Changes in Subantarctic Heard Island Vegetation at Sites Occupied by Poa annua, 1987–2000

Authors: Scott, J. J., and Kirkpatrick, J. B.

Source: Arctic, Antarctic, and Alpine Research, 37(3) : 366-371

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(2005)037[0366:CISHIV]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 37, No. 3, 2005, pp. 366–371

Changes in Subantarctic Heard Island Vegetation at Sites Occupied by *Poa annua,* 1987–2000

J. J. Scott[*]† and
J. B. Kirkpatrick[*]

*School of Geography and Environmental
Studies, University of Tasmania,
Private Bag 78, GPO, Hobart,
Tasmania 7001, Australia
†Jenny.Scott@utas.edu.au

Abstract

Poa annua, the only alien plant species recorded on subantarctic Heard Island, considerably expanded its range and abundance along three transects in tundra-like vegetation on the island in the period 1987–2000. This expansion was strongly associated with increased seal disturbance, which also favored *Callitriche antarctica* and damaged *Pringlea antiscorbutica*, leading to a decrease in mean vegetation height. Expansions of *Azorella selago* and *Poa cookii* were independent of the expansion of *P. annua*, relating to colonization of moraines. There was no evidence of displacement of other taxa by *Poa annua* in areas undisturbed by seals.

Introduction

Heard Island lies south of the Antarctic Polar Frontal Zone in the southern Indian Ocean (53°5′S, 73°30′E; Fig. 1). Only a small proportion of its 367-km^2 area is ice free and available for vegetation colonization, although these proportions are increasing due to rapid glacial retreat over the past few decades (Kiernan and McConnell, 1999; Ruddell, in press). However, at low altitudes there are patches of species-poor tundra-like vegetation which cover more than 20 km^2 of the land area (Scott and Bergstrom, in press). The vegetation of Heard Island is unusual in the subantarctic region as there appear to be no human-introduced alien plant species (Scott, 1989). Here, "alien" is defined as "introduced to an ecosystem as a result of human activity (including species that arrive by natural means to a specific ecosystem but are alien to that biogeographical zone)" (Frenot et al., 2005). The one alien species, *Poa annua*, was first recorded in 1987 from two sites on eastern Heard Island, both on moraine outwash deposits near the edges of retreating glaciers which covered the sites in 1947 (Scott, 1990) (Fig. 1). Neither site was directly linked with human presence on the island (Scott, 1989). It appears most likely that seabirds transported seeds of *P. annua* to Heard Island (Scott, 1989), possibly from the closest landmass, Iles Kerguelen, where it is widespread (Frenot et al., 2001). The species typically takes on a perennial habit in the subantarctic (Frenot and Gloaguen, 1994; Gremmen, 1997), although it is usually an annual in temperate locations.

In 1987 one of us (Scott) collected vegetation and environmental data from 61 quadrats along four transects in the two locations where *P. annua* occurred. In November 2000, after a period of 13 years, the two *P. annua* populations on Heard Island were revisited. Scott was able to relocate 37 of the quadrats along three of the transects. Vegetation and environmental parameters were remeasured, the distribution of *P. annua* at the two sites was remapped, and changes in distribution and patterns of colonization were documented. In this paper we report the changes that have taken place in the vegetation of the quadrats; relate *P. annua* expansion to environment, seal disturbance, and floristic variation; and test whether there is any indication that *P. annua* might displace native species.

Methods

The thirty-seven 5 × 2 m quadrats were located along two transects at the Winston Lagoon site and one at the Stephenson Lagoon site (Figs. 1 and 2) which were originally placed to pass through the main populations of *P. annua*. The extent of *P. annua* in these areas was mapped at both times using color aerial photographs and ground observation, in 1987 using pacing and compass bearings, and in 2000 using a GPS unit with an expected accuracy of 10–30 m.

The cover of each vascular plant species, genera or species of bryophytes, filamentous green algae as a class, bare ground, rock cover, and free-standing water was recorded for each quadrat using the following classes: 1, <1%; 2, 1–5%; 3, 5–25%; 4, 25–50%; 5, 50–75%; 6, 75–100%. Two moss genera, *Bryum* and *Pohlia*, were combined during analyses due to insufficient sampling in 2000 to allow accurate identifications. The resulting category "*Bryum* spp./*Pohlia* spp." is characteristic of moist habitats such as springs and seepage lines, and is likely to include *Bryum pseudotriquetrum* and *Pohlia wahlenbergii*. The influence of seal disturbance was visually estimated in four classes (0, none; 1, slight; 2, moderate; 3, heavy) by taking into account relative disturbance from vegetation trampling and manuring, deposition of hair and skin, and creation of bare ground (Scott 1990). The maximum height of the vegetation was measured to the nearest centimeter. Altitude was determined with an altimeter, slope with a clinometer, and aspect with a compass. Soil depth in centimeters was estimated as the maximum penetration of three probes. These latter four variables were measured only in 1987, while the others were measured or estimated in both 1987 and 2000.

Four communities were chosen from a manually sorted table of the quadrat data. Global nonmetric multidimensional scaling (mds) was used to ordinate the floristic data set, using the default options in DECODA (Minchin, 1990). Scores for each quadrat in 1987 were subtracted from the scores for each quadrat in 2000 to give change indices for all variables. Pearsons product moment correlation coefficient, one-way ANOVA, the paired *t*-test, and chi-squared were used to determine the significance of relationships between variables, or the significance of differences between sets of values, as appropriate.

Results

Four intergrading communities were selected from the sorted table. All had quadrats from both sample times (Table 1). Three ordination axes were selected, as the stress declined only a little between axes 3 and 4. The four communities occupy statistically distinct sections of ordination space (Table 2). In general, our communities fit into the broad exploratory classes of Scott and Bergstrom (in press).

In Community 1, *Poa annua* had its highest mean abundance out of all the communities and was the only species with its peak abundance

1523-0430/05 $7.00

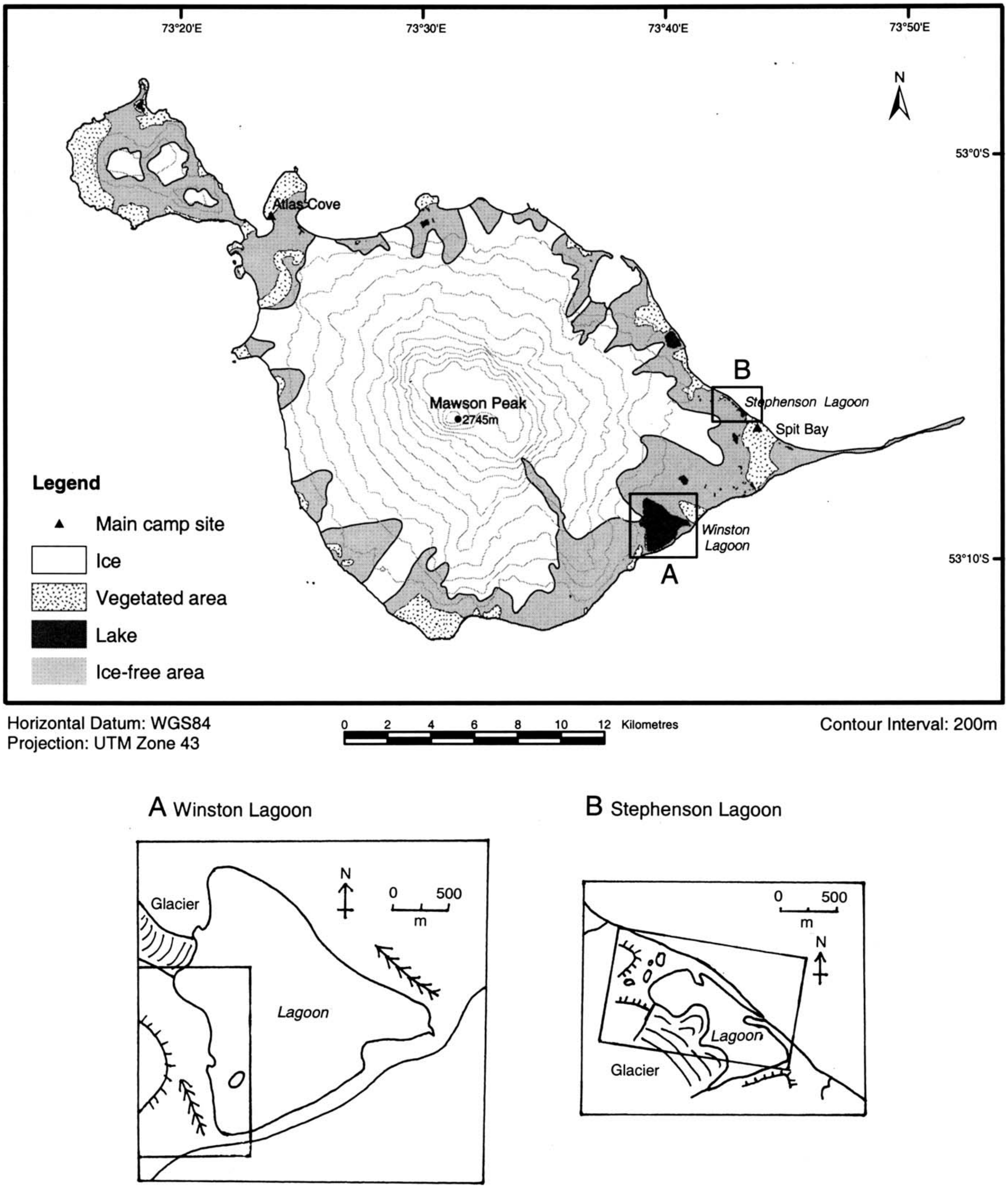

FIGURE 1. Location of Heard Island and study sites. Locations of sites shown in Figure 2 are indicated by boxes on inset maps. Topographic data for Heard Island supplied by Australian Antarctic Data Centre.

in this community. *Poa kerguelensis* and *Pringlea antiscorbutica* had their lowest mean abundance. Community 1 falls within the "coastal biotic vegetation" complex and was located at low altitudes with gentle slopes, low rock cover, high water cover, and a moderate to high level of seal disturbance. Mean vegetation height and species richness were both relatively low (Table 2), and most quadrats were located on the Winston transects. In Community 2, *Callitriche antarctica*, *Deschampsia antarctica*, *Montia fontana*, *Poa cookii*, and *Ceratodon purpureus* had their highest mean abundance, and mean vegetation height and species richness were the highest for the four communities. Community

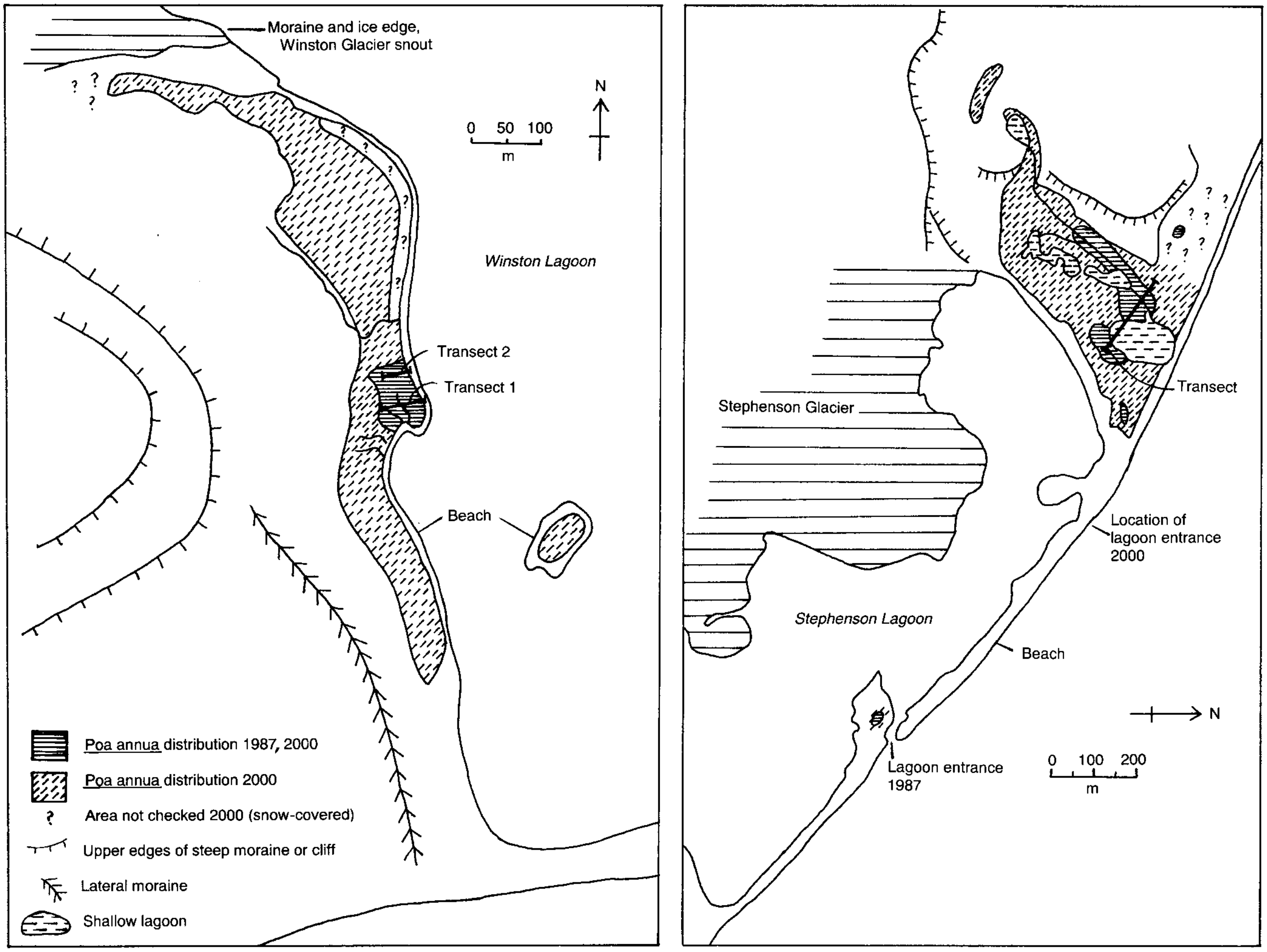

FIGURE 2. Winston Lagoon and Stephenson Lagoon sites: location of transects and changes in *Poa annua* distribution, 1987–2000.

2 is included in the "wet mixed herbfield" complex and occupied low altitudes with moderate slopes, low rock cover, high water cover, and a moderate to low level of seal disturbance (Table 2). All quadrats were from the Winston transects.

In Community 3, *Azorella selago*, *Pringlea antiscorbutica*, and *Ceratodon purpureus* had their highest mean abundance values. Community 3 fits between the "wet mixed herbfield" complex and "open cushionfield" vegetation categories, and occupied drier locations than the previous two communities, at low altitudes with moderate slopes and low rock cover, and a moderate to low level of seal disturbance. Mean vegetation height and species richness were both relatively high (Table 2), and nearly all quadrats were from the Winston transects. In Community 4, *Colobanthus kerguelensis* and *Poa kerguelensis* had their highest mean abundance and *Azorella selago* its second highest mean abundance, while *P. annua*, *Callitriche antarctica*, *Deschampsia antarctica*, *Montia fontana*, *P. cookii*, and *Ceratodon purpureus* had their lowest. Community 4 corresponds to "open cushionfield/unstable fellfield" vegetation and occupied higher altitudes with gentle slopes, high rock cover, low water cover, and moderate to low seal disturbance levels. It had relatively low mean vegetation height and species richness, and nearly all quadrats were located on the Stephenson transect.

Most quadrats that were in Communities 2 and 4 in 1987 remained in these communities in 2000 (Table 1). Of the 12 quadrats in Community 3 in 1987, only six remained in this community in 2000, the remainder moving to Community 1 (four quadrats) and Community 2 (two quadrats). The five quadrats that were in Community 1 in 1987 remained there in 2000 (Table 1), and the community gained another seven quadrats from Communities 2, 3, and 4 (mainly from Community 3). Thus, the major transition in the time period was from Community 3 to Community 1, and the major changes occurred on the Winston transects rather than the Stephenson transect. As indicated in Table 2, the transition was to a less species-rich community characterized by lower vegetation height; a higher abundance of *P. annua*, *Callitriche antarctica*, and *P. cookii*; and a lower abundance of *Azorella selago*, *Colobanthus kerguelensis*, *Deschampsia antarctica*, *Montia fontana*, *P. kerguelensis*, *Pringlea antiscorbutica*, and *Ceratodon purpureus*. In environmental terms, the transition was to a situation where elephant

TABLE 1

Transition matrix of communities, 1987–2000. Cells show the number of quadrats that were classified into one group in 1987 and the same or another in 2000 (e.g., the top left-hand cell records 5 quadrats that fell in community one in both 1987 and 2000).

	Community 2000				
Community 1987	1	2	3	4	Total
1	5	0	0	0	5
2	2	2	0	0	4
3	4	2	6	0	12
4	1	0	1	14	16
Total	12	4	7	14	37

TABLE 2

Mean value of attributes by community. Means for a community are statistically identical at $P > 0.05$ (*t*-test) to another community if the letter(s) next to the first community also occur as a part or whole of the letters next to another community. The probability value in the last column is derived from one-way ANOVA. Cover scores were used as input for bare ground, rock, water and plant species. Visual estimate classes were used for seal disturbance (see Methods), while "mds" represents ordination axis scores.

	Community				
Variable	1	2	3	4	*P*
Altitude (m)	3.1a	3.9a	3.5a	6.3b	0.000
Aspect (deg.)	177a	135a	163a	133a	0.278
Slope (deg.)	4.3a	9.4b	9.5b	5.7a	0.000
Soil depth (cm)	8.1a	7.0a	7.0a	8.2a	0.871
Bare ground	3.8a	3.2a	3.7a	3.7a	0.352
Rock cover	3.4a	3.2a	3.9a	4.8b	0.000
Water cover	1.8a	2.5a	0.0b	0.5b	0.000
Seal disturbance	2.4a	1.8b	1.8b	1.8b	0.004
Vegetation ht (cm)	11.5a	16.9ab	16.3ab	10.5ac	0.003
mds 1	0.45a	0.53a	0.87b	0.26c	0.000
mds 2	1.11a	0.72b	0.72b	0.98a	0.000
mds 3	−0.10a	0.24b	0.15b	−0.04a	0.001
Richness	5.4a	11.0b	9.3b	5.1a	0.000
Poa annua	3.3a	3.2ab	2.0bc	1.7c	0.003
Azorella selago	0.8a	1.6abc	2.8b	1.9c	0.001
Callitriche	1.4a	3.0b	0.4c	0.2c	0.000
Colobanthus	0.2a	1.1b	1.4b	1.6b	0.000
Deschampsia	0.5a	2.2b	1.6b	0.2a	0.000
Montia	1.0a	2.6b	1.8c	0.1d	0.000
Poa cookii	2.9a	3.2a	2.5a	0.5b	0.000
Poa kerguelensis	0.1a	0.2a	1.0b	1.5b	0.000
Pringlea	0.3a	2.2bc	2.8b	1.9c	0.000
Ceratodon	0.6a	1.4b	1.4b	0.0c	0.000

TABLE 3

Means for variables and taxa for 1987 and 2000 and the ratios between them. The probability level is from the paired *t*-test. Cover scores were used as input for bare ground, rock, water, and plant species. Visual estimate classes were used for seal disturbance (see Methods), while "mds" represents ordination axis scores.

Variable	1987	2000	2000/1987	*P*
mds 3	0.16	−0.12	−0.75	0.000
Pringlea antiscorbutica	2.28	1.20	0.53	0.000
Deschampsia antarctica	1.03	0.59	0.57	0.009
Bryum/*Pohlia* spp.	0.31	0.18	0.58	0.230
Ceratodon purpureus	0.77	0.49	0.64	0.020
Marchantia berteroana	0.33	0.21	0.64	0.257
Vegetation height (cm)	14.8	10.3	0.70	0.000
mds 1	1.04	0.81	0.78	0.000
Colobanthus	1.28	1.00	0.78	0.054
Poa kerguelensis	1.00	0.79	0.79	0.073
Bare ground cover	3.97	3.46	0.87	0.001
Montia fontana	1.00	0.95	0.95	0.570
Rock cover	4.13	4.00	0.97	0.442
mds 2	0.91	0.89	0.98	0.617
Richness	6.64	6.64	1.00	1.000
Acaena magellanica	0.15	0.18	1.20	0.786
Poa cookii	1.67	2.00	1.20	0.026
Polytrichastrum alpinum	0.08	0.10	1.25	0.661
Seal disturbance	1.72	2.18	1.27	0.001
Water cover	0.74	1.13	1.53	0.030
Azorella selago	1.31	2.31	1.76	0.000
Poa annua	1.46	3.08	2.11	0.000
Callitriche antarctica	0.51	1.13	2.22	0.000
Ditrichum sp.	0.05	0.18	3.60	0.096
Filamentous green algae	0.08	0.41	5.12	0.014

seal disturbance was greater and there was more free-standing water. The increase in free-standing water is a likely consequence of seal trampling and wallowing, although seasonal snow melt may have also played a role, as the 2000 measurement was done in November with remnant winter snow-cover and the 1987 measurement in December, when all snow had melted.

P. annua, *Callitriche antarctica*, *Azorella selago*, *P. cookii*, and filamentous green algae significantly increased in abundance between 1987 and 2000 (Table 3). *Pringlea antiscorbutica*, *Deschampsia antarctica*, and *Ceratodon purpureus* significantly decreased in abundance over the same time period (Table 3). Despite considerable and consistent compositional change, as shown in significant reductions in mds (ordination) axis one and three scores (Table 3), mean species richness did not change (Table 3). Vegetation height declined significantly (Table 3), a phenomenon largely associated with the destruction of *Pringlea antiscorbutica* by a significant increase in seal disturbance (Table 3). Bare ground significantly decreased ($P < 0.01$), while water cover significantly increased ($P < 0.05$), and rock cover remained relatively constant (Table 3).

In 28 of the 37 quadrats, *P. annua* cover increased between 1987 and 2000. Its cover decreased in three quadrats and remained the same in six. The three quadrats in which it decreased had more than 50% cover of the species in 1987. Four of the quadrats that remained the same had no *P. annua* cover in 1987. The change score for *P. annua* was significantly positively correlated with slope in 1987 ($r = 0.388$, $P = 0.015$), bare ground in 1987 ($r = 0.369$, $P = 0.021$), the change score for the third ordination axis mds 3 ($r = 0.685$, $P = 0.000$), the change score for seal disturbance ($r = 0.414$, $P = 0.009$), and the change score for *Callitriche antarctica* ($r = 0.352$, $P = 0.028$). It was significantly negatively associated with the change score for bare ground ($r = -0.432$, $P = 0.006$) and the change score for the first ordination axis mds 1 ($r = -0.481$, $P = 0.003$). These relationships indicate that the expansion of *P. annua* was associated with expansion and/or intensification of disturbance by seals, which also favored expansion of *Callitriche*, an oft-noted characterizer of the vegetation of old seal wallows (Scott and Bergstrom, in press). *P. annua* expanded more where there was bare ground in 1987, a partial consequence of this expansion being a decrease in bare ground between 1987 and 2000.

The many significant changes in abundance recorded for other taxa do not appear to be the result of the expansion of *P. annua*, given that the only change score that was significantly correlated with the *P. annua* change score seems to be clearly explained by the increased seal activity, which was also associated with *P. annua* expansion. It seems highly likely that the decrease in abundance of *Pringlea*, *Deschampsia*, and *Ceratodon* relates to trampling by molting elephant seals and that the increase in filamentous green algae relates to an increased number of damp, fertile hollows created by their wallowing. The expansion of *Azorella selago* is most logically related to ongoing colonization of glacial moraines in an environment of climatic amelioration, likewise the expansion of *P. cookii*, although the latter is also favored by the ongoing addition of nutrients from molting seals (Scott and Bergstrom, in press). The change scores for a large proportion of the taxa were significantly positively correlated with the change score for species richness and the change score for the second ordination axis mds 2 (Table 4), whereas the change scores for *P. annua* were significantly correlated with change scores for mds 1 and mds 3, indicating independence of the change in *P. annua* from general changes in species richness.

Discussion

Between 1987 and 2000, the areal extent, density, and abundance of *P. annua* in the original two populations at Winston and Stephenson Lagoons increased markedly (Fig. 2). At the Winston site in 1987, the transects had reached to the outer extent of the *P. annua* population, an area of about 100 × 70 m. The greatest concentration of plants in 1987 occurred in a moist area of 20 × 30 m intensively used by molting elephant seals and centered around several springs and stream-lines in a shallow embayment adjacent to the lagoon. Only a scattering of plants occurred beyond this embayment. In 2000, some areas of dense *P. annua* growth had expanded beyond the original outer extent of 100 × 70 m, and a scattering of plants extended for over 600 m north and northwest and over 380 m to the south (Fig. 2).

At Stephenson Lagoon in 1987, *P. annua* occurred within several similar sized areas which were also utilized by molting seals, but growth was less prolific (Scott, 1989). Overall vegetation cover was more sparse, indicative of well-drained moraines, and level of use by molting seals was lower than at the Winston site (H. Burton and J. J. Scott, unpublished data). *P. annua* occurred in several small discontinuous swards on dry gravelly seal-molt areas at the bases of low rocky moraines, and numerous scattered plants occurred along stream-lines connecting shallow lagoons amongst the moraines (Scott, 1989). See Figure 2. In 2000 the range and density of *P. annua* had increased overall in these habitats, although several of the smaller swards noted in 1987 had disappeared and been replaced by scattered *Azorella* cushions. *P. annua* had formed extensive swards, often with *Deschampsia*, on the sand/gravel flats adjacent to the central shallow lagoon, and was also found up to 450 m inland in small patches of mire vegetation on steep rocky moraines away from the influence of molting seals (Fig. 2).

The average rate of spread at the two sites between 1987 and 2000 was >100 m y^{-1}. This is similar to average rates of spread for several introduced plant species documented for Marion Island, although the rate of spread of *P. annua* on Marion was somewhat lower (Gremmen and Smith, 1999). Our data set provides no direct evidence that *P. annua* displaces other plant species in undisturbed vegetation. Rather, *P. annua* is favored by the disturbances of seals (bare ground, manuring), along with some other taxa. Along with *Callitriche antarctica* and *Montia fontana*, *P. annua* was commonly observed invading damaged tussocks of *P. cookii* and *Deschampsia* once bare peat was exposed by seal trampling. However, in November 2000, small *P. annua* plants were occasionally seen growing in undamaged *Azorella* cushions at the Winston site, and also growing on moraines inland of seal-influenced vegetation at both sites, either at the edges of apparently undisturbed mire vegetation or in moist mineral soils on sparsely vegetated moraines. To invalidate the hypothesis that *P. annua* will displace other plants on Heard Island would require frequent temporal data from photographic plots and some critical experimental work. The data analyzed here suggest strongly that the process of establishment and spread of *P. annua* is largely independent of ongoing processes of vegetation change on glacial moraines, apart from sites where vegetation development is influenced by seal disturbance.

Molting elephant seals appear to have had a major influence in the establishment and spread of *P. annua* at its two main sites on Heard Island. The apparent increase in levels of seal disturbance at the two sites as indicated by our data, especially at the Winston site, is unlikely to reflect an overall increase in elephant seal numbers on Heard Island. A population decline documented between 1949 and 1985 appears to have halted, with an intrinsic rate of increase of 0–0.9% per year since 1985 (Slip and Burton, 1999). It is more likely that the recorded increase in seal disturbance on the two sites relates to the development of vegetation which is adapted to a regime of seasonal disturbance and which in turn provides an increasingly attractive molting habitat.

TABLE 4

Correlations between change scores for taxa and those for the scores of the ordination axes and species richness; * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Taxon	Richness	mds1	mds2	mds3
Poa annua	0.234	−0.481**	0.089	−0.628***
Callitriche antarctica	−0.183	−0.247	0.117	−0.246
Azorella selago	0.502**	0.421*	−0.773***	0.246
Colobanthus	0.587***	0.133	−0.341*	0.095
Deschampsia antarctica	0.587***	−0.084	−0.263	0.248
Montia fontana	0.434**	−0.010	−0.142	0.048
Poa cookii	0.450**	−0.138	−0.111	0.055
Poa kerguelensis	0.207	0.323	−0.462**	0.014
Pringlea antiscorbutica	0.483**	−0.081	−0.220	−0.053
Ceratodon purpureus	0.497**	0.073	−0.545***	0.128
Marchantia berteroana	0.582***	0.126	−0.358*	0.274
Bryum/*Pohlia* spp.	0.561***	−0.072	−0.387*	0.020
Ditrichum sp.	0.402*	0.276	−0.348*	0.112
Polytrichastrum alpinum	0.323*	0.033	−0.217	0.106
Filamentous green algae	0.413**	−0.118	−0.054	−0.067

It is apparent from our investigations that *P. annua* can also spread further afield into areas away from the influence of seals. An important factor here is climatic warming (see Thost and Allison, in press) and the new areas of ice-free land, along with the competition-free seedbed which these provide (Scott, 1990; Smith, 1986). On Marion Island, Gremmen (1997) has suggested that the increase in abundance of *P. annua* noted over the past two decades is related to temperature increases during this time, while on subantarctic Iles Kerguelen (Frenot et al., 1997, 1998) and South Georgia (Smith, 2000), *P. annua* has been noted as an early colonizer of recently deglaciated environments. However, on Iles Kerguelen it is relatively transient in primary succession on newly deglaciated land due to a poor ability to access soil nutrients once nutrients leach downwards through the developing soil profile, while deeper-rooting species such as *Poa kerguelensis* are better long-term survivors in such environments (Frenot et al., 1998). *P. annua* usually requires ongoing biotic disturbance to provide bare ground through trampling, and nutrient enrichment through manuring and molting, to become a locally dominant component in subantarctic vegetation. Its dominance in vegetation of biotically influenced sites such as seasonally disturbed elephant seal wallows has been previously noted for Iles Kerguelen and Crozet (Frenot et al., 2001) and Marion Island (Gremmen, 1981, 1997), and for heavily grazed and trampled reindeer areas on South Georgia (Walton and Smith, 1973; Smith, 2000). On Macquarie Island, *P. annua* thrives mainly on sites subject to disturbance such as seal wallows (Selkirk et al., 1990) and areas adjacent to penguin colonies. It also colonizes bare soil on new landslips and sites heavily grazed by rabbits, but it tends to be outcompeted by native species within several years on these sites if disturbance is not continued (Scott, 1995; J. J. Scott and J. B. Kirkpatrick, unpublished data).

On Heard Island, the patterns of *P. annua* establishment and expansion documented so far appear to fit the patterns described for other subantarctic islands. It can be predicted that *P. annua* will continue to spread around the island, colonizing coastal vegetation which is subjected to seasonal disturbance by seals and penguins both in recently deglaciated areas and areas of longer-established vegetation. Unknown factors in predicting its further expansion on Heard Island, especially into areas not affected by biotic disturbance, include the nutrient regimes of soils developing on recently deglaciated areas. This requires testing. For example, the extensive *P. annua* swards which have appeared at the Stephenson site since 1987 have mostly developed on relatively fine morainal outwash material along the edges of shallow lagoons and stream-lines, and may be benefiting from nutrient-rich deposits associated with changing levels in these water-bodies as well as from the presence of molting seals. No *P. annua* was found along a series of well-established and richly vegetated mires at the inland edge of moraines at the Winston site, suggesting that established vegetation communities which lack bare ground and which are not subject to biotic disturbance are not easily invaded by the species. This has certainly been observed at Marion Island (Gremmen, 1981), South Georgia (Walton and Smith, 1973) and Macquarie Island (Scott, 1995).

The rapid environmental changes which Heard Island is currently undergoing as a result of climatic warming and deglaciation makes introduction and establishment of further plant species likely, whether or not they are (a) aliens or indigenous species and (b) introduced by humans or dispersed naturally. Comprehensive quarantine measures applying to all visitors, and provisions for investigating and responding to new species recorded on the island, are a key part of the new management plan being prepared by the Australian Antarctic Division (E. McIvor, personal communication). These measures aim to ensure that Heard Island's status is maintained as a World Heritage subantarctic island still relatively undisturbed by humans.

Acknowledgments

Thanks to the Australian Antarctic Division for Scott's participation in the 1986–1987, 1987–1988, and 2000–2001 Australian National Antarctic Research Expeditions to Heard Island. Thanks also to Ewan McIvor, AAD, for helpful comments on an earlier version of the manuscript and for later discussions, Yves Frenot for useful discussions in the field, and the Australian Antarctic Data Centre for providing the data for Figure 1.

References Cited

Frenot, Y., and Gloaguen, J.-C., 1994: Reproductive performance of native and alien phanerogams on a glacier foreland, Iles Kerguelen. *Polar Biology,* 14: 473–481.

Frenot, Y., Gloaguen, J.-C., and Tréhen, P., 1997: Climate change in Kerguelen Islands and colonization of recently deglaciated areas by *Poa kerguelensis* and *P. annua*. *In:* Battaglia, B., Valencia, J., and Walton, D. W. H. (eds.), *Antarctic Communities: Species, Structure and Survival*. Cambridge: Cambridge University Press, 358–566.

Frenot, Y., Gloaguen, J. C., Cannavacciuolo, M., and Bellido, A., 1998: Primary succession on glacier forelands in the subantarctic Kerguelen Islands. *Journal of Vegetation Science,* 9: 75–84.

Frenot, Y., Gloaguen, J.-C., Massé, L., and Lebouvier, M., 2001: Human activities, ecosystem disturbance and plant invasions in subantarctic Crozet, Kerguelen and Amsterdam Islands. *Biological Conservation,* 101: 33–50.

Frenot, Y., Chown, S. L., Whinam., J., Selkirk, P. M., Convey, P., Skotnicki, M., and Bergstrom, D. M., 2005: Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews,* 80: 45–72.

Gremmen, N. J. M., 1981: *The Vegetation of the Subantarctic Islands Marion and Prince Edward*. The Hague: Junk Publishers, 145 pp.

Gremmen, N. J. M., 1997: Changes in the vegetation of sub-Antarctic Marion Island resulting from introduced vascular plants. *In:* Battaglia, B., Valencia, J., and Walton, D. W. H. (eds.), *Antarctic Communities: Species, Structure and Survival.* Cambridge: Cambridge University Press, 417–423.

Gremmen, N. J. M., and Smith, V. R., 1999: New records of alien vascular plants from Marion and Prince Edward Islands, sub-Antarctic. *Polar Biology,* 21: 401–409.

Kiernan, K., and McConnell, A., 1999: Geomorphology of the sub-antarctic Australian Territory of Heard Island–McDonald Island. *Australian Geographer,* 30: 159–195.

Minchin, P., 1990: *DECODA—Database for Ecological Community Data*, Version 2.02. Canberra: Australian National University.

Ruddell, A., in press: An inventory of present glaciers on Heard Island and their historical variation. *In:* Green, K., and Woehler, E. (eds.), *Heard Island: Southern Ocean Sentinel.* Chipping Norton, Australia: Surrey Beatty and Sons.

Scott, J. J., 1989: New records of vascular plants from Heard Island. *Polar Record,* 25: 37–42.

Scott, J. J., 1990: Changes in vegetation on Heard Island 1947–1987. *In:* Kerry, K. R., and Hempel, G. (eds.), *Antarctic Ecosystems, Ecological Change and Conservation.* Berlin: Springer Verlag, 61–76.

Scott, J. J., 1995: Changes in vegetation on Macquarie Island coastal slopes, 1980–1990. PhD thesis, University of Tasmania, Hobart, 340 pp.

Scott, J. J., and Bergstrom, D. M., in press: Vegetation of Heard and McDonald Islands. *In:* Green, K., and Woehler, E. (eds.), *Heard Island: Southern Ocean Sentinel.* Chipping Norton, Australia: Surrey Beatty and Sons.

Selkirk, P. M., Seppelt, R. D., and Selkirk, D. R., 1990: *Subantarctic Macquarie Island: Environment and Biology*. Cambridge: Cambridge University Press, 285 pp.

Slip, D. J., and Burton, H. R., 1999: Population status and seasonal haulout patterns of the southern elephant seal (*Mirounga leonina*) at Heard Island. *Antarctic Science,* 11: 38–47.

Smith, J. M. B., 1986: Origins of Australasian tropicalpine and alpine floras. *In:* Barlow, B. (ed.), *Flora and Fauna of Alpine Australasia. Ages and Origins.* Melbourne: Commonwealth Scientific and Industrial Research Organisation, 109–128.

Smith, R. I. L., 2000: Plant colonisation on a 45-year sequence of annual micromoraines on a South Georgia glacier foreland. *In:* Davison, W., Howard-Williams, C., and Broady, P., *Antarctic Ecosystems: Models for Wider Ecological Understanding.* Christchurch, New Zealand: Caxton Press, 225–232.

Thost, D., and Allison, I., in press: The climate of Heard Island. *In:* Green, K., and Woehler, E. (eds.), *Heard Island: Southern Ocean Sentinel.* Chipping Norton, Australia: Surrey Beatty and Sons.

Walton, D. W. H., and Smith, R. I. L., 1973: Status of the alien vascular flora of South Georgia. *British Antarctic Survey Bulletin,* 36: 79–97.

Revised ms submitted December 2004