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Source: Arctic, Antarctic, and Alpine Research, 39(3): 500-511

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

URL: https://doi.org/10.1657/1523-0430(06-040)[YELOFF]2.0.CO;2

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Volcanic Ash Deposition and Long-Term Vegetation Change on Subantarctic Marion Island

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DOI: 10.1657/1523-0430(06-040)[YELOFF]2.0.CO;2

Introduction

Owing to their isolation, impoverished biota, and harsh environments, the ecosystems of subantarctic islands are relatively simple and sensitive to disturbance. They can be seen as 'ecological laboratories' for studying the response of ecosystems to environmental change (Smith, 2002). Human visitation to the islands has only occurred in the last two centuries; long-term archives of environmental change can therefore show the response of the islands' ecosystems to environmental perturbation in the absence of any human influence.

Marion Island is an intraplate shield volcano located remotely in the subantarctic region of the southern Indian Ocean, c. 2200 km southeast of Cape Town, South Africa (Fig. 1). Ecological surveys and monitoring campaigns have shown that the main drivers of ecological change on the island include the manuring and trampling of vegetation by seals and seabirds in coastal areas. Like other subantarctic islands, there has been a marked change in climate since meteorological recording began in the middle of the 20th century. The increasing temperatures and lower precipitation have been shown to be exacerbating the interaction of indigenous species with invaders such as the grass Agrostis stolonifera. Climate change may also be playing a role in affecting salt spray in coastal ecosystems through changing atmospheric circulation patterns and wind (Bergstrom and Chown, 1999; Smith et al., 2001a; Smith, 2002). On longer time scales, reconstructions of post-glacial environmental change show

Abstract

A c. 5500 year record of peatland development and vegetation change was generated from a core recovered from an *Agrostis magellanica* peat bog on subantarctic Marion Island, using palynomorph, plant macrofossil, and tephra analyses. Two tephra horizons (both 17 cm thick) were identified and dated to ca. 2900 cal. BP and ca. 1700 cal. BP. Succession of the vegetation as a consequence of tephra deposition, particularly by the pioneer *Azorella selago*, appears to have been very slow, lasting as long as c. 700 yr. The slow pace of vegetation succession highlights the sensitivity of the indigenous Marion Island flora to environmental change, and the vulnerability to the spread of alien invasive species.

the impacts of nutrient enrichment and disturbance by animals on vegetation composition in coastal areas, but do not indicate the influence of other factors on long-term ecosystem change (Schalke and van Zinderen Bakker, 1971; Scott and Hall, 1983; Scott, 1985).

The effects of tephra deposition from volcanism on local vegetation have been noted in the Pacific Rim (e.g. Bush and Whittaker, 1991; Thornton and Walsh, 1992; Whittaker and Walden, 1992; Horrocks and Ogden, 1998; Hotes et al., 2006), North America (e.g. Blong, 1984), Europe (from paleoecological studies, e.g. Birks and Lotter, 1994; Edwards et al., 2004), and Deception Island in the maritime Antarctic (e.g. Collins, 1969). However, volcanic activity has not been previously recognized as a significant influence on vegetation in the subantarctic. This study is therefore unique in the context of the subantarctic, as it presents a record of vegetation change showing that tephra deposition following volcanic eruptions has been a major driver of long-term ecosystem change and succession at one site on Marion Island during the last 5500 yr.

Marion Island and Its Current Vegetation

 ${}^{40}\text{K}/{}^{39}\text{Ar}$ dating suggests the island was formed before 450 ka. ${}^{40}\text{K}/{}^{39}\text{Ar}$ dating has also shown volcanism to have occurred episodically since this date (McDougall et al., 2001). Geological evidence indicates several glaciations corresponding to marine

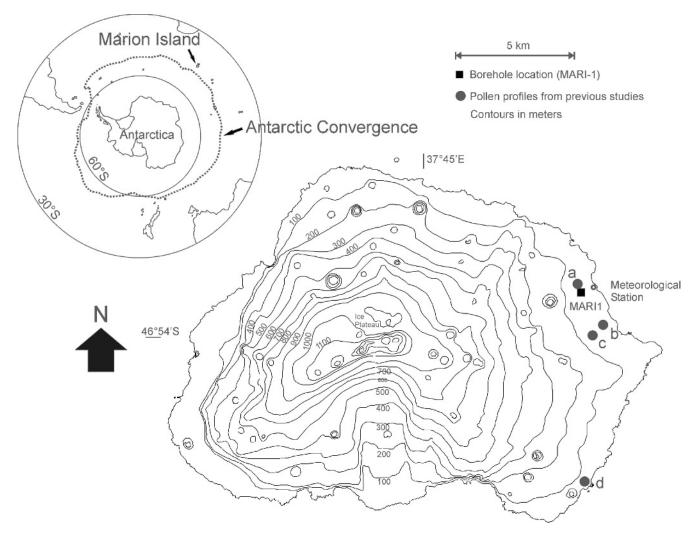


FIGURE 1. Study site location, and location of sites mentioned in the text: (a) Junior's Kop (Schalke and van Zinderen Bakker, 1971); (b) Macaroni Bay (Schalke and van Zinderen Bakker, 1971); (c) Albatross Lakes (Scott, 1985); (d) Kildakey Bay (Scott, 1985).

oxygen isotope stages 2, 4, 6, 8, and 12 (McDougall et al., 2001). Holocene volcanic activity has resulted in the formation of c. 130 scoria cones; with the most recently observed eruptions occurring in 1980 (Verwoerd et al., 1981), 2004, and 2005 (http:// www.up.ac.za/academic/geog/marion_island.html).

The island and its nearby, smaller neighbor, Prince Edward Island, have a cool (mean annual temperature, c. 6°C) oceanic climate with a total annual precipitation of c. 2000 mm. Moreover, the climate is exceptionally thermally stable, the difference between the mean temperature of the coldest and warmest months is 3.6° C, and the mean diurnal temperature variation is 1.9° C (Smith, 2002).

The vegetation of the islands has been described and classified using the Braun-Blanquet approach (Gremmen, 1981; Smith et al., 2001b). Salt-spray complexes dominated by *Cotula plumosa* and *Crassula moschata* exist in coastal areas. In coastal and some inland areas, disturbance from seals and seabirds maintains biotic herbfield and grassland complexes. *Poa cookii* and the nitrophiles *Callitriche antarctica* and *Montia fontana* are dominant in these habitats.

Peat bogs are abundant on the lowland plains of Marion Island, and mire complexes cover around 50% of the island below

300 m a.s.l. Plant communities of the mires form the Juncus scheuchzerioides–Blepharidophyllum densifolium complex. Graminoid species form an important part of the peat-forming plants, notably Agrostis magellanica, Uncinia compacta, and Juncus scheuchzerioides. Bryophytes also occur on the mires, and the most important of these are Drepanocladus uncinatus, Blepharidophyllum densifolium, Jamesoniella colorata, Racomitrium lanuginosum, and Breutelia integrifolia. The mires have a very even surface and do not possess a pattern of hollows and hummocks. Ranunculus biternatus occurs in bog ponds, and Juncus scheuchzerioides and Agrostis magellanica can form pioneer communities in 20- to 80-cm-deep water.

Well drained lava ridges around the edges of mires are covered in fernbrake vegetation dominated by the pteridophyte *Blechnum penna-marina* with *Acaena magellanica*. Exposed ridges and plateaus around the mires, and at higher elevations are covered in a fellfield complex, an open vegetation of isolated, stunted plants, with mosses and lichens. Much of the bare rock and scoria has no vegetation cover except for lichens and cushion dicots including *Azorella selago* and *Colobanthus kerguelensis*, on which grow graminoid species such as *Agrostis magellanica*, *Uncinia compacta*, and *Poa cookii*.

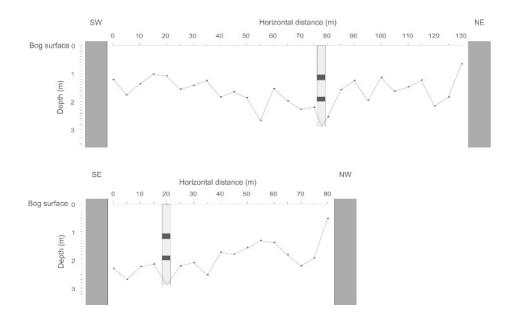


FIGURE 2. Peat depths along two transects. Light gray rectangles are coring location, black bands indicate tephra deposits; dark gray rectangles are lava ridges/outcrops.

Methods

FIELDWORK

Two intersecting transects of peat depth measurements were made across a small bog (135×79 m) and are shown in Figure 2. The main peat core, MARI1 ($46^{\circ}52.7303'S$, $37^{\circ}50.9161'E$), was taken to a depth of 287 cm. At this depth the Russian corer (7 cm \times 50 cm) hit solid lava deposits at the base. The cores were split into contiguous 1 cm slices on Marion Island.

¹⁴C DATING

Seven peat samples were AMS radiocarbon dated by the SUERC and Groningen ¹⁴C facilities (Table 1). With the exception of the sample at 261.5 cm, which contained *Ranunculus biternatus* leaf fragments, the samples were composed of roots of *Agrostis magellanica* and indeterminate humified organic material. The downward growth of these roots would have introduced some contamination, but their ubiquitous presence in the peat samples and the scarcity of other plant macrofossils left no option but to date these components.

TABLE 1

¹⁴C measurements; *weighted average of BCal posterior probability distribution (Buck et al., 1999). With the exception of the sample at 261.5 cm, which contained *Ranunculus biternatus* leaf fragments, the samples were composed of roots of *Agrostis magellanica* and indeterminate humified organic material.

Code	¹⁴ C age (BP)	Mid-point sample depth (cm)	cal. BP*	δ ¹³ C (‰)
SUERC-548	378 ± 38	49.5	482	-27.9
SUERC-549	1260 ± 45	89.5	1231	-27.8
SUERC-550	$1699~\pm~27$	117.5	1573	-28.4
SUERC-552	$1805~\pm~59$	124.5	1721	-28.1
SUERC-553	2716 ± 81	182.5	2819	-27.3
SUERC-554	$2769~\pm~70$	184.5	2933	-26.7
GrA-30781	$4750~\pm~40$	261.5	5495	-26.6

Microfossil samples of c. 1 cm³ volume (volume estimated by immersion) were treated with KOH and acetolyzed (Fægri and Iversen, 1989). To estimate microfossil concentrations, tablets with Eucalyptus spores were added to the samples (Stockmarr, 1971). A total of 300 pollen grains was the pollen sum, where possible, for each of the 71 samples. Pollen identifications were made using Schalke and van Zinderen Bakker (1971), Scott and Hall (1983), and Markgraf and D'Antoni (1978). Selected pollen types are shown in Figure 3. The samples also contained a variety of non-pollen palynomorphs. Some of these, including fungi, testate amoebae, and desmids, have already been described in the literature and were identifiable (e.g. van Geel, 1978; Charman et al., 2000). There were a number of unknown structures that were morphologically distinguishable and could be considered as homogeneous entities. These were classified into 'Types.' These Types are described in the Appendix and shown in Figure 3. Where possible, a sum of at least 100 palynomorphs was recorded

PALYNOMORPH AND MACROFOSSIL ANALYSES

Macrofossil samples were boiled with 5% KOH and sieved (mesh diameter 150 μ m). Macrofossils were identified using a binocular microscope (×10 to ×50), and the abundances of each peat component were expressed using a six point scale: 0, absent; 1, rare; 2, occasional; 3, frequent; 4, common; and 5, abundant. Identifications of plant macrofossils were confirmed using type material of plants collected during fieldwork. Examples of these macrofossils are shown in Figure 4.

for each sample during the pollen counts, and these are expressed

as percentages of the pollen sum for each sample.

ORGANIC CONTENT AND TEPHRA ANALYSES

The organic content of the peat samples was measured using the loss-on-ignition (LOI) technique (Gale and Hoare, 1991). Oven-dried samples were ignited at 430°C for 24 h, and the change in mass determined.

Visible tephra horizons in the sequence were prepared for geochemical analysis using Wavelength Dispersive Spectrometry (WDS). To avoid migration of some major oxides as a result of heating, the material was not combusted (Turney and Lowe, 2001). Samples were acid digested, following the procedure

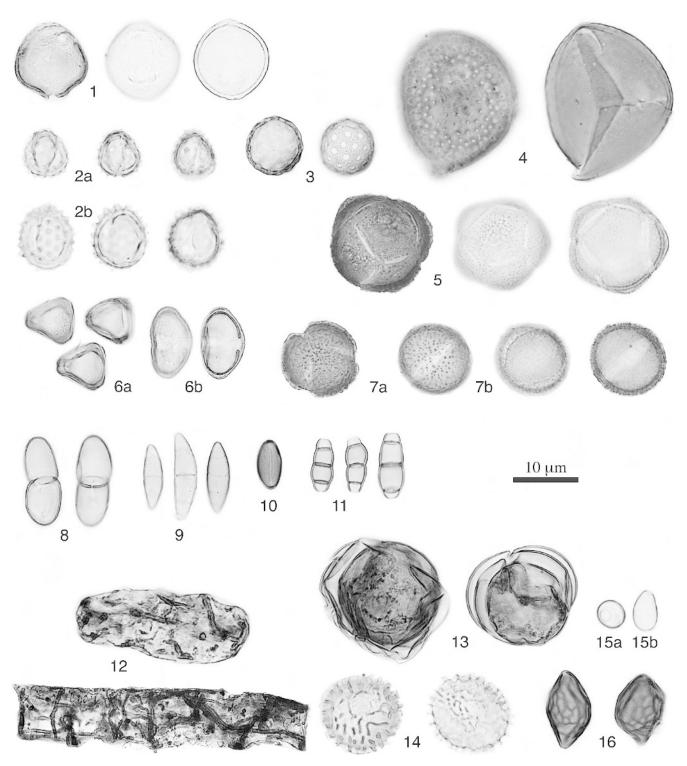


FIGURE 3. Examples of palynomorphs found in the MARI1 profile. (1) *Acaena magellanica* at three different focal depths; (2a) *Cotula plumosa*, polar views; (2b) *Cotula plumosa*, equatorial views; (3) *Colobanthus kerguelensis* at two focal depths; (4) *Hymenophyllum peltatum* at two focal depths; (5) *Montia fontana* at three focal depths; (6a) *Azorella selago*, polar views; (6b) *Azorella selago*, equatorial views; (7a) *Ranunculus biternatus*, polar view; (7b) *Ranunculus biternatus*, equatorial views; (8) Type 815 fungal spores; (9) Type 816 fungal spores; (10) Type 817 fungal spore; (11) Type 823 fungal spores; (12) Type 818, two examples; (13) Type 819, two examples; (14) Type 820, two examples; (15a) Type 822, polar view; (15b) Type 822, equatorial view; (16) Type 821, two examples.

outlined by Dugmore (1989), and the size fraction 70–15 μ m was isolated for analysis. Extracted glass shards were geochemically analyzed on the Jeol 733 Superprobe at the Electron Microscope Unit, Queen's University, Belfast. An accelerating voltage of 15 kV, a beam current of 10 nA, and a slightly defocused beam diameter of c. 8 μ m were used, and a lipari standard was analyzed

at regular intervals during the analysis period. A ZAF correction was applied to correct for atomic number, absorption, and fluorescence effects (Sweatman and Long, 1969). Counter dead time was also corrected for. All analyses exceeded 95% totals (Hunt and Hill, 1993). The detection limits of the major oxides were of the order of 0.01-0.05 wt%.

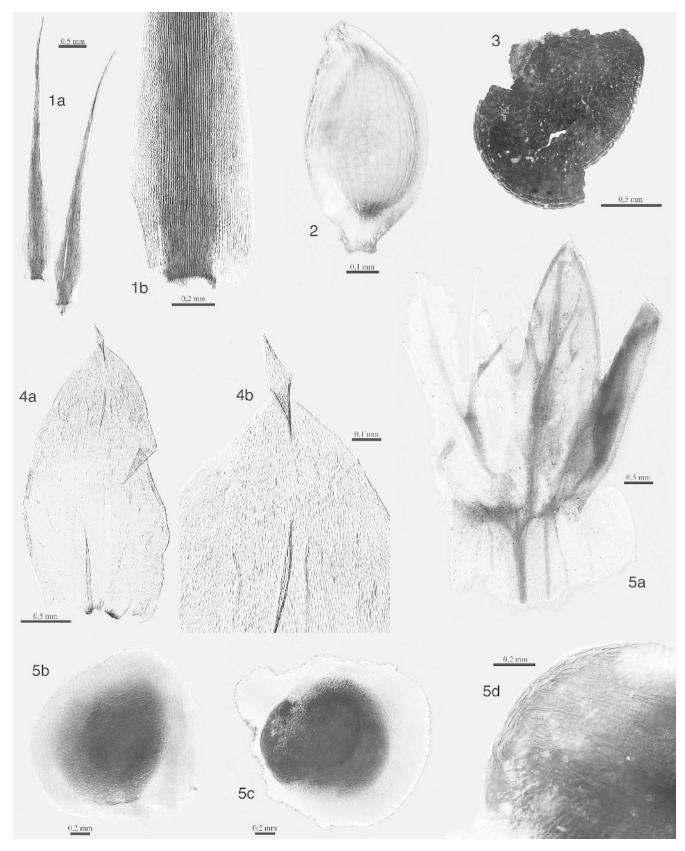


FIGURE 4. Examples of macrofossils found in the MARI1 profile. (1a, 1b) *Campylopus clavatus* leaves; (2) *Juncus scheuchzerioides* seed; (3) *Montia fontana* seed; (4a, 4b) *Ptychomnion densifolium* leaf; (5a) *Ranunculus biternatus* leaf; (5b, 5c, 5d) *Ranunculus biternatus* seeds.

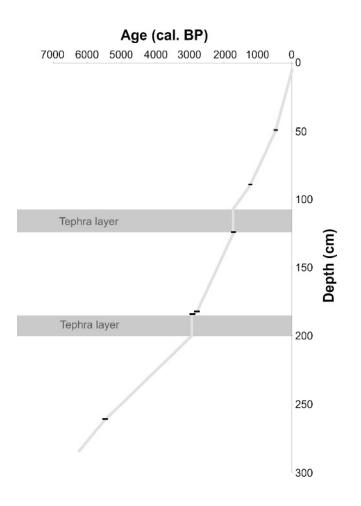


FIGURE 5. MARI1 Age-depth model. ¹⁴C dates were calibrated using BCal, black lines indicate the 95% confidence interval for each calibrated date. The weighted average of each date was used for the age-depth model produced by Psimpoll 4.25 (Bennett, 2005), using linear interpolation between dated levels.

Results

¹⁴C CHRONOLOGY

The ¹⁴C ages of the samples (Table 1) have been converted to calendar ages by online BCal calibration (Buck et al., 1999) using the Intcal04 calibration data set (Reimer et al., 2004). The probability density plots for each age were then imported into Psimpoll 4.25 (Bennett, 2005), and an age/depth model was constructed by linear interpolation between the weighted averages of the calibrated ages (Figure 5). Owing to the deposition of the tephra layer at 124–107 cm (being assumed to be instantaneous), the ¹⁴C date at 117.5 cm was excluded from the age model. Ages are expressed as calibrated radiocarbon years (cal. BP). It is recognized that these dates lie within a range and are not precise; and therefore are rounded to the nearest 100 years.

PALYNOMORPHS AND MACROFOSSILS

The pollen spectra are dominated by Poaceae and Azorella selago, in addition to varying proportions of Uncinia compacta, monolete psilate fern spores, Acaena magellanica, and Lycopodium spp. (Fig. 6). Exotic pollen grains were also identified, and these form between 0 and 2% of the whole assemblage. Type 91 and Type 820 palynomorphs were most frequently encountered in addition to varying proportions of Type 821, Type 823, and fungal types (Types 815, 816, 817, 818, 819, and 824). Remains of Corythion-Trinema type testate amoebae (Charman et al., 2000) were only observed in the layers containing tephra. This may be due to special preservation conditions, or the deposition of the ashes producing favorable conditions (relatively dry; see Charman et al., 2000). With the exception of the levels between 263 and

242 cm where macrofossil remains of *Ranunculus biternatus* and *Montia fontana* were frequently encountered, very few identifiable macrofossils were present (Fig. 7). Leaves of the moss species *Campylopus clavatus* and seeds of *Agrostis magellanica* were restricted to the sample at 3 cm depth, suggesting these macrofossil components do not survive the decomposition processes that occurred in the bog. Zonation of the pollen, palynomorphs, and macrofossils was made by eye and by optimum splitting by information content using Psimpoll version 4.25 (both resulted with similar zone boundaries), and are described in Tables 2 and 3, respectively.

TEPHRA ANALYSES

Two distinct tephra horizons were identified in the Marion Island sequence between 200-183 cm and 124-107 cm using the LOI record (Fig. 8). Samples were extracted from 184 and 121 cm using the methods outlined above and geochemically analyzed using WDS (Tables 4 and 5). None of the glass had any visible phenocrysts. Brown vesicular glass shards (up to sand size particles) were identified in both units. Lavas on the island possess typical oceanic island basalt (OIB) geochemical characteristics (Verwoerd, 1990). There are two types of lavas: 'older grey lavas' (Pleistocene) and 'younger black lavas' of Holocene age (McDougall et al., 2001). Petrologically, all these lavas have SiO₂ values ranging between 45 and 55%, and are overwhelmingly basalt and hawaiite. Trachyte has been found only on nearby Prince Edward Island (Verwoerd, 1990). The two tephra horizons in the MARI1 core can best be characterized as basaltic in composition, at the lower end of the OIB with 46-48% SiO₂ content. Although the mean results for both horizons are

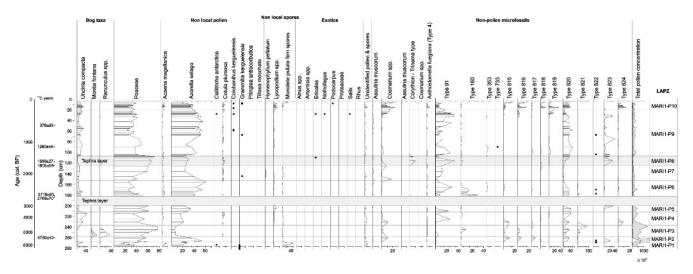
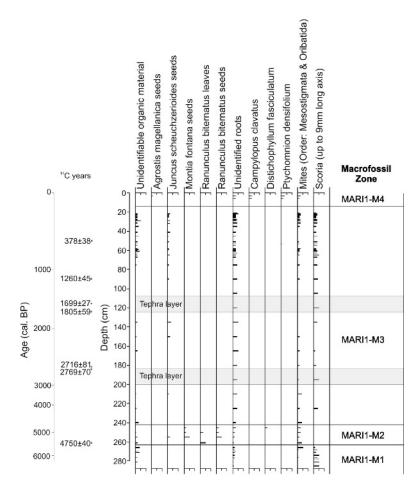


FIGURE 6. MARI1 Palynomorph stratigraphy. Values of pollen are expressed as percentages based on a sum of 300 pollen grains. Nonpollen palynomorphs are presented as percentages related to the pollen sum for each sample. The total pollen and spore concentration is plotted with a $\times 20$ exaggeration. *Montia fontana* and *Cotula plumosa* are plotted with a $\times 3$ exaggeration.

statistically indistinguishable, the individual data points do, however, record significant differences between the two horizons, suggesting separate eruptions. The horizon at 184 cm has variable Al_2O_3 values ranging from 19.2 to 14.1 wt%, while the horizon at 121 cm is significantly more limited in its range, with values between 15.8 and 14.2 wt%. Similar differences are seen in most of the other major oxides, while CaO values tend to be higher than those from 121 cm. The two distinct eruptions are dated to ca. 2900 cal. BP and ca. 1700 cal. BP.

INTERPRETATION OF THE LOCAL AND REGIONAL VEGETATION RECORD

The first stage of organic accumulation in the basin between 274 and 269 cm (ca. 5900–5700 cal. BP in zone MARI1-P1) appears to show the presence of an early successional sequence representing a fellfield/fernbrake habitat, given the high values of monolete psilate fern spores (*Blechnum penna*-marina) and *Acaena magellanica*. Free drainage of soils is highly likely to have occurred



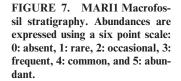


TABLE 2Local Pollen Assemblage Zones (LPAZ).

Pollen zone	Depth (cm)	Age (cal. BP)	Pollen	Non-pollen microfossils		
MARI-P10	20-5	ca. 200-modern	Low values of <i>Azorella selago</i> , Poaceae. High values of <i>Uncinia compacta</i> (peak at 14 cm), Monolete psilate fern spores (peak at 6 cm), <i>Acaena magellanica</i> (peak at 13 cm), <i>Lycopodium</i> spp. (peak at 15 cm).	High values of Type 819, and fungi (Types 815, 816, 817, 818, and 823.		
MARI1-P9	107–20	ca. 1700–200	Low values of Poaceae, Polypodiceae. Fluctuating values of Uncinia compacta, Acaena magellanica. High values of Azorella selago above 80 cm.	High values of Types 818 (rises above 32 cm) and 819, fluctuating Type 822.		
MARI1-P8	124–107	ca. 1700	Low values of <i>Azorella selago</i> , <i>Uncinia compacta</i> , Monolete psilate fern spores. High values of Poaceae, rise in <i>Acaena magellanica</i> after 115 cm.	High values of Corythion-Trinema type, Type 822		
MARI1-P7	152–124	ca. 2200–1700	Low values of <i>Azorella selago</i> . High values of Poaceae, Uncinia compacta, Monolete psilate fern spores and Acaena magellanica.	High values of Type 91. Low values of Type 819.		
MARI1-P6	183–152	ca. 2900–2200	Low values of Poaceae. High values of Uncinia compacta, Monolete psilate fern spores, Azorella selago, and Acaena magellanica.	High values of Types 91 and 160, Type 819, Type 820.		
Tephra layer	200-183	ca. 2900	Tephra laver	Tephra laver.		
MARI1-P5	212–200	ca. 3400–2900	Fluctuating values of Poaceae. Low values of Uncinia compacta. High values of Azorella selago, Lycopodium spp.	High values of Type 91, Type 819.		
MARI1-P4	236–212	ca. 4400–3400	Fluctuating values of Poaceae. High values of Azorella selago, Uncinia compacta.	High values of Type 91. Fungi (Type 815, Type 823).		
MARI1-P3	258–236	ca. 5300–4400	Low values of <i>Azorella selago</i> . High values of Poaceae, <i>Ranunculus</i> spp. (peak at 255 cm), <i>Montia fontana</i> (peak at 255 cm).	High values of Type 820, fungi present (Type 815, Type 816).		
MARI1-P2	269-258	ca. 5700-5300	High values of Azorella selago.	High values of fungi (Types 815, 816, 819, and 822).		
MARI1-P1	274–269	ca. 5900–5700	Relatively high values of <i>Uncinia compacta</i> , Monolete psilate fern spores (peak at 271 cm) and <i>Acaena magellanica</i> .			

due to the presence of coarse scoria deposits (up to 9-mm-long axis) identified in this zone.

The pollen spectra in MARI1-P2 (269–258 cm, ca. 5700–5300 cal. BP) are largely composed of Poaceae and *Azorella selago* and may reflect the slow growth of the latter pioneer species as the lava/scoria deposits were further stabilized. The highest pollen concentrations were identified in this zone, possibly indicating low peat accumulation rates and/or the position of the site in an isolated depression during this interval (Fig. 2).

Mire surface wetness appears to have been consistently high in the overlapping macrofossil and pollen zones MARI1-M2 and MARI1-P3 (263–236 cm, ca. 5500–4400 cal. BP) given the high values of *Ranunculus* pollen and *Ranunculus biternatus* seeds and leaves. These remains indicate the presence of a pool forming in the low-lying depression, possibly as a result of organic material accumulation blocking the pores in the lava/scoria deposits and therefore impeding drainage (Smith, 1987). The presence of *Montia fontana* seeds may indicate the local influence of animals, possibly wandering albatross and/or giant petrels (the site is too far inland for penguins), since this plant occurs in biotic mud habitats (Smith et al., 2001b). Relatively high pollen concentrations were also identified in this zone, again indicating low peat accumulation rates.

The absence of *Ranunculus* pollen during MARI1-P4 (236–212 cm, ca. 4400–3400 cal. BP) suggests a shift to drier conditions in the mire. Type 91 microfossils are present from the beginning of this zone, indicating oligotrophic conditions in the bog (van Geel, 1978), possibly related to the decline of the mire as an animal habitat.

In zone MARI1-P5 (212–200 cm, ca. 3400–2900 cal. BP), the higher values of *Azorella selago* may reflect a change from purely local to extra-local pollen deposition, since below c. 220 cm depth the coring site was an isolated depression measuring only c. 5×10 m (see Fig. 2). Given the widespread occurrence of *Azorella selago* from sea level to the limit of vascular plant growth at 765 m elevation (it occurred in 71% of the 457 quadrats examined in the vegetation survey of Huntley, 1972), the increase of its pollen values may indicate an influx of pollen from a greater area around the sampling site.

Following deposition of a 17-cm-thick tephra layer at 200– 183 cm depth, *Uncinia compacta* and *Acaena magellanica* initially increase at the expense of Poaceae, and *Azorella selago* gradually increases throughout the zone (MARI1-P6, 183–152 cm, ca. 2900–

TABLE 3								
Macrofossil zonation								

Macrofossil zone	Depth (cm)	Age (cal. BP)	Macrofossils			
MARI1-M4	14–5	ca. 100-modern	Fresh litter of mosses (<i>Ptychomnion densifolium</i> and <i>Campylopus clavatus</i>) and <i>Agrostis magellanica</i> seeds.			
MARI1-M3	242-14	ca. 4700-100	Relatively constant records of unidentifiable roots, scoria, and Juncus scheuchzerioides seeds.			
MARI1-M2	263-242	ca. 5500-4700	High values of mites, Ranunculus biternatus leaves and seeds, and Montia fontana seeds.			
MARI1-M1	285-263	ca. 6300-5500	High values of scoria and unidentifiable organic material.			

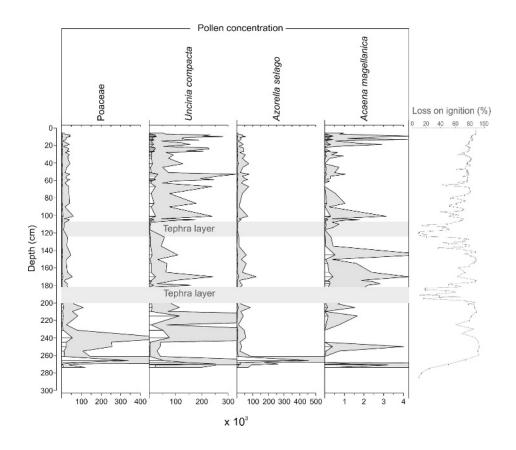


FIGURE 8. Pollen concentrations of selected pollen types, and loss on ignition (LOI) data. Gray shading on pollen concentration diagram indicates $\times 10$ exaggeration.

2200 cal. BP). This may represent the response of the vegetation to the deposition of the tephra. Concentration data (Fig. 8) reflect this pattern. On the bog surface, there was a decrease in the recruitment of Poaceae above 180 cm, while *Uncinia compacta* increased in concentration during the interval 178–165 cm. On the slopes around the bog, the cover of *Azorella selago* increased after tephra deposition and remained high relative to Poaceae (compare with the interval before the tephra deposition, when Poaceae concentrations were higher than *A. selago*). Type 160 microfossils also increase in this interval. Type 160 is characteristic of mesotrophic moorland pools in Europe (van Dam et al., 1988), and its presence may be related to a change in pH and trophic state of the bog water favoring the organism that produced it.

In zone MARI1-P7 (152–124 cm, ca. 2200–1700 cal. BP), the pollen spectra closely resemble those found in MARI1-5 before the volcanic eruption, with relatively low levels of *Azorella selago*. The tephra layer above this, in zone MARI1-P8 (124–107 cm, ca. 1700 cal. BP), complicates any vegetation reconstruction.

In the penultimate zone, MARI1-P9 (107–20 cm, ca. 1700–200 cal. BP), there is a gradual increase in the representation of *Azorella selago* at the expense of Poaceae up to 41 cm depth (ca. 400 cal. BP). On the bog surface, *Uncinia compacta* shows high values relative to those recorded in MARI1-P7, before the tephra layer. Concentration data (Fig. 8) reflect the increase of *Azorella selago* cover on the slopes around the bog up to c. 101–90 cm (ca. 1500–1200 cal. BP); which may be a response to the deposition of

TABLE 4

Relative concentrations (wt. %) of oxides of the eight major elements in glass shards from 184 cm depth, as determined by electron microprobe.

Marion Island 184 cm	SiO_2	TiO_2	Al_2O_3	FeO	MgO	CaO	Na ₂ O	K_2O	Total
1	47.2	4.5	14.1	12.5	4.5	9.0	3.8	1.9	97.5
2	47.6	4.5	14.3	12.1	4.4	8.7	3.6	2.0	97.1
3	49.6	2.7	19.2	8.2	4.6	9.1	4.3	1.2	98.9
4	48.4	4.2	16.1	11.2	3.9	8.9	3.9	1.7	98.2
5	50.0	3.6	15.0	11.4	6.5	5.8	4.8	1.8	98.9
6	47.7	4.4	14.2	12.6	4.4	8.9	3.9	1.9	97.9
7	46.7	4.5	13.9	12.9	4.6	8.8	3.6	1.9	96.8
8	47.2	4.3	14.4	11.9	4.4	8.8	3.8	1.9	96.7
9	47.8	4.3	14.6	12.1	4.5	8.9	3.7	1.8	97.6
10	47.9	4.5	14.4	12.4	4.5	8.9	3.3	1.8	97.7
11	47.8	4.3	14.4	12.2	4.5	8.6	3.8	2.0	97.5
12	48.4	3.7	15.8	11.4	4.1	9.0	3.9	1.6	98.0
13	48.0	4.1	14.7	12.1	4.4	8.7	3.9	1.9	97.7
Mean	48.0	4.1	15.0	11.8	4.6	8.6	3.9	1.9	97.7
SD	0.9	0.5	1.4	1.2	0.6	0.9	0.4	0.2	0.7

508 / Arctic, Antarctic, and Alpine Research

TABLE 5

Relative concentrations (wt. %) of oxides of the eight major elements in glass shards from 121 cm depth, as determined by electron microprobe.

Marion Island 121cm	SiO_2	TiO ₂	Al_2O_3	FeO	MgO	CaO	Na ₂ O	K_2O	Total
1	45.9	4.2	14.1	13.5	4.5	9.7	3.6	1.8	97.3
2	45.6	4.2	15.1	13.0	5.0	10.1	3.5	2.4	98.9
3	46.5	4.1	14.7	13.0	4.6	8.5	3.7	1.8	96.8
4	45.9	4.3	15.0	12.8	4.7	8.9	3.8	1.8	97.0
5	47.5	3.7	15.8	11.8	4.1	8.6	3.6	1.6	96.8
6	46.6	4.1	15.0	12.7	4.8	10.1	3.8	1.6	98.8
7	46.5	4.0	14.5	12.9	4.8	10.1	3.5	1.6	97.8
8	45.9	4.1	14.7	13.0	4.8	9.9	3.7	1.6	97.7
9	46.4	4.3	14.9	13.0	4.5	8.8	3.9	1.8	97.6
10	46.6	4.4	14.9	13.3	4.6	9.1	3.5	1.8	98.3
Mean	46.3	4.1	14.9	12.9	4.6	9.4	3.7	1.8	97.7
SD	0.6	0.2	0.4	0.5	0.2	0.7	0.1	0.2	0.7

the tephra. The greatest diversity of exotic pollen was also discovered in MARI1-P9 and is likely to reflect the larger pollen source area of the expanding peatland.

The final zone, MARI1-P10 (20–5 cm, ca. 200 cal. BP to modern), records an increase in monolete psilate fern spores and *Acaena magellanica*, and may indicate the presence of a fernbrake/ dwarf shrub habitat and drier conditions.

Discussion

The results suggest that tephra deposition has been a major influence on long-term vegetation succession in and around the study site. The effects of tephra deposition close to the source of eruption include the mechanical impact upon the land surface (including the burial or partial burial of plants), the encouragement of erosion in freshly coated surfaces and the chemical 'scorching' of leaves (Edwards et al., 2004; Hotes et al., 2006). After volcanic ash deposition ca. 2900 cal. BP, total vegetation cover initially decreased and then *Uncinia compacta* increased in cover as a pioneer on the disturbed mire surface. On the slopes around the bog, *Acaena magellanica*, and particularly *Azorella selago*, increased in cover. Ash deposition can alter topography and therefore influence stream patterns (Collins, 1969); a change in drainage lines would favor *Acaena magellanica*, since this species occurs where subsurface water flows on slopes (Smith et al., 2001b).

The slow increase of Azorella selago pollen after volcanic ash deposition ca. 2900 cal. BP (MARI1-P6, with a duration of c. 700 yr) represents the long-lived nature and extremely slow growth of Azorella selago (small 15-cm-diameter cushions were estimated to be 83 years old by Huntley [1972], although there are no age estimates for the larger cushions which can exceed 1 m diameter). The volcanic ash itself can also absorb moisture and cause desiccation; resulting in the slow growth of Azorella selago. Furthermore, the exposed periglacial conditions on the island may explain the slow vegetation succession. The low annual temperature ranges experienced on Marion Island combined with high precipitation and cloudiness result in high frequencies of shortduration freeze-thaw cycles with shallow frost penetration. The presence of patterned ground and solifluction features and the incidence of debris flows, peat slides, and frost creep associated with needle ice activity highlight the dynamic nature of geomorphological processes on Marion Island (Boelhouwers et al., 2003; Holness, 2004). The general pattern of long-term vegetation change described in this study may be compared with arctic tundra landscapes, where rates of directional vegetation change are extremely slow, often of the order of a 1000 years or more (e.g. Billings and Peterson, 1980). In the Arctic, episodic environmental

events slow or reverse successional development so that the "successional clock" is continually being reset by disturbance (Forbes and Jefferies, 1999). The slow pace of vegetation succession highlights the sensitivity of the indigenous Marion Island flora to environmental change, and the importance of controlling the introduction and spread of alien invasive species, which by contrast, can respond faster. This has been shown by the rapid spread of the grass *Agrostis stolonifera* between the 1980s and 1990s, possibly as a result of the ongoing climate change (Bergstrom and Chown, 1999). The ongoing climate change may also affect the growth and distribution of *Azorella selago* both directly through decreased rainfall, and indirectly by increased shading from faster growing grass species (Le Roux et al., 2005).

Examination of pollen diagrams from previous studies suggests that increases of Azorella selago after tephra deposition have occurred at other sites around the island. These include Macaroni Bay (at c. 250 cm depth), Albatross Valley on nearby Prince Edward Island (at c. 325 cm, c. 275 cm, and c. 185 cm depth), and Juniors Kop from the early study of Schalke and van Zinderen Bakker (1971), in addition to Albatross Lakes (4th boring) (at c. 175 cm depth) (Scott, 1985). However, these pollen diagrams have relatively low resolution (10 cm), making these changes not so noticeable, and were therefore not discussed in the publications. Schalke and van Zinderen Bakker (1971) used a sum including both pollen and spores, which may have also confused the interpretation of the diagrams. Due to the low number of indigenous taxa (and consequent pollen types) on the island, there has been less motivation to calculate a pollen sum distinguishing local bog pollen types from extra-local taxa. In particular, increases of extra-local A. selago at Albatross Lakes (3rd boring) after the tephra deposition at c. 378 cm (Scott, 1985) may have been masked by the dominance of the pollen spectra by the local aquatic Ranunculus spp.

The evidence for a major effect of volcanic ash deposition on the vegetation of other areas of the island is therefore not entirely conclusive, and this may also be due to the pollen recruitment characteristics of the sites studied. A review of basin characteristics and estimated pollen source area by Davies and Tipping (2004) suggests that the coring site, even at its current dimensions of c. 130×80 m, would only record local vegetation mosaics within a radius of c. 1 km. The pollen records reported here and in previous studies are therefore not representative of the entire island's vegetation. However, there are c. 130 volcanic cones on the island marking centers of eruption, and even relatively recently in 1980 (Verwoerd et al., 1981), 2004, and 2005 (http:// www.up.ac.za/academic/geog/marion_island.html), small eruptions have occurred; leading to the speculation that tephra deposition and the consequent effects on the local vegetation have been repeated on numerous occasions around the island since the last glacial. The results of this study outline the sensitivity of ecosystems on Marion Island to disturbance from tephra deposition and associated effects including the burial of plants, chemical 'scorching' of leaves, and alteration of trophic status through acidification and nutrient enrichment.

Acknowledgments

The South African National Antarctic Program provided financial and logistic support for this research, and NERC provided ¹⁴C dating support (Allocation No. 987,1002). We thank Jan Boelhouwers for suggesting and encouraging this research in the first instance and for fieldwork assistance with Steve Holness and Werner Nel. We also thank Valdon Smith for collecting additional plant type material and for valuable discussions on Marion Island peatland ecology. Louis Scott offered useful suggestions in the identification and interpretation of the pollen records, and both Melodie McGeoch and Peter Le Roux gave useful advice on the ecology of Azorella selago. Louise Coetzee kindly confirmed the identifications of the mites encountered in the samples. Randy Miller examined possible tardigrade eggs, and identifications of the mosses were made by Ryzard Ochyra. We thank Annemarie Philip for preparing the pollen samples, Jan van Arkel for creating the digital illustrations of the micro/macrofossil samples, and Stephen McFarland for help in operating the electron microprobe at Queen's University Belfast. We also thank Anne Jennings and two anonymous reviewers for constructive comments on the manuscript.

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Ms accepted September 2006

Appendix-Descriptions Of Palynomorphs

TYPE 815

Two-celled fungal spores, each cell 10–25 μ m in length and 5– 12 μ m in width. Constriction at septum. The spores often show two germ slits running parallel along the long axis of each cell. Some spores have cells that vary in proportion from one another.

TYPE 816

Three-septate elongate fungal spores, $15-33 \mu m$ in length and $5-8 \mu m$ in width. Septa are often barely visible and are spaced out evenly along the long axis. Type 816 spores occur in the lower and the upper part of the core only.

TYPE 817

Elliptical fungal spores, $\sim 20 \ \mu m$ in length and $\sim 7.5 \ \mu m$ wide. The spores often show a germ slit along the long axis.

TYPE 818

Irregular and angular shaped microfossils, $58-220 \mu m$ in length and $16-30 \mu m$ in width. Appears to be plant cells infested with fungal hyphae. Shows relatively high frequencies of occurrence in the upper 30 cm of the core.

TYPE 819

'Winged' microfossils with a center composed of a doublewalled globose object, $\sim 68 \ \mu\text{m}$ in diameter. This is often filled with dark material, frequently smaller globose objects. The wings are relatively thin walled compared to the center. Type 820 appears to be quite fragile, and is more often than not found in a broken state, with two components: (1) the two 'wings' joined together, $\sim 55 \ \mu\text{m}$ in length, and $\sim 33 \ \mu\text{m}$ in width; and (2) the double-walled center piece, sometimes filled with dark material.

TYPE 820

Spores/eggs $28-36 \,\mu\text{m}$ in diameter. Covered with small hyaline ridges; ridges often green/white. Objects are sometimes folded. May be a tardigrade egg (R. Miller, personal communication, 2004).

TYPE 821

Egg-shaped objects, 15–23 μm in length and 8–13 μm in width. Pits on surface at varying depths.

TYPE 822

Hyaline egg- or cigar-shaped objects, 13–32 μ m in length and 8–13 μ m in width. A relatively large pore (diameter 2.5–5 μ m) and distinct annulus at one end. Possibly a testate amoeba.

TYPE 823

Fungal spores 20–24 μ m in length and 7.5–12 μ m in width. Composed of four cells. Two central cells are relatively large. Terminal cells are relatively small and almost hyaline.