CHAPTER 9

TERRESTRIAL VEGETATION AND DYNAMICS

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From offshore the Prince Edward Islands appear bleak and barren with monotonous vegetation, mainly due to the absence of trees or shrubs. Closer inspection, of the low altitude regions at least, reveals dense and often complex vegetation consisting of a variety of plant communities distributed along gradients of moisture, exposure and soil nutrient status. Vascular plants determine the physiognomy of the vegetation at low altitudes, but in almost all the communities there is a diversity and abundance of bryophytes. At higher altitudes cryptogams become dominant. Above 600 m only one vascular species occurs and the vegetation is sparse and consists mainly of mosses and lichens.

The impoverished flora and harsh climate of the islands result in a close coupling of plant community structure with abiotic and biotic factors. Soil moisture and exposure to wind (the latter through its direct effect on the plants through chilling, drying, mechanical injury, as well as its indirect effects through changing the micro- and mesoclimate) are the most important of these, so that the pattern of variation in species composition and vegetation structure between plant communities is dominated by a conspicuous gradient from dry-exposed to wet-sheltered conditions (Smith & Steenkamp 2001). Related to this gradient is a change in soil type, from organic peats at sheltered sites to mineral soils at exposed ones. At any point along the wet/sheltered/organic to dry/exposed/mineral gradient the type of vegetation that develops depends

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on the intensity to which the site is influenced by wind-blown saltspray and manuring and trampling by seals and seabirds. This interaction of abiotic and biotic gradients gives rise to a complex mosaic of habitats and plant communities. Other factors are also important. For instance, soil hydrology strongly influences community composition, so that ombrotrophic (rainwater-influenced) mires have a very different species composition to minerotrophic (groundwater-influenced) mires, and drainage lines in slopes support a very different vegetation to that of the slopes (Gremmen 1981). Differences in geological substratum also add to the complexity of the vegetation cover.

In this chapter we describe the flora of the two islands and give an overview of the ecology and distribution of the vegetation types on Marion Island. We present the main patterns of vegetation succession and how the vegetation has changed due to changes in the population sizes of seals and seabirds and the impact of human activities, including the introduction of alien plant species.

9.1 The Flora

Only 23 indigenous vascular plant species occur on Marion Island and 21 on Prince Edward Island (Appendix IV). The bryophyte and lichen floras are much more diverse: 90 mosses and 44 liverworts have been recorded on Marion Island and 63 mosses and 29 liverworts on Prince Edward Island (Appendices II & III). For both islands together, 118 lichen species have been recorded (Appendix V). About 5% of the island's indigenous plant species appear to be restricted to the Prince Edward Islands, while about 20% are endemic to the Southern Indian Ocean Province islands (the Prince Edward Islands, Heard and Macdonald Islands, Îles Kerguelen, Îles Crozet). This is a preliminary estimate of the flora's endemism, because the bryophyte and lichen floras of many of the sub-Antarctic islands have been insufficiently studied and many taxonomic problems need to be resolved. Biogeographical relationships of the islands' biota are discussed by Chown *et al.* (2008).

Eighteen "alien" (introduced by humans) vascular species have been recorded on Marion Island and three on Prince Edward Island (Table 9.1). Six of these have disappeared again or have been eradicated. There are another three vascular species on Marion Island whose status is unclear and which do not occur on any other sub-Antarctic island. *Juncus* cf. *effusus* occurs at three widely separated sites in the north-eastern coastal plain. The other two species with unknown status (*Luzula* cf. *multiflora* and an unidentified thorny shrub) were discovered only recently, at sites far away from the meteorological station, the most likely place for the introduction of plants by humans.

Table 9.1 Status and distribution of the introduced vascular plants at the Prince Edward Islands. (WS) means the species was introduced at the weather station after 1948. (SS) means it was introduced by sealers or shipwrecked parties, at a site or sites other than the weather station and probably in the 1800s. From Gremmen (1975, 1982), Gremmen & Smith (1999) and Ryan *et al.* (2003).

Species	Distribution and locality of introduction
Transient aliens	
<i>Avena sativa</i>	Meteorological station (WS)
<i>Holcus lanatus</i>	Meteorological station (WS)
<i>Hypochoeris radicata</i>	Meteorological station (WS)
<i>Plantago lanceolata</i>	Meteorological station (WS)
Naturalised aliens with a restricted distribution	
<i>Agropyron repens</i>	One large patch at Ship's Cove, c. 250 m ² ; eradication in progress (SS)
<i>Alopecurus geniculatus</i>	One small (< 1 m ² patch) at Mixed Pickle Cove (SS)
<i>Festuca rubra</i>	One patch at Ship's Cove, a group of patches 1500 m inland (SS)
<i>Rumex acetosella</i>	4 sites; meteorological station, Skua Ridge, Sealer's Cave, and Goney Plain (SS)
Naturalised aliens with a widespread distribution	
<i>Agrostis castellana</i>	At meteorological station, Albatross Lakes and Trypot Beach (WS)
<i>Agrostis stolonifera</i>	Widespread on Marion Island (WS)
<i>Cerastium fontanum</i>	Widespread on Marion Island; on western part of Prince Edward Island (SS)
<i>Poa annua</i>	Widespread on Marion and Prince Edward Islands (SS)
<i>Poa pratensis</i>	Between Ship's Cove and Stony Ridge (WS)
<i>Sagina procumbens</i>	Widespread on both islands (WS)
<i>Stellaria media</i>	Widespread on Marion Island (SS)
Unclassified aliens	
<i>Agrostis gigantea</i>	At meteorological station in 1994 about 4 m ² , increased to about 200 m ² in 1996. Eradicated by 2006 (WS)
<i>Senecio sp.</i>	At meteorological station in 1988; all plants removed (WS)
<i>Sonchus sp.</i>	At meteorological station in 1983, 1984, 1998; all plants removed each time (WS)
Status unknown	
<i>Juncus cf. effusus</i>	Three patches: near Trypot Beach, east of Ship's Cove, Goney Plain
<i>Luzula cf. multiflora</i>	Several large and many small patches in a c.1 ha area north of Sealer's Cave
<i>Unidentified shrub</i>	One patch (plant?) discovered between Arthur's Hill and Kildalkey Bay in 2004.

Seven of the alien vascular species on Marion Island were introduced at sites of sealers' camps or shipwreck sites (Gremmen 1975, 1981) and three of those were widespread on the island when the vegetation was first surveyed in 1965/66 (Huntley 1971). Since the establishment of the weather station at Transvaal Cove in 1948, 14 new introductions have been observed there, some being re-introductions of species that had been eradicated previously (Gremmen & Smith 1999). Some of the introduced species have not spread far from the station but others have dispersed widely, at rates of up to 400 m per year. Two have crossed the 22 km of ocean between Marion and Prince Edward Island, apparently without human assistance (Bergstrom & Smith 1990; Ryan *et al.* 2003). The influence of alien vascular species on the vegetation is discussed later.

Despite the preventative measures that have been put in place (De Villiers & Cooper 2008) new species continue to be recorded at or near the station. Since 1990 there have been four successful introductions, i.e. that resulted in the species becoming established (Gremmen & Smith 1999). In all four cases the plants were eradicated.

Only two moss species are suspected as being human-introduced, mainly because of their highly disjunct global distribution (Ochyra *et al.* 2003). *Thuidium delicatulum* occurs only in a small area near the meteorological station, and nowhere else in the sub-Antarctic, or in Africa, southern South America and Oceania. *Leptodontium gemmascens* is a European species that is not found anywhere between Europe and the island. It is consistently sterile and is dispersed over short distances by gemmae, which are too large to be good candidates for long-distance transoceanic dispersal (Ochyra *et al.* 2003).

9.2 Vegetation, plant communities and habitats

Huntley (1971) classified the islands' vegetation on floristic composition and autecological characteristics of the dominant species and recognized 13 plant communities (which he called "noda"). He grouped these into five complexes, based on the most important factor controlling their distribution (salt-spray, manuring and trampling, exposure, and drainage). Gremmen (1981) used floristic data in a phytosociological approach to classify the island's vegetation into 41 communities and then combined the floristic data with environmental information (soil depth, moisture content, pH, loss-on-ignition, depth of groundwater, severity of manuring and trampling by animals and of salt spray) to group the plant communities in six community complexes. Smith & Steenkamp (2001) applied ordination and clustering methods to vegetation and soil chemistry information to compile a classification of Marion Island's terrestrial habitats. They grouped the habitats into six habitat complexes and added one more complex in order to accommodate polar desert, the most widespread of the island's vegetation types.

In the recently produced map of the vegetation of South Africa, two biomes were recognized on the islands, the sub-Antarctic Tundra Biome and the

Polar Desert Biome (Smith & Mucina 2006). The vegetation mapping units defined for sub-Antarctic Tundra Biome were Coastal Vegetation, Biotic Herbfield and Grassland, Mire, Drainage Line & Spring Vegetation, Fernbrake Vegetation, Fellfield Vegetation and Cinder Cone Vegetation. The Polar Desert Biome comprises only one vegetation unit, sub-Antarctic Polar Desert. The distributions, important taxa, geology, soils, hydrology, climate and landscape patterns of these units are described by Smith & Mucina (2006). However, the units are too broad to allow a detailed account of the ecology, distribution and successional pattern of the islands' vegetation types. To achieve this, we hybridised the ecological classification of Huntley (1971), the floristic classification of Gremmen (1981) and the habitat classification of Smith & Steenkamp (2001). Since edaphic and ecological criteria, and not only floristics, were important in defining the categories in the hybridised classification, we prefer to term the categories "habitats" rather than plant communities or vegetation types. Table 9.2 lists the habitats and the total areas they occupy on Marion Island and provides some information on the chemical composition their soils. Fig. 9.1 shows the positions of the habitats on two ordination axes from a Canonical Correspondence Analysis that defined the habitats. Interpretations of the edaphic gradients represented by the axes are given, as are the directions of the main ecological forcing variables that determine vegetation succession on the islands. Table 9.3 gives the areas occupied by the various habitat complexes at different altitudes.

9.2.1 Mire Complex

Oligotrophic mires form a conspicuous and extensive component of the islands' lowland areas (Plate 9.1, 9.2). The habitats in the Mire Complex have vegetations that are physiognomically almost identical (dominated by bryophytes) and they have similar soil characteristics (highly organic, wet peats that may be deep and are mostly very nutrient-poor). One or more of three graminoid species (*Agrostis magellanica*, *Uncinia compacta* and *Juncus scheuchzerioides*) generally form a canopy over the bryophyte layer. High moisture content is the principal soil characteristic of mire habitats but the nature of the soil water (ombrotrophic, directly from rain or minerotrophic, from surrounding slopes) is cardinal to what type of mire develops. Also, subtle differences in soil moisture content, watertable depth, and the degree to which watertable depth fluctuates, result in marked differences in plant species composition. These changes may occur over short distances (meters) to produce areas with a fine-scale spatial mosaic of mire communities that may extend over many thousands of square meters. Gremmen (1981) distinguished 18 mire communities. We have grouped them into four habitats, following Smith & Steenkamp (2001); Wet mires, Mesic mires, Dry mires and Mire drainage lines. Together, these mire habitats occupy about 22 km² of the total island area, but are almost wholly restricted to the area where closed vegetation can occur (below 300 m a.s.l., Table 9.3). Biotic mires and Saline mires, which Smith & Steenkamp (2001) grouped in the Mire Complex, are here considered as part of the Biotic and the Saltspray Complexes, respectively.

Table 9.2 Terrestrial habitats of the Prince Edward Islands. Area is the total area occupied by the particular habitat on Marion Island, from measurements made in the 1990s. Area and soil chemistry values extracted from Smith *et al.* (2001). Habitat abbreviations in the first column are used in Fig. 9.1. Soil chemistry concentrations (min.-max.) are on an oven-dry mass basis. Exch. = exchangeable form of the particular cation.

Habitat	Area (ha)	pH	Moisture (%)	Organic C (%)	Organic N (%)	Total P (mg g ⁻¹)	Inorganic N (µg g ⁻¹)	Inorganic P (µg g ⁻¹)	Exch. Ca (% CEC)	Exch. Mg (% CEC)	Exch. K (% CEC)	Exch. Na (% CEC)
Mire Complex												
M.d.	792	4.5-5.3	506-1332	7-37	0.5-2.6	0.9-2.2	0-6	4-105	2-18	5-13	0-1.6	1-2
M.m.	570	4.2-5.3	725-1667	34-48	1.8-2.7	0.6-2.0	0-18	7-1.3	4-10	5-13	0.7-3.0	1-5
M.w.	597	4.3-5.5	1124-2263	31-41	1.0-2.5	0.8-2.0	1-59	12-198	0-23	4-15	0.1-1.1	1-3
M.dl.	246	5.5-6.2	433-1399	8-25	0.5-1.6	0.8-2.1	0-17	0-16	4-13	3-8	0-0.7	0.7-1
Slope Complex												
Sl.ofb.	429	4.5-5.0	238-870	13-32	0.9-2.6	0.5-2.4	0-15	4-44	0-13	2-14	0.2-1.2	0.5-5
Sl.cfb	1765	4.0-5.2	484-735	17-44	1.2-2.5	0.7-3.9	0-3	4-100	1-21	2-40	0.1-7.0	0.2-5
Sl.mfb.	111	5.0-5.4	610-812	23-25	1.6-2.0	1.5-1.9	6-9	4-11	1-9	4-9	0.5-0.7	0.2-1
Sl.dsfb.	113	4.4-4.6	545-782	21-28	1.8-2.3	2.0-2.9	0-0.3	1-16	6-13	3-7	0.2-0.3	0.3-1
Sl.d&s.	119	4.5-6.5	495-1002	5-43	0.3-2.5	0.7-2.8	3-13	6-23	4-27	6-32	0-2.0	1-4
Sl.s&f.	8	6.0-6.4	1049-1407	13-20	1.4-2.0	2.2-3.1	10-14	12-16	9-15	6-10	0.2-0.5	1-3

Table 9.2 Continued.

Habitat	Area (ha)	pH	Moisture (%)	Organic C (%)	Organic N (%)	Total P (mg g ⁻¹)	Inorganic N (µg g ⁻¹)	Inorganic P (µg g ⁻¹)	Exch. Ca (% CEC)	Exch. Mg (% CEC)	Exch. K (% CEC)	Exch. Na (% CEC)	
Fellfield Complex													
Ex.	Xeric Fellfield	7963	5.5-6.2	46-371	2-14	0.1-1.0	0.9-1.6	0-4	0-18	3-49	1-10	0-0.3	0.4-5
F.m.	Mesic Fellfield	5749	4.9-5.9	217-453	6-25	0.5-1.0	0.4-1.9	0-1	0-25	3-18	2-9	0.1-2.0	0.1-4
Polar Desert													
	Polar Desert	10876	-	-	-	-	-	-	-	-	-	-	
Coastal Saltspray Complex													
C.h.	Coastal Herbfield	57	4.8-7.1	121-770	8-36	0.5-2.5	0.9-1.7	2-34	13-180	14-38	18-37	0.3-2.0	14-35
C.f.	Coastal Fellfield	36	4.5-6.2	162-1107	9-44	0.7-3.1	0.5-1.2	2-2	23-100	11-17	16-50	0.2-0.6	8-46
C.sm.	Saline Mire	14	4.4-5.2	1225-2247	39-54	1.8-2.4	0.7-1.3	39-45	98-131	4-18	16-58	0.5-1.7	6-17
	Coastal Rock Habitat	?	-	-	-	-	-	-	-	-	-	-	-

Table 9.2 Continued.

Habitat	Area (ha)	pH	Moisture (%)	Organic C (%)	Organic N (%)	Total P (mg g ⁻¹)	Inorganic N (µg g ⁻¹)	Inorganic P (µg g ⁻¹)	Exch. Ca (% CEC)	Exch. Mg (% CEC)	Exch. K (% CEC)	Exch. Na (% CEC)
Biotic Complex												
	Pedestalled Tussock Grassland	13										
B.ptg.	(a) Pedestals	4.2-4.3	437-548	36-34	3.4-4.0	1.6-2.5	22-43	154-291	5-14	2-5	0-0.2	1-4
	(b) Mud between pedestals	4.5-4.9	295-849	13-30	1.1-3.2	1.3-1.9	12-92	70-257	10-24	8-22	0-0.1	2-4
B.ctg.	Coastal Tussock Grassland	75	3.8-4.7	429-610	32-40	2.4-4.7	2-18	33-997	6-13	1-4	0-0.1	0.5-3
B.itg	Inland Tussock Grassland	12?	3.8-4.9	355-960	19-32	1.5-3.7	8-61	11-347	0-14	1-13	0.1-1.0	1-5
B.Coth.	<i>Cotula</i> Herbfield	221	4.0-5.9	181-887	10-45	0.7-4.1	9-57	33-822	0-38	5-24	0.1-1.7	1-13
B.mud	Biotic Mud	27	3.7-5.6	520-1441	34-43	4.0-12.1	29-109	41-234	7-10	4-15	0-0.1	1-4
B.l.	Biotic Lawn	66	4.6-7.7	155-1194	12-37	1.2-4.1	15-27	40-1350	5-21	6-11	0-0.7	1-3
B.mire	Biotic Mire	41	4.7-5.6	1066-2015	38-42	2.2-3.4	8-48	159-281	0-9	8-14	0.2-1.5	2-4

Table 9.3 Percentages of the areas occupied by the various habitat complexes in four altitudinal zones on Marion Island.

Complex	0-100 m	100-300 m	300-500 m	>500 m
Mire	30	5	<0.1	0
Slope	26	11	<0.5	0
Fellfield	33	75	68	15
Polar Desert	1	8	32	85
Saltspray	2	0	0	0
Biotic	7	<0.1	<0.1	0
Total area:	61 km ²	81 km ²	60 km ²	98 km ²

Figure 9.1 Distribution of the terrestrial habitats of Marion Island along the first two axes of the ordination of soil and botanical variables that defined the habitats. Interpretations of the gradients in soil conditions represented by the axes are provided at the ends of the axes. The direction of the main ecological forcing variables that drive ecological succession on the island is shown by the dashed arrows. Modified from Smith & Steenkamp (2001).

The Wet Mire Habitat occurs on very wet peat soils. *Agrostis magellanica*, *J. scheuchzerioides* and *Ranunculus biternatus* are the dominant (and often the only) vascular species. There is usually a well-developed bryophyte stratum, dominated by *Sanionia uncinata*, *Distichophyllum fasciculatum*, *Blepharidophyllum densifolium* and/or *Clasmatocolea humilis*. The wet mire habitat comprises a range of plant communities, from pioneer communities dominated by graminoids and dense mats of bryophytes around ponds, lava-lakelets and lakes, through bryophyte-dominated, very wet depressions where the watertable is at or just below the surface for much of the time, to a high cover of both graminoids and bryophytes on deep consolidated peats where the watertable can be up to 20 cm below the surface but where capillarity ensures that the surface layer remains saturated.

Mesic Mire Habitat has lower soil moisture content than wet mire. The dominant bryophyte is usually *Jamesoniella colorata*, but wet mire species such as *B. densifolium* are often important. *Agrostis magellanica* and *J. scheuchzerioides* are the dominant vascular species.

Dry Mire Habitat occurs on relatively dry peats. *Jamesoniella colorata*, *Racomitrium lanuginosum* and *Ptychomnion densifolium* (= *P. ringianum*, see Appendix III) are usually the dominant bryophytes, and *Agrostis magellanica* and *U. compacta* the dominant vascular plants. Dry mire is the only mire habitat in which *Blechnum penna-marina* and the cushion plant *Azorella selago* may be significant components of the vegetation. Dry mire represents a transition between mire and fernbrake (specifically the Mesic Fernbrake Habitat), but also contains some sites that have floristic (presence of cushion dicots and pteridophytes) and soil chemistry (relatively low organic C, high total Ca and Mg contents) affinities with the Mesic Fellfield Habitat.

The mire habitats dealt with above are ombrotrophic so lateral water flow from surrounding areas does not affect the surface layers in which the vegetation is rooted. Where there are water tracks draining water from higher parts of the mire, or there is subsurface flow of water into the mire from an adjacent slope, the Mire Drainage Line habitat occurs, mostly in a narrow ribbon but sometimes over an extensive area (Plate 9.2). Mire drainage line peats are less acidic and possess higher Ca and Mg concentrations than peats of the other mire habitats. A number of bryophytes (e.g. *Breutelia integrifolia*, *Bryum laevigatum*, *Riccardia* spp. and, on more mineral soils, *Cryptochila grandiflora*) are restricted to, and dominant in mire drainage lines. Mire drainage lines become the predominant mire type with increasing altitude; between 0 to 100 m altitude they account for 7%, between 100 and 300 m for 16% and above 300 m for 80% of all the of mire vegetation in these zones. However, this does not mean that drainage line mires are a common habitat above 300 m; in total they occupy only about 5 ha.

Mire complex habitats all occupy that part of the ordination space in Fig. 9.1 where wetness and shelter (the two are partly confounded since protection

from wind reduces desiccation, but shelter also implies greater warmth) are the important ecological factors, and where manuring by seabirds or seals does not occur. This is consistent with the distribution of mires on the islands – restricted to wet, oligotrophic peats in sheltered, low-altitude areas away from the heaviest influence of saltspray.

9.2.2 Slope Complex

Most slopes at low and middle altitudes are covered by dense vegetation dominated by *B. penna-marina* and/or *Acaena magellanica*. Soils are well drained and, while still very organic, have a greater mineral content than mire soils, except for the surface layer which usually consists only of organic matter. The impact of animals or saltspray is negligible at all Slope Complex habitats. The main edaphic factors which distinguish the different slope habitats are related to water, especially soil moisture content and whether the hydrological regime is ombrotrophic or minerotrophic. Together, slope habitats occupy about 18% of the area where closed vegetation can develop (< 300 m altitude), about 25 km² in total. Above 300 m they are rare, occupying only about 20 ha.

Open Fernbrake occurs on shallow, mineral soils of dry slopes and on flat areas. The vegetation is open and has a scrubby appearance. *Blechnum penna-marina* shares dominance with other vascular species, mainly *A. selago*, *Agrostis magellanica* (usually growing epiphytically on *A. selago* cushions) and *Acaena magellanica*. Lichens and cushion-forming mosses occur, unlike at the other slope complex habitats. With regards to vegetation and soil development, Open Fernbrake represents a stage in the ecological succession from Mesic Fellfield to Closed Fernbrake, as is clear from its position in Fig. 9.1 and from comparisons of the rates of ecological functional processes (primary production, nutrient cycling, decomposition and soil respiration) between fellfield, Open Fernbrake and Closed Fernbrake (Smith 1987a, 1988a, b, 2003; Smith *et al.* 1993).

Closed Fernbrake is the most conspicuous and widespread slope habitat on the island and is the climax vegetation on inland slopes that are not directly influenced by seabirds or seals (Plate 9.3). It occurs on relatively dry, well-drained soils covered by a dense carpet of the fern *B. penna-marina*. Only 5-10 species (vascular plants and bryophytes) are found per 9 m² in Closed Fernbrake.

Mesic Fernbrake is found on damper slopes that are generally less steep than those occupied by Closed Fernbrake. It is also common on flat areas. The vegetation is still a carpet of *B. penna-marina*, but species diversity (up to 25 species per 9 m² plot) is higher than at Closed Fernbrake. Graminoids such as *U. compacta*, *Agrostis magellanica* and *Poa cookii* occur, as do ombrotrophic mire bryophytes (e.g. *S. uncinata*, *Lepidozia laevifolia*, *B. densifolium*), although never abundantly. Ecologically, Mesic Fernbrake represents a transition between closed fernbrakes and dry mire.

The Dwarf Shrub Fernbrake Habitat occurs in sheltered depressions on slopes otherwise dominated by Closed or Mesic Fernbrake. As well as *B. penna-marina*,

it is dominated by *Acaena magellanica* which although actually a suffruticose herb, is the only woody plant on the island and fulfils the same ecological role as deciduous dwarf shrubs in more temperate vegetations and shrub tundras of the Northern Hemisphere. The most common mosses are *Brachythecium rutabulum* and *S. uncinata*. Dwarf Shrub Fernbrake is intermediate between the Mesic Fernbrake Habitat and the Slope Drainage Line and Streambank Habitat described next.

The Slope Drainage Line and Streambank Habitat occurs on slopes where percolation of water down the soil profile is impeded (for example by an impermeable rock layer on grey lava slopes or a hard plinthic layer on some black lava slopes) so that there is substantial subsurface lateral movement of water. Stream banks form essentially the same habitat, where groundwater from the surrounding area drains into the stream. Such areas are minerotrophic, rather than an oligotrophic, and support a closed cover of *Acaena magellanica*, often with a lush understory of bryophytes (mainly species of *Brachythecium* but *S. uncinata* may also be abundant). Sometimes whole slopes (especially on grey lava) are occupied by the Drainage Line Habitat.

At the foot of steep slopes, water wells up locally as springs and flushes. Sometimes the same happens in sites away from the slopes, e.g. at the source of some tributaries of the Van den Boogaard River. In these very minerotrophic Spring and Flush Habitats, bryophyte mats dominated by *Brachythecium subplicatum*, *Philonotis* spp. and *Drepanocladus aduncus* occur. Vascular plants (*Acaena magellanica*, *Montia fontana* and sometimes *P. cookii* are the most common) are usually of minor importance.

Slope habitats are not that well separated from mire habitats along the wet/organic – dry/mineral and the low soil fertility – high soil fertility gradients represented by the axes in Fig. 9.1. However, the two types occupy distinctly different regions of an ordination space formed by Axis 1 and an axis representing a gradient from ill-drained amorphous peats to well-drained mineral soils with clear horizon development (data not shown – see Fig. 3 in Smith & Steenkamp 2001).

9.2.3 Fellfield Complex

Cushions of *A. selago* are the characteristic aspect of fellfield vegetation (Plates 9.4, 9.5). Fellfield soils are mineral and often contain a large proportion of scoria or lava rocks. During heavy rains some fellfield areas can become very wet, even locally inundated, but during dry periods the soils become quite dry. Cushion-forming mosses (*Andreaea acuminata*, *Andreaea acutifolia*, *Bucklandiella* spp., *Ditrichum* spp., *Bartramia patens*, *Grimmia kerguelensis*) and crustose lichens (*Coccotrema stellata*, *Fuscidea asbolodes*, *Lecanora disjungenda*, *Lecidea lygomma*, *Lecidea medusula*, *Lithographa* spp., *Ramonia sub-Antarctica*, *Stephanocyclos henssenianus*) are common. Species richness in fellfield communities can be high, (15-25 species of vascular plants and bryophytes per 25 m²), related to the wide range of

microhabitats in the fellfield habitat. Bare soil, the tops, sides and bottoms of rocks, the edges of *Azorella* cushions and spaces in the cushions between the stems all offer different microhabitats and support different assemblages of species. Most fellfield in lowland areas (< 300 m a.s.l.) belongs to the Mesic Fellfield Habitat, which may have a substantial (up to 50%) plant cover. Xeric Fellfield Habitat is also found at low altitudes, but is the dominant fellfield at higher altitudes. Xeric Fellfield rarely has more than 10% plant cover. Fellfield vegetation covers about 137 km², or 47%, of the total area of Marion Island, and is the dominant vegetation type between 100 and 300 m a.s.l., occupying 72% of that altitudinal zone. The two fellfield habitats occupy the cold/dry, infertile mineral soil extremes of the gradients represented in Fig. 9.1, well separated from all other habitats except Open Fernbrake.

9.2.4 Polar Desert

Polar Desert is the characteristic, almost only, habitat of the mid to high altitude regions of the islands. The vegetation consists of very open communities of bryophytes and lichens, with total plant cover rarely exceeding 1% (Plate 9.6). Few vascular plants extend above 600 m altitude (Huntley 1970) and only one, *A. selago*, occurs in Polar Desert. Common bryophytes are *Ditrichum strictum*, *A. acutifolia*, *A. regularis*, *B. patens*, *Bucklandiella orthotrichacea*, *Guembellia kidderi*, *Hymenoloma antarcticum*, *Notoligotrichum australe* and *Philonotis scabrifolia*. Most of these form balls or cushions. On some scoriae slopes bryophytes grow under the scoria surface, protected from the drying and chilling effects of wind. At sheltered, moist localities (e.g. depressions where snow-melt accumulates) a more luxuriant bryophyte vegetation occurs, dominated by *Dicranella gremmenii* and *C. grandiflora*.

Vegetation ecologists have avoided using the term polar desert when describing a vegetation type on sub-Antarctic islands, all of which are at mid-latitudes and receive substantial rainfall. Huntley (1971) referred to the vegetation of what we call polar desert as *Ditrichum-Bartramia* montane desert and included it with *A. selago* fellfield in a Wind Desert Complex. Corresponding vegetation formations on other sub-Antarctic islands have been considered to be fellfield (Taylor 1955; Hughes 1987; Bergstrom 1998) or included with fellfield in a Fellfield Formation (Lewis Smith 1993). However, fellfield (*Fjældmark*, *Felsenfluren* or *Felsentundra*) was originally used to describe vegetation in which vascular plants, especially cushion-forming ones, are dominant. This is certainly not the case for the Marion Island Polar Desert Habitat, which contains only one vascular species, and then only at lower altitudes. Rather, on the basis of its environmental and botanical characteristics (a barren unstable surface caused by frequent freeze-thaw cycles and frost heaving, and an extremely sparse vegetation dominated by mosses and lichens), the habitat conforms well with the definitions of high Arctic polar deserts given by Aleksandrova (1970) and Bliss (1981). With its single vascular species, it is even more polar desert-like than many high Arctic polar deserts. For instance the uplands of Devon,

Bathurst, Cornwallis and Ellesmere islands (all $> 75^\circ$ N and considered to be true polar deserts) possess 4-12 vascular plant species (Bliss 1981). Hence, the Polar Desert Habitat on the island resembles the most extreme northern hemisphere polar deserts; those dominated by mosses and lichens and which have been termed “polar barrens” (Benninghof 1974) or simply “barrens” (Longton 1998), to distinguish them from fellfield where vascular plants are more important. Polar Desert occupies about 109 km² of Marion Island. Polar Desert and fellfield thus occupy 246 km², or 85% of the island’s total surface, so the two can be considered to be the archetypical vegetation types for the island.

9.2.5 Coastal Salt spray Complex

This complex is restricted to the islands’ coastal zone at sites subjected to salt spray and inundation by waves. On the eastern and southern coasts it occurs within 50 m of the shore, but on the northern and western coasts, which are more exposed to the prevailing sea and wind, it is found up to 300 m inland. The complex occupies about 1 km² of Marion Island. Coastal Herbfield (Plate 9.7) is dominated by the halophyte *Crassula moschata*, a small reddish chamaephyte with succulent leaves, which occurs on fibrous, black or dark-brown peats with high sodium and magnesium contents. *Cotula plumosa* is often co-dominant (in some cases dominant) and forms short, compact rosettes. Few other vascular species occur, and bryophytes are important only in very wet areas where the effect of salt spray is diluted by incoming freshwater.

On rocky exposed locations with skeletal soils in the salt spray zone an open Coastal Fellfield occurs, dominated by *C. moschata* and the cushion-forming dicot *A. selago*. *Colobanthus kerguelensis* and *P. cookii* may also occur. Rocks closer to the shore and subject to very intense salt spray form a distinctive Coastal Rock Habitat where lichens such as *Amandinia subplicata*, *Arthothelium evanescens*, *Mastodia tessellata* and several species of *Verrucaria* and *Caloplaca* form distinct zonation from the intertidal to several meters above sea level (De Villiers 1976). These lichen zonation are best developed on grey lava coastal rocks and are fragmentary on black lava. On exposed coasts, *Mastodia* and *Caloplaca*-communities may be found up to 50 m a.s.l. Characteristic mosses on coastal rocks are *Eriopus apiculatus* and *Muelleriella crassifolia*.

On very wet peat soils along the inland margins of Coastal herbfield are Saline Mires, dominated by the hepatic *Clasmatocolea vermicularis*. *Crassula moschata*, *Agrostis magellanica* and *R. biternatus* also occur here, but never abundantly. Coastal herbfield and Coastal fellfield are well separated from all other habitats in the ordination space occupied by the habitats (Fig. 9.1). Saline mire is closer to habitats of the mire complex, which is why Smith & Steenkamp (2001) included it in the Mire Complex.

9.2.6 Biotic Complex

The impact of seabirds or seals on vegetation and soil ranges from moderate enrichment of nutrient status on inland slopes inhabited by burrowing prions or petrels, to complete eutrophication of the soil and complete destruction of the plant cover, as in penguin rookeries, Elephant Seal wallows and some areas occupied by Fur Seals. Following terminology commonly used in the island's ecological literature (e.g. Huntley 1971; Gremmen 1981; Smith & Steenkamp 2001) the term *biotic* is used here to indicate sites, vegetation or habitats that are influenced by seals and seabirds. About 4.5 km² of Marion Island is occupied by such habitats, which predominantly occur on the coastal lowlands. Some biotic habitats are found at higher elevations around albatross nests and on slopes colonized by burrowing bird species, but in total they occupy only about 3 ha of the area above 100 m altitude.

Characteristic vascular species in biotic vegetation are the tussock grass *P. cookii*, *Callitriche antarctica*, *M. fontana* and *C. plumosa*. Unlike in the Saltspray Complex, the *Cotula* plants occur as large (up to 30 cm tall) lax rosettes. *Poa annua* and/or *Agrostis stolonifera* dominate in one habitat of the complex. Other than in the biotic mire habitat (see below) bryophytes are not an important component of biotic vegetation, although *B. rutabulum*, *Marchantia berteroana*, *Schizymenium campylocarpum*, and *L. gemmascens* occur.

In heavily trampled areas around penguin rookeries and seal wallows Pedestalled Tussock Grassland occurs, consisting of *P. cookii* tussocks on peat pedestals up to 1 m high, formed by peat erosion between the tussocks. Heavy trampling prevents the development of vegetation between the *Poa* pedestals, except for *C. antarctica* and, less frequently, *P. annua*. Bryophytes are rare, except for *M. berteroana* which is sometimes found on the sides and eroded crests of the pedestals.

On flatter areas where erosion due to the activities of seals and penguins is less intense, or on shore-zone slopes occupied by burrowing petrels, a Coastal Tussock Grassland occurs (Plate 9.8). Here, *P. cookii* forms smaller tussocks that are not, or are only slightly, pedestalled. *Callitriche antarctica*, *M. fontana* and *C. plumosa* are common under the grass canopy but are rarely abundant. Bryophytes such as *C. vermicularis*, *L. gemmascens*, and *B. rutabulum* occur, but are also not abundant. Where burrowing birds colonise inland slopes, Inland Tussock Grassland occurs. Trampling is less intensive than in the other two tussock grassland habitats and the grass is never pedestalled. Burrow densities are generally lower than in Coastal Tussock Grassland and, other than both having a dense canopy of *P. cookii*, the two habitats carry distinctly different vegetations. Inland Tussock Grassland has a greater vascular plant diversity, with *Acaena magellanica*, *M. fontana*, *B. penna-marina* and *A. stolonifera*. Bryophytes are common and often abundant; *B. rutabulum* is the most usual one, but *Lophocolea randii*, *S. campylocarpum* and *L. gemmascens* frequently occur. Although most common on slopes, small stands of Inland Tussock Grassland also occur

on level areas surrounding wandering albatross and giant petrel nests. Inland Tussock Grasslands have become scarce on Marion Island over the last 20 years, for reasons suggested later in this chapter. This is why a question mark occurs in Table 9.2 against the estimate (made in the mid 1990s) of the total area occupied by this habitat.

The *Cotula* Herbfield habitat occupies the greatest total area of all the coastal habitats on the islands, occurring as large expanses up to a kilometer inland and also as smaller stands between tussock grasslands. The intensity of animal influence seems to be less here than in the tussock grassland habitats, but this might be true only with respect to trampling, rather than manuring. The characteristic (and often only) species is *C. plumosa*. *Poa cookii* is sometimes co-dominant, but few other vascular plants occur. Bryophytes are rare, except for *M. berteriana* and *C. vermicularis*. The soils have high Na and K concentrations and very high levels of N and P.

Where heavy trampling churns up wet organic soils (seal wallows and the edges of penguin rookeries are typical examples), a eutrophic Biotic Mud habitat occurs (Plate 9.8). It is dominated by *C. antarctica* and/or *M. fontana*, but few other species are able to withstand the high level of disturbance and intense nutrient enrichment. There are no bryophytes. On more mineral soils, or where the substrate is fibrous peat rather than mud, heavy trampling (especially by seals) results in compaction of the soil and a Biotic Lawn habitat is found (Plate 9.8). The vegetation consists of a very dense lawn of the introduced grasses *P. annua* and/or *A. stolonifera*. Soils of this habitat are extremely nutrient-enriched.

Where very wet peats are influenced by animals to a lesser extent than is the case for the two previous habitats, Biotic Mire occurs, dominated by the hepatic *C. vermicularis*. *Agrostis magellanica*, *M. fontana* and *R. biternatus* are the most common vascular species, but are rarely important. The Biotic Mire community does not tolerate trampling and most nutrients come from surrounding, animal-inhabited slopes, rather than through direct deposition of excreta. Even so, concentrations of soil nutrients in this habitat are appreciably higher than in any of the other mire habitats.

In Fig. 9.1 the biotic habitats are clearly separated from all other habitats on the soil fertility axis, with the exception of Biotic Mire which occurs between the main biotic group and non-biotically influenced mires.

9.2.7 Aquatic communities

The islands' freshwater bodies (lakes, lava-lakelets, crater lakes, wallows and streams) are described by Smith (2008). Macrophytic aquatic vegetation is poorly developed and generally originates from the terrestrialization of the water body. Plants (especially *Agrostis magellanica*, *A. stolonifera*, *J. scheuchzerioides*, *R. biternatus*) encroach into the water body from the shore. *Limosella australis* and *Ranunculus moseleyi* grow on the bottom of shallow lakes and ponds, but are quite rare. *Potamogeton nodosus* occurs in two of the Albatross Lakes on Marion

Island, forming dense stands in 50-100 cm deep water. The species does not reproduce sexually and is not found in any other of the island's water bodies, or on Prince Edward Island. *Drepanocladus aduncus*, *Drepanocladus polycarpus*, and *S. uncinata* are the most common submerged mosses in ponds. In rivers, aquatic vegetation is limited to mosses (*Schistidium falcatum*, *Schistidium rivulare*, *Orthotheciella varia*, *Blindia magellanica*, *Bucklandiella didyma*) attached to rocks and mats of *A. stolonifera*.

9.3 Vegetation dynamics

9.3.1 Autogenic succession

The earliest colonizers of lava flows are generally mosses. On the 7 ha lava flow that resulted from the 1980 volcanic eruption near Kaalkoppie (Verwoerd *et al.* 1981), a careful search in 1981 yielded only a few stems of a single species of moss (*Bryum* sp.). By 1994, sheltered localities on the flow supported a lush growth of bryophytes and lichens, with *R. lanuginosum* as the most common moss, and *Stereocaulon cymosum* as the most common lichen. Total vegetation cover in a series of 1 m² sample plots ranged from < 1% to 95% and the plots contained up to three species, with 10 species being recorded in a 1 ha area on the flow. By 1998, 14 species were found in the same area, including 4 vascular species; *B. penna-marina*, *Agrostis magellanica*, *P. annua* and *Cerastium fontanum*. In 1998 there were three to four species, on average, per 1 m² plot, but one plot contained nine species. By 2003, 23 years after the eruption, most of the lava flow was covered by vegetation, often dense and mainly comprised of bryophytes. The rapid colonisation and subsequent succession to an almost complete vegetation cover of the Kaalkoppie lava flow is probably due to the fact that the flow is at less than 100 m altitude. Succession at higher altitudes is probably much slower, and instigated by cushion- and ball-forming mosses and *A. selago*, rather than fast-growing species such as *R. lanuginosum* and *Bryum* species, which are restricted to lower altitudes and are relatively dependent on continuously moist conditions.

The pattern of vegetation succession on Marion Island is depicted in Fig. 4 of Smith (1987b). Scoria or solid lava are generally colonised first by *A. selago*, the cushions of which are crucial to further vegetation succession since they accumulate organic matter which is added to fine volcanic ash to form a loamy-textured soil in which other plant species can establish and add further organic matter. A similar type of soil formation has been described for glacier forelands on Kerguelen Island (Frenot *et al.* 1998). Other plant species root in living or dead *A. selago* cushions and add to the accumulation of organic debris, which eventually fills the crevices and porous structure of the lava or scoria and impedes drainage, ultimately leading to peat formation. If the rate of water acquisition by the area is greater than the rate of drainage, bryophyte-dominated mire develops. Peat accumulation may raise the mire surface above the watertable, resulting in a dry mire dominated by graminoids and bryophytes. Further peat accumulation may make the surface even drier,

and fernbrake vegetation then develops. However, closed fernbrake on flat, level areas is rare. Dry mire communities dominated by *B. penna-marina*, *R. lanuginosum* and *U. compacta* generally represent the culmination of the wet-dry succession on level surfaces.

Where drainage from the fellfield area is unimpeded, the cushion plants develop a stable peat for fernbrake elements to develop. At first these elements may arise epiphytically on, or in the shelter of, the cushions, but eventually extend across the peat to form an open fernbrake that is often succeeded by a closed carpet of *B. penna-marina*. This sequence from fellfield to fernbrake occurs predominantly on slopes. On flat plateaus, impeded drainage (caused by peat blocking the drainage channels) diverts the fellfield-fernbrake succession to the one toward mire vegetation.

At rocky coastal sites subjected to salt-spray, *A. selago* and *M. crassifolia* first occur, followed by *C. moschata*. Peat accumulation in these areas results in the coastal herbfield vegetation dominated by *C. moschata* and sometimes also *C. plumosa*. Impeded drainage in such areas diverts the succession to a saline mire dominated by *C. vermicularis*.

Strong lateral flow of water (for instance, in drainage lines, water tracks, flushes and springs) may modify the vegetation at any level of succession, leading to a group of plant communities characterized, on slopes and stream banks, by a dominance of *Acaena magellanica* in the herb layer, and *B. subplicatum* or *B. rutabulum* in the bryophyte layer. In mires, drainage lines are dominated by *B. integrifolia* and *B. laevigatum*.

Seabird and/or seal activity may have a marked influence at any stage of succession. Other than Salvin's Prions (*Pachyptila salvini*), animals seldom establish nests or otherwise exploit fellfield areas, preferring mires and well-vegetated slopes (Schramm 1986). In the coastal zone, a *C. plumosa*-*P. cookii* dominated vegetation, or a *P. cookii* tussock grassland, develops at sites influenced by animals, except at very wet sites where communities of coprophilous, trampling-tolerant species (mainly *C. antarctica*, *M. fontana* and *P. annua*) occur. Where fernbrake communities are colonized by burrowing birds, tussock grassland dominated by *P. cookii*, *Acaena magellanica*, *B. penna-marina* and *B. rutabulum* develops (Smith 1976a).

9.3.2 Vegetation and climate change

The climate of the entire sub-Antarctic region is currently undergoing marked change (Jacka & Budd 1998). Marion Island (and presumably also Prince Edward Island) has become significantly warmer and drier over the past 35 years (Smith 2002; Sumner *et al.* 2004). Table 9.4 shows how the islands' terrestrial habitats might respond to changes in temperature and moisture. The suggested responses of the habitats to the various perturbations are based on an analysis of the positions of the habitats on the axes of the ordinations on which the habitat classification was based (Fig. 9.1) and a prediction of how a particular habitat would move on the axes in response to a particular

perturbation or combination of perturbations. The predictions were also based on soil chemistry information, a re-appraisal of botanical and environmental data for 510 sites studied by Gremmen (1981) and a consideration of soil and air temperature data in Huntley (1971), Smith (1987a, c), Chown & Crafford (1992), Smith *et al.* (1993) and Blake (1996). Some predictions are simply subjective, based on an appreciation of how vegetation pattern on the island, and on colder sub-Antarctic islands such as Heard Island and South Georgia, is related to environmental forcing variables.

Climate change might also affect the vegetation in less direct ways. For instance, changing atmospheric and oceanic circulation patterns that underlie the changing climate at the islands (Smith & Steenkamp 1990; le Roux 2008) could influence the seabird and seal populations by moving their feeding grounds or, in the case of the birds, changing the positions and frequencies of the atmospheric frontal systems they use to reach the feeding grounds (Ryan & Bester 2008). Such alterations in the trophic dynamics of the islands' seal and seabird populations might result in a change in the amounts of nutrients transferred from the ocean to the terrestrial ecosystem, an important determinant of both the structure and function of the islands' vegetation (Smith & Froneman 2008; Smith 2008). Similarly, easterly winds are becoming more common (and also stronger; le Roux 2008) and this might increase the extent of salt-spray dominated habitats on the eastern side of the islands. Table 9.4 suggests how the habitats might respond to a change in levels of manuring and saltspray.

9.3.3 Changes in population sizes of indigenous animals

Large changes have occurred in the numbers of burrowing prions and petrels at Marion Island, and in the size of Fur Seal populations on both Marion and Prince Edward Islands. Both groups of animals have a major impact on the islands' vegetation, specifically on the tussock grasslands.

Tussock grassland is the climax vegetation of slopes occupied by petrels and prions, and results from the nutrients deposited by the birds (Smith 1976a). The populations of all the burrowing species on Marion Island were severely affected by predation by Domestic Cats, which were introduced in 1949 and quickly became feral (Skinner *et al.* 1978). The cat population increased to about 2 000 by 1975, when they killed an estimated 450 000 birds per year (Bester & Skinner 1991). Transects on the north-eastern lowlands of Marion Island (between the Van den Boogaard River and Fred's Hill, and between 100 m and 2 500 m from the shore) showed that tussock grassland occupied c.1% of the area in 1971/72 (Smith 1976b, 1977). This had decreased to 0.1% by 1991 (Smith *et al.* 2001) and by 2005 no inland tussock grasslands occurred in the area. Mostly, the inland tussock grasslands have been replaced by closed fernbrake or dwarf-shrub fernbrake. Hence, although the cats were eradicated in 1991 (Bester *et al.* 2000) and the petrel and prion populations appear to be recovering (Cooper *et al.* 1995), this has not yet reversed the decline of the tussock grasslands.

Table 9.4 Suggested response of habitats to environmental change. The number shows the habitat that replaces the one in the first column should the environment change in the way specified by the column heading. – indicates that no change is expected. L and H indicate what may happen to a habitat in the lower and higher parts, respectively, of its altitudinal range. More/less biotic indicates a greater/lesser intensity of seabird or seal manuring and more/less salt indicates an increase/decrease in the intensity of salt spray deposition. From Smith *et al.* (2001).

	Habitat	Warmer & Drier	Warmer & Wetter	Colder & Drier	Colder & Wetter	More Biotic	Less Biotic	More Salt	Less Salt
1.1	Coastal Herbfield	1.2	6.6	1.2	6.6	5.1	-	-	3.1, 3.2, 3.3, 6.1, 6.2
1.2	Coastal Fellfield	-	1.1	-	1.1	4.1, 5.1	-	-	2.2
2.1	Xeric Fellfield	-	2.2	7.1	-	-, 4.2	-	1.2	-
2.2	Mesic Fellfield	2.1	3.1	2.1	-	5.1, 4.2	-	1.2	-
3.1	Open Fernbrake	2.2	3.2	2.2	(1,3,2, 6.1) (H; 2.2)	4.2	-	1.2	-
3.2	Closed Fernbrake	3.1	3.3	3.1	3.3	4.2	-	1.1	-
3.3	Mesic Fernbrake	3.2	6.1	3.2	3.4, 6.1	4.2	-	1.1?	-
3.4	Dwarf Shrub Fernbrake	3.2	3.5	3.2	3.5	4.2	-	1.1?	-
3.5	Slope Drainage Line and Streambank	3.4?	-, 3.6?	?	-, 3.6?	4.2	-	1.1,	-
3.6	Spring and Flush	3.3, 3.4, 3.5	-	3.5	-	5.2?	-	6.6	-
4.1	Coastal Tussock Grassland	-	-	-	-	-, 4.3	5.1	-	4.2
4.2	Inland Tussock Grassland	-	-	-	-	-	3.2, 3.1	4.1	-
4.3	Pedestalled Tussock Grassland	-	-	-	-	-	4.1, 5.1	-, 5.1	-

Table 9.4 Continued.

	Habitat	Warmer & Drier	Warmer & Wetter	Colder & Drier	Colder & Wetter	More Biotic	Less Biotic	More Salt	Less Salt
5.1	Cotula Herbfield	-, 4.1	-, 6.5	-, 1.2?, 4.1	-, 6.5	4.1, 5.2, 5.3	1.1, 3.2	-, 1.1?	-, 3.2
5.2	Biotic Mud	5.1, 5.3	-	5.1, 5.3	-	-	5.1, 6.5	-	-
5.3	Biotic Lawn	-	5.2, 6.5	-	5.2, 6.5	-	5.1, 3.5	-	-
6.1	Dry Mire	3.3	6.2	3.1	6.2	4.2	-	1.1	-
6.2	Mesic Mire	6.1	6.3	6.1	6.3	4.2, 6.5	-	1.1, 6.6	-
6.3	Wet Mire	6.2	-	6.2	-	6.5	-	6.6	-
6.4	Mire Drainage Line	-, 6.3	-	-, 6.3	-	6.5	-	6.6	-
6.5	Biotic Mire	5.1	-	5.1	-	5.2	6.6, 6.2, 6.3	-, 6.6	-
6.6	Saline Mire	1.1	-	1.1	-	6.5	-	-	6.1 to 6.4
7.1	Polar Desert	2.1	2.1	-	(1.; 2.1), (H; -)	-?	-	-	-

Fur seals have increased on Marion Island from less than a thousand in the early 1950s (Rand 1956) to 7 000 in 1975 (Condy 1978) and *c.* 50 000 in 1995 (Hofmeyr & Bester 1997). Fur Seal numbers have also increased on Prince Edward Island (Ryan & Bester 2008). The area occupied by these animals on the islands has increased immensely and, as on Bird Island, South Georgia (Bonner 1985), this has led to widespread destruction of tussock grassland. This is especially conspicuous on the west coast of Marion Island and all the coastal areas of Prince Edward Island. Fur seals have not yet significantly encroached inland on the east coast of Marion Island and are not responsible for the disappearance of tussock grasslands in the area considered above.

9.3.4 Impact of changing human activities

With the deployment of field huts on Marion Island the amount of fieldwork increased markedly and a network of tracks has developed. The effect of trampling in and around the tracks depends on habitat type and the nature of the soil. On dry soils, trampling results in soil compaction, but the tracks remain quite narrow and disturbance is slight. In contrast, wet soils and peat are churned up and become difficult or impossible to traverse. The tracks become wider as people skirt around their edges. Most trampled areas have less plant species than the surrounding undisturbed habitats, but there are exceptions. For instance, trampling in closed fernbrake opens up the dense *Blechnum* mat and increases species richness by as much as 30% (Gremmen *et al.* 2003).

9.3.5 Impact of invasions by alien plants

The greatest modification of Marion Island's vegetation by invasive plants has been caused by two species, *A. stolonifera* and *Sagina procumbens*, which are widespread on the island (Gremmen 1997) and can be found in almost all of the 23 habitats. *Agrostis stolonifera* has become dominant in seven, and *S. procumbens* in 11, of the habitats (Table 9.5). *Poa annua* has been found in 16 habitats, but it is dominant in only two. *Agrostis gigantea*, observed for the first time in 1993 at the weather station, has invaded seven habitats and was dominant in three. It reduced species richness in the invaded plant community to less than half that of uninvaded communities (N.J.M. Gremmen, unpublished data). The species has been eradicated.

There is no clear relationship between the 'invasiveness' of an alien plant species (the number of habitats it can invade and the total area in which it occurs) and the impact that it has on the communities it invades. Some species have a very restricted distribution, but have a major impact on the vegetation of the localities where they occur. For instance, *Festuca rubra* (two localities) and *Agropyron repens* (one locality) have invaded more than one habitat at the localities where they occur (Table 9.5) and both grasses form dense stands that smother the native plants. For instance, 4 m² sample plots in the *Festuca* stands contain only 3-5 species of vascular plants and bryophytes, whereas uninvaded vegetation in the same habitat has 7-15 species per 4 m² plot.

Table 9.5 Status of alien vascular species in the Marion Island habitats. See Table 9.1 for full names of the species. * = present; d = attains dominance.

Habitat	Species												Total dominant aliens	Total aliens
	<i>Agro rep</i>	<i>Agro cas</i>	<i>Agro gig</i>	<i>Agro slo</i>	<i>Alop gen</i>	<i>Cera fon</i>	<i>Fest rub</i>	<i>Poa annu</i>	<i>Poa prat</i>	<i>Rumex ac</i>	<i>Sagi pro</i>	<i>Stel med</i>		
Coastal Herbfeld				d				*			d		3	2
Coastal Fellfield				*							d	*	3	1
Xeric Fellfield				*		*					*		3	0
Mesic Fellfield				*		*		*			d		4	1
Open Fernbrake			*	d		*		*		d	*		6	2
Closed Fernbrake			*	*		*	*	*		*	*		7	0
Mesic Fernbrake			*	*		*	*	*		*	*		7	0
Dwarf Shrub Fernbrake			*	d		*	*	*		d	*		7	1
Slope Drainage Line and Streambank	d	*	d	d		*	d	*	d		*	*	10	5
Spring and Flush				d				*					2	1
Coastal Tussock Grassland				d		*		*	*		*	*	5	1
Inland Tussock Grassland				d		*		*	*		*	*	5	1
Pedestalled Tussock Grassland				*		*		*	*		*		4	0
Cotula Herbfeld	*	*	d	*	d		*		d		*		8	3
Biotic Mud				d				*			*		3	1
Biotic Lawn				d				d			*		3	2
Dry Mire				*									1	0
Mesic Mire			d	*						*	d		4	2

Table 9.5 Continued.

Habitat	Species										Total aliens	Total dominant aliens
	<i>Agro rep</i>	<i>Agro cas</i>	<i>Agro gig</i>	<i>Agro sto</i>	<i>Alop gen</i>	<i>Cera fon</i>	<i>Fest rub</i>	<i>Poa annu</i>	<i>Poa prat</i>	<i>Rumex ac</i>	<i>Sagi pro</i>	<i>Stel med</i>
Wet Mire				d					*		d	
Mire Drainage Line								*			*	
Mesic Mire Drainage Line				d		*			*		*	
Biotic Mire				*				*			d	
Saline Mire				*							d	
Polar Desert												
Number of habitats invaded:	2	2	7	22	1	11	5	16	3	5	21	4
Number of habitats in which dominant:	1	0	3	11	1	0	1	2	1	2	7	0

Where *A. stolonifera* invades drainage lines and streambanks the number of native plant species is reduced by 50% compared to undisturbed sites (Fig. 9.2). The composition of the soil fauna is also significantly affected (Gremmen *et al.* 1998). *Poa pratensis* has had a similar impact on parts of north-eastern lowlands of Marion Island (Gremmen 1997). On the other hand, some widespread alien plants, e.g. *Stellaria media* and *C. fontanum* most commonly occur only as scattered individuals in the communities they invade, and they do not displace the native species. Coastal habitats are particularly susceptible to invasion by alien plants, but the invasions generally have little effect on the native species diversity. For instance *S. procumbens* readily invades, and frequently becomes dominant in, coastal herbfield and *Cotula* herbfield without significantly reducing the number of native plant species (Gremmen 1997). Similarly, where *S. procumbens*, *C. fontanum* or *A. stolonifera* have invaded fellfields, usually none of the native species are eliminated since the alien colonists occupy the open spaces in these communities.

Figure 9.2 Vegetation structure of a Drainage Line and Streambank Habitat a) before and b) after invasion by *Agrostis stolonifera* (from Gremmen *et al.* 1998).

Although the impacts of alien plants may be considerable in the areas at which they occur, the total area affected by alien plants is still relatively small, at present less than 5% of the total island area. Polar Desert is at present the only habitat not colonised by invasive species.

We conclude with some subjective considerations based on our experience of the Prince Edward Islands' vegetation, which we consider to be as trustworthy as the conclusions from our research results. Like most botanists acquainted with the islands' vegetation (starting with Sir Joseph Hooker in the 19th century; Hooker 1847), when we started working on the islands we thought that the vegetation was extremely slow-growing and that succession was too slow to be easily discerned in as short a period as the lifetimes of our expected research careers. Dogma at the time was that it took thousands of years for a new lava flow to become vegetated, that the island vegetation was unproductive and largely unchanging, and that the forcing variables driving ecosystem structure and function (especially the climate) were also static, or at least would not change noticeably in our lifetime.

Thirty four years later, we have a completely different view. We know that the lowland vegetation is productive and that succession is extremely dynamic. We have seen large sections of barren lava becoming substantially vegetated (Santa Rosa Valley), and partially vegetated areas become almost completely covered with fernbrake (Hoppie's Hell). We had the privilege of standing on a still-fuming lava eruption, and subsequently being able to witness how rapidly it became colonised and covered by plants. Over 30 years we witnessed most of the mesic fellfields on the eastern lowlands become mires and open fernbrakes, and open fernbrakes become mesic fernbrakes, closed fernbrakes or mires. Pipelines have disappeared under dense carpets of vegetation and become covered by up to 20 cm of peat. We have seen the terrestrialization of large ponds and, in some instances, the subsequent reappearance of the ponds. We have seen the almost total disappearance of tussock grasslands on inland slopes, and the total disappearance of a plant community that was common in the 1970s (*Azorella-Poa* montane grassland, a cushion plant-tussock grass community on the crests of slopes; Huntley 1971). Alarming, on Marion Island we have seen the spread of alien plant species from the meteorological station so that two of them are now found all over the island's lowlands and have come to dominate the vegetation of large areas.

What has perhaps surprised us most has been the extent to which, and rapidity with which, the climate has changed at the islands. Over 20 years we saw the Marion Island summit change from white to red as the ice cap was lost and the scoria peaks exposed; the temperature record since 1970 tells why this was so. Rainfall declined by about 25% in the same period and we saw large, waterlogged expanses of mire become traversable. The results of our studies have allowed us to predict how ecological structure and functioning might respond to these climatic changes and we have even seen particular predictions proved true. Islands have always been particularly satisfying and rewarding subjects for studying biological and ecological processes. We have been exceedingly fortunate in the opportunity and support that enabled us to work on the Prince Edward Islands over all these years.

9.4 References

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