua* is the most common and widespread non-native plant and present in all vegetation communities (Copson 1984). It was likely introduced accidentally by sealers in packing material in the 1880s (Taylor 1955). On Macquarie Island it grows in dry to wet peat, free water, sand, gravel and rock flour (Taylor 1955) but primarily inhabits disturbed or grazed areas, especially in bare ground exposed by landslips, walking tracks and around elephant seal wallows and penguin colonies (Taylor 1955; Copson 1984; Scott & Kirkpatrick 1994; Copson & Whinam 2001) (Figure 1.5, 1.6). Its distribution is limited by high winds and taller vegetation (Taylor 1955).

Figure 1.5 (Left) Mature *Poa annua* growing in sand on Macquarie Island, (right) seed heads

Figure 1.6 *Poa annua* growing around Macquarie Island (left-right) low-altitude coastal vegetation; wildlife disturbed coastal vegetation; penguin rookery; mid-altitude short grassland; seal colony; land slip; walking track, high-altitude feldmark vegetation

The distribution of *P. annua* on Macquarie Island has been linked to the presence of rabbits (Copson 1984), which facilitate its spread (Copson & Whinam 2001; Whinam et al. 2014). It is abundant under severe grazing (Taylor 1955) yet can't compete with native species in the absence of continued disturbance on coastal slopes (Scott & Kirkpatrick 2008). *Poa annua* is predicted to decrease in abundance and even disappear in some areas of Macquarie Island following the eradication of rabbits and associated grazing and disturbance, however it will continue to inhabit the coastal fringe where wildlife disturbance will continue (Copson & Whinam 1998; Scott & Kirkpatrick 2008). Whinam et al. (2014) suggest active management of *P. annua,* is not required on Macquarie Island as it should decrease in the absence of rabbits. However, it is important to note that *P. annua* is abundant on sub-Antarctic islands that do not have rabbits (Frenot et al. 2001; Chapuis et al. 2004; le Roux et al. 2013).

Control of invasive species

Control of invasive species is often a necessary requirement. Control methods can be generally classified as chemical control; or non-chemical control which includes physical control, biological control and ecosystem management (Tu et al. 2001; Simberloff 2002).

Chemical weed control is a time-efficient and cost effective means of weed control (Ferrel *et al.* 2004). However, there are concerns around herbicide resistance (Preston 2000) and health and environmental impacts (van der Werf 1996; Monaco et al. 2002) which are a particular concern in high conservation areas such as the sub-Antarctic. Leaching can carry the dissolved herbicide away from the treated area where it can contaminate ground water (Kent & Preston 2000; Monaco et al. 2002). Herbicides can also impact on non-target organisms, having potential adverse impacts on the soil microfauna, birds (secondary poisoning) and mammals (feeding on contaminated sources), cause major damage to aquatic life (van der Werf 1996) and impact on non-target plants through soil persistence and drift (Rao 2000). Despite the potential hazards that herbicides may present, when applied properly they can be successfully utilised in natural areas to kill weeds without impacting on native systems (Weed Management CRC 2003; Department of Environment and Conservation 2006).

In cold climates, the efficacy and behaviour of herbicides may be altered and so is an important consideration in polar environments. Cooler temperatures increase the time a herbicide remains in solution on leaves, decrease vaporisation, decrease the rate of soil degradation through decreased microbial activity (Ditomaso 2011) and can affect efficacy and leaching rates (Veeh et al. 1996). A number of herbicides have been documented to have decreased degradation rates at lower (although not extreme) temperatures (Walker 1976, 1992; Obrigawitch et al. 1982; Welander 2005; Stenrød et al. 2008). However, the behaviour of herbicides in the extreme cold temperatures of high latitudes (Newton et al. 2008) and cold climates (Stenrød et al. 2008) is little known and can't be extrapolated from warmer regions.

Non-chemical control methods are often used where there are concerns over herbicide resistance and health and environmental impacts (van der Werf 1996). They can play an important role in integrated management plans (Simberloff 2002). Physical methods are a form of non-chemical control which can be applied selectively, resulting in minimal damage to desirable biota and are often used successfully in combination with other techniques such as herbicides (Tu et al. 2001). Tillage (the mechanical disturbance of soil to stimulate germination) (Pratley 2000; Monaco et al. 2002), heat treatment (use of an intense wave of heat to rupture plant cells) (Ascard 1995; Bond et al. 2003), solarisation (use of plastic over soil to trap solar radiation and kill seed) and hand weeding or hoeing (Monaco et al. 2002) are all effective forms of non-chemical control.

Biological control involves the use of certain animals, fungi and other microbes to feed upon, parasitize or interfere with a target species while causing little harm to other plants (Tu et al. 2001; Ferrel et al. 2004). It is generally considered practical, safe and environmentally beneficial (Charudattan 2001) as it leaves behind no chemical residues, however it is rarely effective on its own and can sometimes result in significant, irreversible ecological harm (Briese 2000; Tu et al. 2001). Ecosystem management involves the manipulation of environmental conditions such as water availability, nutrient levels or mowing, to promoting the growth and development of the desired plant species while slowly displacing the weed (Lemerle et al. 2000).

The control of *P. annua* has mostly been studied in temperate turf grass, where despite research over several decades, control remains difficult due to the high plasticity of the species (Breuninger 1993; Branham & Calhoun 2005; Christians 2006). Many pre and post emergent herbicides are effectively used to control *P. annua* in temperate turf grass (summarised in Appendix 3). However, their efficacy and selectivity can be variable depending on the variant of *P. annua*, environmental conditions and non-target species (McCarty & Estes 2005; McCullough & Hart 2006, 2010).

Physical control methods such as the application of boiling water, litter and salt and surface tillage were used to control *P. annua* before herbicides (Beard et al. 1978). Heat treatment is unsuccessful for *P. annua* as plants quickly recover due to lack of competition (Ascard 1995;

Andreasen et al. 1999). Solarisation can provide effective control of the *P. annua* seed bank in temperate climates, but possible only at shallow depths (Standifer et al. 1984; Peachey et al. 2001). Hand weeding can be used to give some control of *P. annua* (Itoh et al. 1996). The biological control agent *Xanthomonas campestris* pv *poannua* , and a biocide based on this parasite have been found to give various levels of control of *P. annua* in turf (Zhou & Neal 1995; Johnson et al. 1996; Imaizumi et al. 1999; McRae et al. 2000), as has a mycorrhizal fungi (Gange & Whitfield 2004; Hart et al. 2007). Ecosystem management is widely used in golf courses to either control or promote *P. annua* and includes varying nitrogen levels, soil moisture and aeration; and mowing height and frequency (Beard et al. 1978; Beard 1996).

No research was identified regarding the control of *P. annua* in cold climates. Herbicides such as bispyribic-sodium, benefin, DCPA, EPTC and dichlobenil, used for the control of *P. annua* in turf, have reduced efficacy under cooler temperatures (Downing et al. 1970; McCarty & Estes 2005; McCullough & Hart 2010) which is likely to be more profound in polar regions.

Controlling invasive species in the sub-Antarctic

The control or eradication of non-native plant species from the sub-Antarctic and Antarctica is a current management focus (de Villiers et al. 2006, Committee for Environmental Protection 2011, Hughes et al. 2015, McGeoch et al. 2015). Indeed, the control of *P. annua* is being attempted in the Antarctic Peninsula (Chwedorzewska unpublished data) and is also being considered in parts of the sub-Antarctic (de Villiers et al. 2006; Commonwealth of Australia 2014). While isolated plants and small populations have been eradicated from some islands and the Antarctic Peninsula (Shaw 2013, Hughes et al. 2015), eradication of more widespread species is difficult, largely due to established seed banks (Cooper et al. 2011, Shaw 2013, Molina-Montenegro et al. 2015).

To date, most non-native plant control or eradication programs throughout the Antarctic and sub-Antarctic have utilized physical removal – digging out the plant or population (Hughes et al. 2015). However, herbicides are beginning to be used more widely, particularly on South Georgia (Government of South Georgia and the South Sandwich Islands 2015), with little understanding of the environmental impacts.

Implications

Throughout the sub-Antarctic and Antarctic, managers are considering eradicating or controlling several more established non-native species, including *P. annua* (Commonwealth of Australia 2014; Government of South Georgia and the South Sandwich Islands 2016; Pertierra et al. 2016). However, there are gaps in the knowledge of the ecology of *P. annua* in the sub-Antarctic, particularly its seed bank dynamics. *Poa annua* is notoriously difficult to control, largely due to its high morphological plasticity (Downing et al. 1970, Wu et al. 1987, Lush 1988, Christians 2006). The efficacy of various chemical and non-chemical control methods are likely to differ in the sub-Antarctic environment, yet little is known about the efficacy of control methods for *P. annua* in cold climates. Additionally, whilst small populations of non-native plants have been controlled and eradicated in the sub-Antarctic, the impact of control methods on non-target organisms and the sub-Antarctic environment has rarely been assessed, particularly for herbicides.

Eradication and control of non-native species is becoming increasingly common (Foxcroft et al. 2013), including in the sub-Antarctic and Antarctic (Hughes et al. 2015, McGeoch et al. 2015. However, successful eradication or control is often thwarted by three major shortcomings (Wagner et al. 2016). Firstly, a lack of information on the ecology of the target species, such as longevity, reproductive strategy, reproductive output and seed bank dynamics which can help inform management (Hughes et al. 2015). Second, the efficacy of control methods are rarely researched prior to management programs, but rather a trial-and-error approach is used, wasting time and resources (Rippey et al. 2002; Milne 2007; Hilton & Konlechner 2010; Cooper et al. 2011; Lombard et al. 2012; Ryan et al. 2012; Hamilton et al. Turner 2015). Third, the impact of control methods on non-target organisms and the environment is seldom assessed (Downey et al. 2010; Buckley & Han 2014; Simberloff 2014; Lindenmayer et al. 2015).

To date, successful eradication programs on non-native plants in the sub-Antarctic have been undertaken on small, restricted populations (Hughes et al. 2015). In these cases, knowledge of the ecology of the plant and efficacy and impact of control was unnecessary as management had a restricted footprint. However, as the control or eradication of widespread species is being considered in the sub-Antarctic and Antarctic, it is essential for management programs to address these shortcomings to enable effective, efficient control, particularly in remote wilderness areas where access is difficult and logistics complicated and costly.

Given this, my thesis aims to:

- examine the ecology of *P. annua* on Macquarie Island – the longevity of the species in the sub-Antarctic (annual vs perennial), its growth, morphology and biomass allocation and how this varies across small scales in response to environmental and soil variables, and the impact of *P. annua* on native plant communities
- quantify the seed bank dynamics of *P. annua* – the density, depth distribution, viability and persistence of the seed and how this varies across different infestation densities and with environmental and soil drivers
- test the efficacy of various chemical and non-chemical control methods on *P. annua* in sub-Antarctic conditions and assess their impact on native species; and
- investigate the mobility of glyphosate through Macquarie Island soils when used for *P. annua* control and assess its potential impact on the sub-Antarctic environment

This will increase understanding of the ecology of *P. annua* in the sub-Antarctic, where due to the high variability of *P. annua* it is likely to perform differently to more temperate areas of the world, and help explain why *P. annua* is such a successful invader in the sub-Antarctic. This information will also inform future management of *P. annua* in the sub-Antarctic and Antarctic by providing information on successful control methods and off-target impacts.

On a broader scale, this research will expand knowledge of invasive species in the sub-Antarctic and provide information on the traits enabling these species to be such successful invaders in the sub-Antarctic environment. It will also highlight the importance of conducting detailed research on the ecology of invasive species prior to management and assessing the efficacy of control methods and their impact on off-target species to enable successful control and eradication of invasive species in wilderness areas throughout the world.

Chapter 2

Longevity, growth and community ecology of invasive *Poa annua* across environmental gradients on sub-Antarctic Macquarie Island

Plate 2 King Penguins observing vegetation monitoring of *Poa annua* on Macquarie Island

Chapter submitted as an original research paper to *Plant Ecology* (8th November 2016)

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Abstract

Poa annua is a cosmopolitan weed and is well studied in turf grass systems. Its longevity, morphology and reproductive capacity are known to be highly variable across both its invaded and native range. The species is widespread and abundant in the sub-Antarctic and present in the Antarctic Peninsula. Across the Antarctic region its distribution, seed bank dynamics, colonisation processes, response to grazing and competitive ability are reasonably well understood. However, less is known about the ecology of *P. annua* in the sub-Antarctic, particularly its longevity, morphological variation across small spatial scales and competitive ability. I aimed to fill these knowledge gaps by monitoring individual *P. annua* plants on sub-Antarctic Macquarie Island to assess their longevity. I quantified morphology and biomass allocation of *P. annua* plants across environmental gradients by collecting measurements of plant traits in the field and drying and weighing different plant components. I also assessed community diversity indices in areas of varying *P. annua* densities by undertaking vegetation surveys. I show that *P. annua* plants on sub-Antarctic Macquarie Island are perennial, and their morphology and impact on native plant communities 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 suppress native plant diversity. Conversely, at high altitude sites *P. annua* plants are smaller with no detectable impact on native plant communities. This new information helps to explain the success of *P. annua* as in invader in the sub-Antarctic and quantifies the characteristics needed by an invasive species to function well beyond its natural range.

Introduction

Poa annua is a cosmopolitan weed (Heide 2001). It is a particular problem in temperate turf grass throughout the world, and therefore much research has focused on its ecology and population dynamics in turf to better understand the species and develop effective control methods (Law et al. 1977; Beard et al. 1978; Wu et al. 1987; Lush 1988; Mitich 1998; Heide 2001). The longevity, morphology and reproductive capacity of *P. annua* vary greatly across its invaded and native range, largely in response to environmental conditions (Warwick 1979; Soreng and Peterson 2012).

Poa annua is the most common and widespread non-native vascular plant in the sub-Antarctic (Williams et al. 2013; McGeoch et al. 2015) and it also grows in the Antarctic Peninsula (Chwedorzewska 2015). In the Antarctic Peninsula, the colonisation, distribution, seed bank and germination dynamics and competitive ability of *P. annua* have been well studied (i.e. Olech and Chwedorzewska 2011; Molina-Montenegro et al. 2014; 2016; Wódkiewicz et al. 2014). In the sub-Antarctic, its distribution and spread between and within island groups and its ability to tolerate grazing, wildlife disturbance and trampling and colonise bare ground, deglaciated areas and landslips have been well documented (i.e. Copson 1984; Bergstrom and Smith 1990; Frenot et al. 1997; 1998; Scott and Kirkpatrick 2013; Hausmann et al. 2013; Whinam et al. 2014). Despite this previous body of work knowledge gaps remain, particularly about plant longevity, determinants of growth form and its competitive ability.

The longevity of *P. annua* is an important and variable characteristic influencing population dynamics that is often closely aligned with the plant's morphology. A continuum of growth forms has been described from annual, erect, compact plants that flower young and have dormant seed; to perennial, prostrate plants that flower late and have non-dormant seed (Youngner 1959; Gibeault 1970; Beard 1996; Vargas and Turgeon 2004). Anecdotal observations suggest that there are both annual and perennial populations of *P. annua* in the sub-Antarctic (Frenot *et al.* 2005). On South Georgia, some plants are annual but the majority are considered to be perennial (Walton 1975). It has been suggested that the Macquarie Island population is likewise 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 Antarctic and sub-Antarctic has never been quantified *in situ*.

The morphology of *P. annua* plants has been found to vary both within the Antarctic and sub-Antarctic region and compared with populations elsewhere in the world. Plants growing in the Antarctic Peninsula had different morphology to plants from Poland (likely source location), possibly due to differences in environmental factors between the sites, but were similar to plants from sub-Antarctic Kerguelen and Crozet (Galera et al. 2015). A recent study by Molina-Montenegro et al. (2016) found that *P. annua* populations in the Antarctic Peninsula had high phenotypic plasticity across a number of traits, which was partly manifested in morphological variability. When *P. annua* plants sourced from different populations around the world (including sub-Antarctic Macquarie Island) were grown under standard 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 sub-Antarctic Iles Crozet and Kerguelen, and plants also differed in morphology within each archipelago in response to environmental factors. In contrast, plants from Kerguelen and Crozet grown under standard conditions in France showed no morphological variation between populations, but morphology did differ between plants grown in different years (and at different temperatures), providing further evidence of phenotypic plasticity in response to environment (Frenot et al. 1999). Whilst variability in the morphology of *P. annua* in the Antarctic region is well known, variability at small spatial scales (i.e. between populations within an island) and the environmental correlates behind this variability is little understood.

Several studies have explored the competitive ability of *P. annua* and its impacts on native plant communities in the Antarctic region. Some show that although *P. annua* is the first species to colonise open ground in the sub-Antarctic, it does not directly compete with native species (Gremmen 1997; Frenot et al. 2001; Scott and Kirkpatrick 2005) but rather is outcompeted over time in established native vegetation (Scott and Kirkpatrick 2008; 2013; Whinam et al. 2014). Other studies report that in the highly disturbed, nutrient enriched areas around elephant seal wallows on sub-Antarctic La Possession and Kerguelen Islands *P. annua* forms low grasslands and strongly dominates the native vegetation (Frenot et al. 2001). *Poa annua* from the Antarctic Peninsula has been found to compete directly with native species in pot trials, and this is likely to increase under future climate change scenarios (Molina-Montenegro et al. 2012; 2016). The research therefore suggests there is variability in competitive ability and that competitive effects may depend on specific environmental factors. This information is critical for predicting invasion dynamics and site-specific management.

Despite prior research on the ecology of *P. annua* in the Antarctic region, a number of knowledge gaps remain. As the most widespread invasive plant species in the sub-Antarctic, it important to understand its ecology as this has implications for management, conservation and invasion biology in the region and more broadly. We aimed to fill three of the major knowledge gaps for the ecology of *P. annua* in the sub-Antarctic by quantifying the longevity of *P. annua* on Macquarie Island (perenniality vs annuality), understanding its morphological variation in response to fine-scale environmental variables, and quantifying the community dynamics in order to determine its competitive ability and impact on native species diversity.

Methods

Study sites

Macquarie Island (54°30’ S, 158°57’ E) has a cool, wet and windy climate which varies little throughout the year. The mean annual temperature is 4 °C, precipitation is 980 mm and wind speed 30 km h^{-1} (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 a narrow coastal band, and thus has a highly variable altitudinal range and topography that determines vegetation and plant growth (Selkirk *et al.* 1990).

Six sites were established in the austral summer of 2013 (Jan/Feb) to encapsulate different plant communities containing *P. annua* across topographic, altitudinal and *P. annua* density gradients (Figure 2.1). Two sites were located at low altitude (< 50 m a.s.l.) and high *P. annua* cover (> 60 %), Bauer Bay Beach and Tractor Rock. Two mid altitude (100-150 m a.s.l.) sites with medium *P. annua* cover (15-50 %), Bauer Bay Slope and Doctor’s Track, and two high altitude sites (> 250 m a.s.l.) with low *P. annua* cover (< 10 %), Lower Boot Hill and Upper Boot Hill, were also established. An additional three sites were established in December 2013 for the community floristics study, a low altitude site with high *P. annua* cover (The Nuggets), a mid-altitude site with medium *P. annua* cover (Sawyer Creek) and a high altitude site with low *P. annua* cover (Mount Power) (Figure 2.1).

At each site location, elevation and aspect were determined by handheld GPS (Garmin GPSMap 78). Soil depth was measured by inserting a graduated steel rod randomly into the soil ten times/site until it reached bedrock or soil depth was greater than the length of the rod (85 cm). Animal disturbance (i.e. old rabbit burrowing, trampling by wildlife) was visually estimated as low – soil and vegetation intact (value of 1); medium – some soil and vegetation disturbance (value of 2) or high – much of the soil and vegetation highly disturbed (value of 3). Exposure was inferred based on prevailing winds and topography and determined as low – sheltered from prevailing winds (value of 1); medium – some exposure to prevailing winds (value of 2) or high – exposure to much of the prevailing winds (value of 3).

All soil characterisation was undertaken on air dried soil sieved to 2 mm. Soil pH and electrical conductivity were determined using the method adopted from Rayment and Higginson (1992); soil particle analysis was assessed using the pipette method (Day 1965). Soluble sulphur was assessed using the method adopted from Blair et al. (1991) and absorbance measured using an 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) (Raymont and 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. Three replicates were analysed for each test, with the exception of soil particle analysis where a single replicate was sufficient. A single replicate was analysed for exchangeable cations at the Nuggets due to logistical issues. Soil particle analysis was not possible for the Nuggets and Sawyer Creek as the organic matter level was very high.

Plant sampling

In February 2013, 20 *P. annua* plants of various vegetative and reproductive stages were randomly tagged over an area less than 200 m x 200 m at each of the six established sites (two low, two mid and two high altitude) (Figure 2.1). Plant locations were recorded with a handheld GPS and each was marked with a wooden peg and had a coloured paper clip attached to the base or a tiller of each plant (except Upper Boot Hill where plants were too small). The number of tillers (the stem emerging from the soil surface), maximum tiller length (to tip of the longest leaf), number of reproductive stems and plant stage (vegetative/flowering/seeding) were recorded. Each plant and peg was photographed to document the effect of frost heave, erosion and sand deposition. In December 2013, March 2014 and April 2015 plants were re-measured and re-photographed.

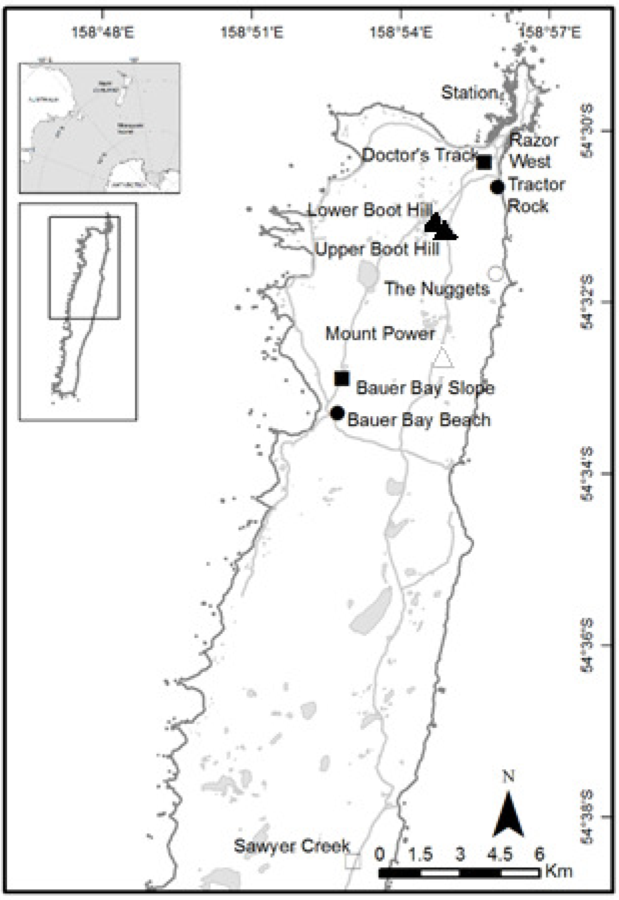

Figure 2.1 Inset: location of Macquarie Island in the Southern Ocean (Australian Antarctic Data Centre 2005); and location of study sites on Macquarie Island. Sites were either at low elevation (< 50 m above sea level) with high *Poa annua* cover (> 60 %) (●), mid altitude (100-150 m) with medium *P. annua* cover (15-50 %) (■) or at high altitude (> 250 m) with low *P. annua* cover (< 10 %) (▲), filled symbols are sites established in 2013, unfilled symbols are sites established in 2014

Resource allocation was assessed by harvesting 120 *P. annua* plants. In February 2013, twenty 1 m x 1m quadrats were randomly selected within a 20 x 20 m area at each of the six sites. Quadrat locations were marked with handheld GPS. One *P. annua* plant (or a 5 x 5 cm clump of *P. annua* when cover was dense i.e. at Bauer Bay Beach and Tractor Rock) were collected from each quadrat (20 plants/site), except at Upper Boot Hill where some quadrats didn't contain plants in which case multiple plants were collected from other quadrats. Plants (including roots) were extracted to a depth of 15 cm and rinsed of soil. The number of tillers, maximum tiller length, maximum root length, plant stage and number of reproductive stems were recorded. Plants were sectioned into reproductive parts; roots; and shoots, dried in paper bags at 80 °C for 48 hours and weighed.

To study the community floristics at each site, vegetation was assessed within each of the twenty 1 m x 1 m quadrats at each of the 9 sites in Jan/Feb 2014. The species present (richness) and percentage cover of each species was recorded and each quadrat photographed.

Data analysis

All statistical analysis were conducted in R version 3.1.3 (R Core Team 2014). Species diversity of each site was estimated using Simpson diversity which is one of the most meaningful and robust diversity measures available as it captures both species richness and the variance of the species abundance distribution (Magurran 2014). It was calculated as $D = \sum (n/N)^2$, where n is the total percentage cover of a particular species and N is the total percentage cover of all species, and was presented in the complement form, 1-D. Simpson diversity was not calculated at Upper Boot Hill due to most quadrats being bare ground with little or no plant cover and so skewing the index.

Longevity data, plant measurements, biomass allocation, diversity indices between sites, and *P. annua* cover and total species richness between sites and years, were analysed using analysis of variance (ANOVA). Variances were checked by plotting residual versus fitted values to confirm the homogeneity of the data and normality was checked by quantile-quantile comparison plots. Significant means were separated using Tukey's highest significant difference (HSD) test where P values were considered significant when < 0.05. Linear regression was used to assess correlations between plant traits and diversity indices, and environmental and soil characteristics. Correlations with a P value > 0.05 were not considered to be significant. Environmental variables that were highly correlated with plant traits or diversity indices ($R^2 > 0.25$) were selected as loadings in a principal component analysis (PCA) to assess differences in plant traits between study sites and underlying environmental drivers of traits. Sand content could not be included in the PCA due to missing values at The Nuggets and Sawyer Creek.

Results

Environmental characteristics varied with elevation across the study sites (Table 2.1). Low altitude sites tended to have deeper, sandy soils (except for The Nuggets which was peaty), were moderately exposed and had high animal disturbance. Mid altitude sites had deep, peaty soils with greater soil water content, no animal disturbance and moderate exposure. High altitude sites generally had shallower soil with low sand content, no animal disturbance and high exposure. Soil chemistry was variable.

Table 2.1 Environmental and soil characteristics of study sites on Macquarie Island, DL = detection limit

Characteristic	Tractor Rock	Bauer Bay Beach	The Nuggets	Doctor's Track	Bauer Bay Slope	Sawyer Creek	Lower Boot Hill	Upper Boot Hill	Mount Power
Latitude °	-54.5106	-54.5548	-54.5281	-54.5061	-54.5481	-54.6417	-54.5192	-54.5204	-54.5428
Longitude °	158.9326	158.8786	158.9313	158.9278	158.8803	158.9003	158.9152	158.9151	158.9108
Elevation (m)	2	24	23	115	136	109	258	278	338
Aspect (° from N)	90 (E)	225 (SW)	45 (NE)	45 (NE)	135 (SE)	260 (W)	45 (NE)	90 (E)	45 (NE)
Animal disturbance	2	3	3	1	1	1	1	1	1
Exposure	2	2	1	1.5	2	2	2.5	3	3
Average soil depth (cm)	> 85	83	> 85	> 85	63	> 85	56	9	> 85
SOIL									
Carbon (%)	0.2 ± 0.0	0.3 ± 0.1	61.2 ± 0.8	44.0 ± 1.0	13.2 ± 0.2	48.2 ± 0.1	7.6 ± 0.4	0.5 ± 0.0	9.6 ± 0.4
Nitrogen (%)	< DL	< DL	5.1 ± 1.5	3.7 ± 1.0	1.2 ± 0.0	4.2 ± 0.0	0.6 ± 0.0	< DL	0.6 ± 0.0
Phosphorus (µg g^{-1})	45.3 ± 1.5	90.7 ± 17.6	8.8 ± 0.2	8152 ± 275	244 ± 10.0	155 ± 23.7	48.1± 32.2	24.7± 0.6	39.6 ± 25.9
Sulphur (µg g^{-1})	16.2± 0.9	9.8 ± 0.2	123.2± 2.1	43.5 ± 1.1	49.8 ± 1.8	50.5 ± 1.0	6.5 ± 0.1	2.4 ± 0.1	4.4 ± 0.1
Exchangeable potassium (cmol^{+} kg^{-1})	0.3 ± 0.0	0.4 ± 0.2	0.3	1.4 ± 0.0	1.0 ± 0.1	0.9 ± 0.2	0.4 ± 0.1	1.0 ± 0.2	0.4 ± 0.2
Exchangeable calcium (cmol^{+} kg^{-1})	2.6 ± 0.0	1.9 ± 0.1	8.1	8.7 ± 0.1	18.6 ± 0.3	7.8 ± 0.2	2.9 ± 0.0	17.9 ± 0.2	2.6 ± 0.1
Exchangeable magnesium (cmol^{+} kg^{-1})	1.4 ± 0.0	16.4 ± 0.1	7.6	10.6 ± 0.5	16.4 ± 0.3	9.8 ± 0.2	4.3 ± 0.1	29.1 ±0.7	2.5 ± 0.1
Exchangeable sodium (cmol^{+} kg^{-1})	0.6 ± 0.0	2.6 ± 0.2	2.7	3.0 ± 0.0	2.6 ± 0.1	2.9 ± 0.0	0.8 ± 0.0	2.0 ± 0.2	1.0 ± 0.2
pH (1:5 H_20)	6.9 ± 1.7	8.2 ± 0.1	4.8 ± 0.3	5.1 ± 0.1	4.8 ± 0.1	4.9 ± 0.3	5.5 ± 0.0	6.2 ± 0.0	7.6 ± 0.0
Electrical conductivity $_{(1:5)}$ (µs cm^{-1})	59.5 ± 2.1	43.0 ± 1.0	356.3 ± 81.3	379.3 ± 11.8	558.7 ± 8.6	482.7 ± 5.7	58.4 ± 2.4	55.3 ± 2.8	105.1 ± 1.1
Sand content (%)	99.3	99.1	n/a	70.5	64.1	n/a	77.0	72.5	80.9
Clay content (%)	0.2	0.3	n/a	14.8	15.8	n/a	12.9	14.1	9.8
Silt content (%)	0.5	0.6	n/a	14.7	20.1	n/a	10.1	13.4	9.3

The longevity study indicated that some of the *P. annua* plants on Macquarie Island were perennial as they had survived for more than 27 months, with at least 20 % of tagged plants still present at the end of the monitoring period (Figure 2.2). As some of these were well established and even reproducing at the start of the experiment, it is likely that *P. annua* plants can survive for more than 27 months. The main apparent cause of the loss of tagged plants appears to be isolated factors that tended to be specific to a site 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 *P. annua* and other species (Bauer Bay Beach, Tractor Rock – 2014/15).There were only 5 out of 120 plants observed as dead *in situ.*

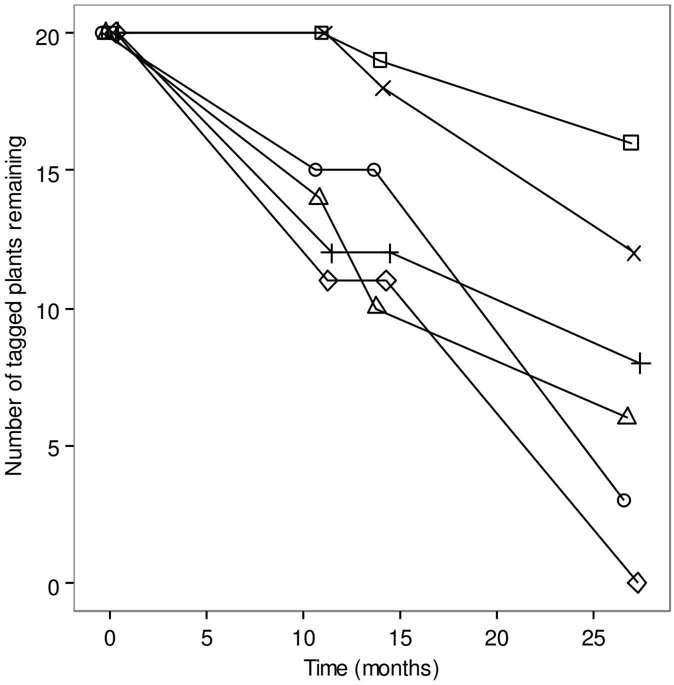

Figure 2.2 Number of tagged *Poa annua* plants remaining at Tractor Rock (◇); Bauer Bay Beach (○); Bauer Bay Slope (△); Doctor's Track (□); Lower Boot Hill (×) and Upper Boot Hill (+) after 0 (February 2013), 11 (December 2013), 14 (March 2014) and 27 (April 2015) months

The morphology of *P. annua* plants varied between the study sites (Table 2.2). Plants at the high altitude sites of Lower Boot Hill and Upper Boot Hill were smallest, weighing 1.8 and 1.1 g on average respectively and having few tillers per plant (15.3 and 12.5 tillers). Plants at Upper Boot Hill had the shortest tillers (3.7 cm) and the lowest number of reproductive tillers per plant (3.2) while plants at Lower Boot Hill had the shortest roots (11.0). Conversely, larger plants were found at the low altitude sites of Tractor Rock and Bauer Bay Beach. The largest plants were found at Tractor Rock, weighing 19.2 g, having 85.4 tillers per plant, 28.0 reproductive tillers and a root length of 21.8 cm. Plants at Bauer Bay Beach had the longest tillers, around 28.7 cm in length. 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 shoots/tillers (18.3-31.6 %), with relatively little allocated to reproductive material (1.6-7.6 %) (Table 2.2).

PCA indicated that environmental variables were strong drivers of the differences in plant morphological traits between sites (indicated by the proximity of the arrow loadings, Figure 2.3). Elevation was the strongest driver of these differences as indicated by regression analysis ($P \leq 0.01$). In general, large plants 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 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) (Figure 2.3).

Table 2.2 Morphological characteristics (mean ± standard deviation/plant) of plants at study sites, significant differences ($P < 0.05$) are between sites and shown by different letters, * Antarctica morphology data from 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 ± 12.1^{a}	10.9 ± 5.8^{b}	12.1 ± 7.5^{b}	4.9 ± 2.3^{c}	1.8 ± 1.6^{d}	1.1 ± 1.2^{d}	3.0 ± 1.0
% shoots	22.5 ± 9.2^{bc}	31.6 ± 15.1^{ab}	18.3 ± 17.8^{bc}	31.2 ± 13.7^{ab}	20.3 ± 12.2^{bc}	23.6 ± 17.1 ^{bc}	
% roots	75.8 ± 10.1^{ab}	60.8 ± 18.6^{c}	80.0 ± 18.5^{ab}	65.7 ± 14.8^{bc}	74.3 ± 14.9^{bc}	74.0 ± 17.6^{bc}	
% reproductive	1.7 ± 1.1^{bc}	7.6 ± 15.5^{ab}	1.6 ± 0.9^{bc}	3.1 ± 1.8^{ab}	5.4 ± 9.7^{bc}	2.4 ± 2.9^{ab}	
No. tillers	85.4 ± 28.2^{a}	58.0 ± 20.6^{b}	46.6 ± 24.9^{bc}	42.3 ± 29.1^{c}	15.3 ± 16.8^{d}	12.5 ± 10.8^{d}	7.6 ± 6.7
Tiller length (cm)	21.4 ± 17.2^{bc}	28.7 ± 10.8^{ab}	14.7 ± 7.5^{cd}	19.2 ± 5.3^{c}	9.1 ± 5.7^{d}	3.7 ± 1.7^{e}	
No. reproductive tillers	28.0 ± 9.0^{a}	23.9 ± 16.3^{a}	12.2 ± 6.8^{b}	8.6 ± 7.7^{bc}	5.1 ± 6.8^{bc}	3.2 ± 3.7^{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 ± 3.3^{a}	15.1 ± 3.5^{b}	14.8 ± 4.3^{b}	13.0 ± 3.5^{c}	11.0 ± 3.7^{d}	13.0 ± 5.2^{c}	

Table 2.3 Mean diversity indices (m^{-2} ± standard deviation) for each site

Species	Tractor Rock	Bauer Bay Beach	The Nuggets	Doctor's Track	Bauer Bay Slope	Sawyer Creek	Lower Boot Hill	Upper Boot Hill	Mount Power
Species richness	2.5 ± 1.5	3.2 ± 0.8	1.5 ± 0.7	7.9 ± 1.6	6.3 ± 1.0	6.0 ± 1.0	8.0 ± 1.6	3.9 ± 2.4	6.4 ± 1.3
Simpson diversity	0.3 ± 0.3	0.6 ± 0.2	0.2 ± 0.3	0.8 ± 0.0	0.8 ± 0.1	0.7 ± 0.1	0.9 ± 0.1	*	0.9 ± 0.1

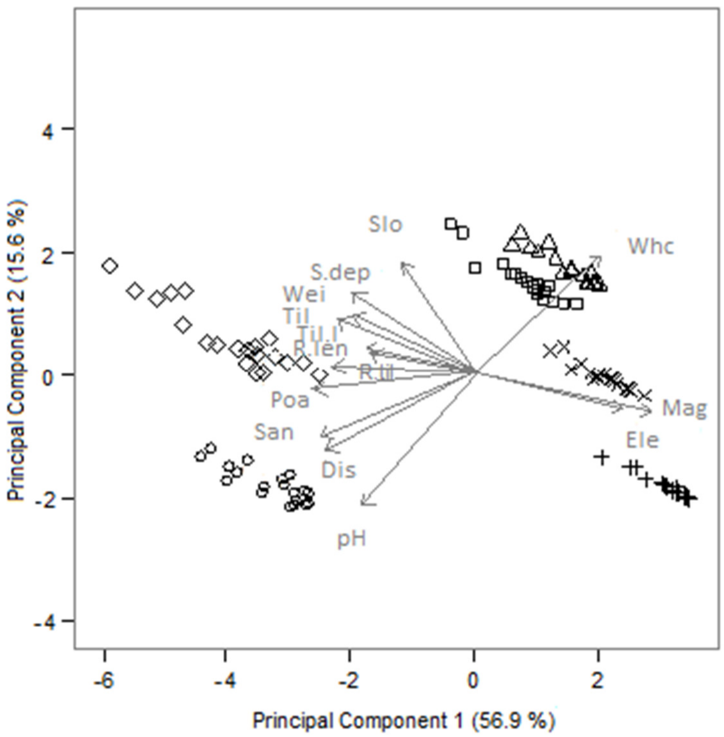

Figure 2.3 Principal component analysis of *Poa annua* cover Poa; plant morphological traits: Dry weight Wei; number of tillers Til; Tiller length Til.l; Number of reproductive tillers R.til; Root length R.len; and environmental characteristics: Animal disturbance Dis; Elevation Ele; Soil magnesium Mag; 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: Bauer Bay Beach (○); Bauer Bay Slope (△); Doctor's Track (□); Lower Boot Hill (×); Tractor Rock (◇) and Upper Boot Hill (+)

Species richness and Simpson diversity varied between the study sites (Table 2.3). The three low altitude sites, Bauer Bay Beach, Tractor Rock and The Nuggets had low species richness (< 3.2 m^{-2}). The high altitude site Upper Boot Hill also had low species richness (3.9 m^{-2}) while Lower Boot Hill, also at high altitude, had the highest species richness (8.0 m^{-2}). The other sites had intermediate species richness. Two of the low altitude sites, Tractor Rock and The Nuggets, had very low Simpson diversity (< 0.4 m^{-2}) whilst the high altitude sites Lower Boot Hill and Mount Power had the highest Simpson diversity (0.9 m^{-2}). Bauer Bay Beach and the mid altitude sites had intermediate species richness.

PCA was used to describe which environmental and soil characteristics influenced the variation in diversity indices between the sites (indicated by the closeness of the arrow loadings, Figure 2.4). In general, sites which had low species richness and Simpson diversity

(Bauer Bay Beach, Tractor Rock, The Nuggets) were very strongly correlated with high animal disturbance and high *P. annua* cover and correlated with low soil water content, low potassium and low exposure. Conversely, sites with high species richness and Simpson diversity (all other sites) were found at higher elevations with high exposure, high soil water content, high 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 diversity ($P < 0.01$, $R^2 = 0.89$), with high *P. annua* cover correlating with lower species richness and Simpson diversity.

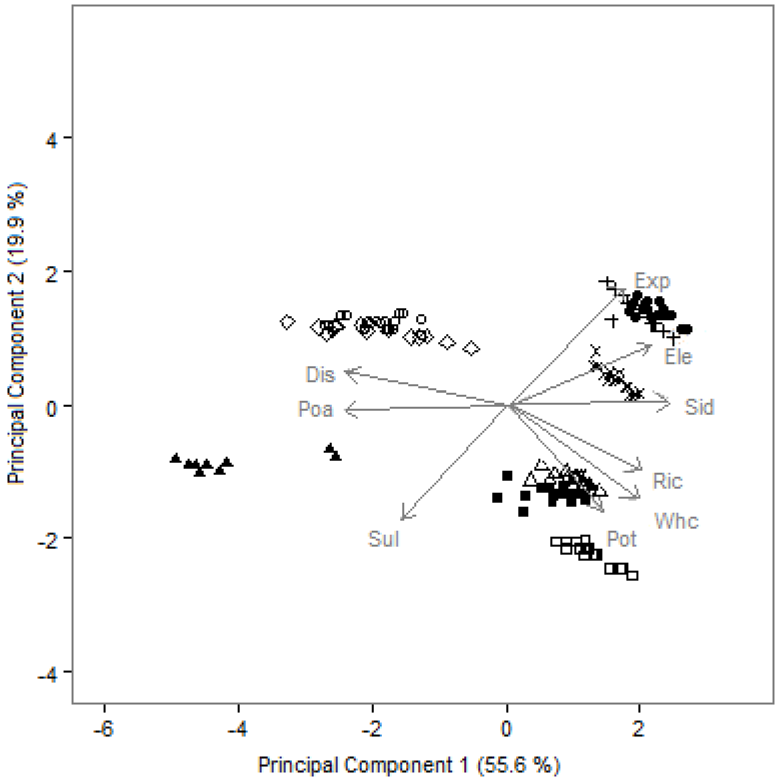

Figure 2.4 Principal component analysis of *Poa annua* cover Poa, community indices: species richness Ric; Simpson's diversity SiD; and various environmental characteristics: Animal disturbance Dis; Elevation Ele; Exposure Exp; Potassium Pot; Sulphur Sul; Water content Whc, according to the first two components. Study sites: Bauer Bay Beach (○); Bauer Bay Slope (△); Doctor's Track (□); Lower Boot Hill (×); Mt Power (●); The Nuggets (▲); Sawyer Creek (■); Tractor Rock (◇) and Upper Boot Hill (+)

Discussion

Longevity

Previous researchers have suggested that some sub-Antarctic *P. annua* populations are annual (Walton 1975; Frenot et al. 2005). We have quantified the lifespan of *P. annua* on Macquarie Island in the sub-Antarctic and shown it to be a perennial. Most plants in the sub-Antarctic, both native and invasive 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 shoots and roots when the growing season begins, especially from nodes along the tillers of grasses (Ellis et al. 1971; Frenot et al. 2001; Convey et al. 2006b). This perenniality provides an advantage over annual species which need to quickly germinate, emerge and grow to avoid competition from established perennial species (Billings and Mooney 1968; Billings 1974), particularly if the level of disturbance is not mainitained. The perenniality of *P. annua* helps it to compete with other perennials on Macquarie Island where it would be difficult for it to establish each season without continuous disturbance and where it would be outcompeted by the longer-lived, taller native species.

Morphology

The high morphological plasticity of *P. annua* at both a species level (Youngner 1959; Gibeault 1970; Callahan and McDonald 1992; Breuninger 1993; Beard 1996; Vargas and Turgeon 2004) and within island populations (Frenot et al. 1999; Galera et al. 2015; Molina-Montenegro et al. 2016) is well documented. Here we show that *P. annua* morphology is also highly variable across small spatial scales in response to environmental gradients. Altitude is the most important driver of variation in the morphology of *P. annua* on Macquarie Island. At the low altitude coastal sites, the warmer, more protected conditions enhance plant growth (Tweedie and Bergstrom 2000). Conversely, at high altitude sites plant growth is restricted by the strong winds and colder temperatures (Hunter and Grant 1971; Barcikowski et al. 1999; Hautier et al. 2009).

Animal disturbance and associated high nutrient levels are important drivers of *P. annua* abundance in the sub-Antarctic (Walton 1975; Ryan et al. 2003; Haussmann et al. 2013). We have identified that animal disturbance is also a key correlate of morphological variation amongst *P. annua* on Macquarie Island. *Poa annua* is enhanced by animal distrubance (Walton 1975; Leader-Williams *et al.* 1987; Haussmann *et al.* 2013) and associated nutrient enrichment at coastal sites but the processes are largely absent at high altitude sites on Macquarie Island. We did not identify nutrients as a key driver of growth, despite the presence of large plants at sites with high animal distrubance and high nutrient inputs. Most likely, nutrients are leached to deeper soil depths than what was sampled yet they are still accessible to plants (Lehmann and Schroth 2003). Soil characteristics such as depth, pH and water content also determine morphological variation of *P. annua* on Macquarie Island. On sub-Antarctic Iles Kerguelen, variation of *P. annua* plants between sites was attributed to differences in soils, with a more vigorous form growing at a site with higher fine particle content (Frenot et al. 1999).

Previous research shows that *P. annua* on Macquarie Island can produce very dense soil seed banks (Williams et al. 2016), with seed densities of up to 130 000 seeds m^{-2}. Seed bank density was driven most strongly by *P. annua* cover and soil wetness, but also by 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 *P. annua* plants allocate considerably more to root biomass than to reproductive structures. This was consistent across all sites, despite environmental differences between sites. On Iles Kerguelen, *P. annua* also had very little reproductive biomass (8 %), with the majority of the biomass composed of shoots (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). Both the Kerguelen and Macquarie populations allocated a high proportion of their resources to persistence rather than reproduction. This is a common survival strategy for plants growing in colder, harsher conditions (Baret et al. 2004; Hautier et al. 2009) and it may also enable them to quickly recover from the winter (Scott and Billings 1964). The high biomass allocation to roots on Macquarie Island is also likely to aid persistence in the presence of established perennial native flora and may enable plants to access nutrients at greater depths (Ericsson 1995).

Community dynamics

Vegetation assemblages throughout the sub-Antarctic 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 and Kirkpatrick 2005). On Macquarie Island, environmental and soil characteristics were also drivers of plant community diversity. However, increasing *P. annua* cover was most strongly correlated with lower plant species diversity.

When *P. annua* occurs at high densities, it both reduces the presence of native species and reduces their abundance. This contrasts with much of the previous research regarding the competitive ability of *P. annua* in the sub-Antarctic. 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 and 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

(Scott and Kirkpatrick 2005). With the eradication of invasive rabbits from Macquarie Island in 2014 (Terauds et al. 2014) and the cessation of the associated vegetation grazing (Scott and Kirkpatrick 2008), community dynamics will greatly change. Studies on *P. annua* from the Antarctic Peninsula also indicate direct competition with native species in pot trials (Molina-Montenegro et al. 2012, 2016). We show that on Macquarie Island at low altitiudes where there is high animal disturbance, *P. annua* occurs at very high densities and supresses the diversity of native vegetation.

Summary

Poa annua has many traits which make it a successful invader within the sub-Antarctic (Rejmánek and Richardson 1996; Pyšek and Richardson 2008; Moravcova et al. 2015). The species can tolerate wildlife disturbance (Walton 1975; Haussmann et al. 2013) and grazing by introduced mammals (Leader-Williams *et al.* 1987; Whinam et al. 2014) and can produce large quantities of seed and have persistent seed banks (Williams et al. 2016).

Here we quantified the ecological drivers of *P.* annua and its persistence on Macquarie Island. We now know it is perennial on Macquarie Island and is highly plastic in its morphology, even 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 suggest that *P. annua* is strong competitor against the perennial native flora of Macquarie Island. The largest, most vigorous plants grow at low altitudes where there is high wildlife disturbance and deep, sandy soils. At these sites, *P. annua* can suppress the diversity of native species. At the more exposed high altitude sites with no animal disturbance and shallow, gravelly soils, *P. annua* plants are small and have no detectable impact on native species.

These newly quantified traits along with those previously documented give us a better understanding of why *P. annua* is the most widespread and abundant non-native on Macquarie Island and why it is a successful invader in the sub-Antarctic.

Chapter 3

Quantifying the seed bank of an invasive grass in the sub-Antarctic: seed density, depth, persistence and viability

Plate 3 Thick lawn of seeding *Poa annua* at Bauer Bay on Macquarie Island

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Williams, L., Kristiansen, P., Sindel, B., Wilson, S., & Shaw, J. (2016). Quantifying the seed bank of an invasive grass in the sub-Antarctic: seed density, depth, persistence and viability. *Biological Invasions*, 18(7), 2093-2106.
http://dx.doi.org/10.1007/s10530-016-1154-x

Chapter 4 Efficacy and impact of invasive grass management in a protected area: *Poa annua* in the sub-Antarctic

Plate 4 A healthy ecosystem on Macquarie Island uninvaded by *Poa annua*

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