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Impact of Trampling on the Vegetation of Subantarctic Marion Island

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Abstract

We assessed the impact of human trampling in three different habitats on Marion Island (46°50'S, 37°50'E). The habitats were (1) mires with wet, peaty soils and grass- and bryophyte-dominated vegetation; (2) slopes with relatively dry mineral soils, dominated by small ferns and dwarf shrub; and (3) feldmark on dry mineral soils with an open vegetation of cushion dicots and bryophytes. We examined existing walking tracks on the island. Track width (25 to 800 cm) increased with soil moisture content. Trampling reduced vegetation height, total cover, and species richness in mires and feldmark and vegetation height and herb layer cover (but not bryophyte cover or species richness) in slopes. In mires, most species were negatively affected by trampling, but in slopes trampling increased the cover of 6 out of 9 significantly affected species. The total number of species in all trampled plots in mire and feldmark communities was ~10% lower, but in slopes 28% higher, than in control plots. The impact of trampling differed between growth forms. Cushion dicot, shrub, and fern covers were reduced, whereas graminoid and pleurocarpous moss covers were unaffected or increased with trampling. Trampling reduced the cover of most bryophyte species, but it did increase the cover of some. In the slope habitat, destruction by trampling of the closed herb canopy allows increased light penetration and makes the habitat more favorable for small plants such as bryophytes. We attribute the differences in how the vegetation of different habitats responds to trampling to differences in the structure of the original vegetation as well as differences in soil characteristics, especially the soil's structural stability under pressure.

Introduction

Trampling is considered a major negative impact of tourist visits in the Antarctic and subantarctic, and it certainly is one of the most obvious (Cessford and Dingwall, 1998). The demand for tourist visits to subantarctic islands has been increasing rapidly, including recent proposals to develop ecotourism on subantarctic Marion Island. As part of a study for the Environmental Impact Assessment of Tourism on Marion Island (Heydenrych and Jackson, 2000), we studied the effect of trampling on the vegetation of the island, using the network of walking tracks between the research station and a number of study sites.

Marion Island is uninhabited, with a small, annually rotated complement of researchers and meteorologists staying at the island's weather station. Until the 1980s, people traveled little on the island, and rarely along fixed routes. In the 1980s and early 1990s, an intensive cat eradication program took place, which involved intensive movement of people through all of the lowlands of Marion Island. As a result, tracks developed between the station and the field huts. Since the end of the cat eradication program in 1994, only a few tracks, mainly close to the weather station, are still in use.

Although trampling is a naturally occurring phenomenon in many areas of the island where vast numbers of penguins and/or seals congregate, human trampling differs from trampling by animals because the latter is always associated with heavy manure deposits and other forms of nutrient enrichment (Gremmen, 1981). Although in antarctic and subantarctic environments the impact of human trampling is highly visible, very little is known about its ecological effect. In this study we aim to answer the following questions: (1) what impact does trampling by people have on vegetation structure and soil characteristics; (2) is there an impact on species richness and on species composition of the vegetation; and (3) does this impact differ between habitats?

Study Area

Marion Island (46°50'S, 37°50'E) is a relatively young volcanic island, 290 km² in area, situated in the Southern Indian Ocean, just north of the Antarctic Convergence. The island has a cool, extremely oceanic climate, characterized by a mean annual temperature of ca. 7°C, with little diurnal and seasonal variation, high precipitation (>2500 mm annually, mainly as rainfall), and high wind speeds (Schulze, 1971; Smith, 2002). The island's flora is relatively species-poor. Forty-two species of vascular plants have been recorded, 18 of which are considered introduced (Gremmen and Smith, 1999). At this time, well over 80 species of mosses (Ochyra and Hertel, 1990), 42 hepatics (Grolle, 2002), and 87 lichens (Øvstedal and Gremmen, 2001) are known.

Marion Island does not have any permanent inhabitants. Sealers were active on the island in the 19th and early 20th centuries (Cooper and Avery, 1986). In 1948 a meteorological station was established at Transvaal Cove, which has been in use continuously since then and houses an annually rotated complement of between 10 and 30 people. There is no vehicular transport. All tracks have been made by people traveling on foot.

Methods

FIELD OBSERVATIONS

From the research station at Transvaal Cove several tracks run toward a number of often visited study sites. In April–May 1997 at 50 sites, we compared the vegetation of these tracks with the vegetation in the areas immediately next to the tracks. Two sample plots measuring 300 × 20 cm were set up at each site: one trampled plot lengthwise on the center of the track, the other in undisturbed vegetation 1 m from the

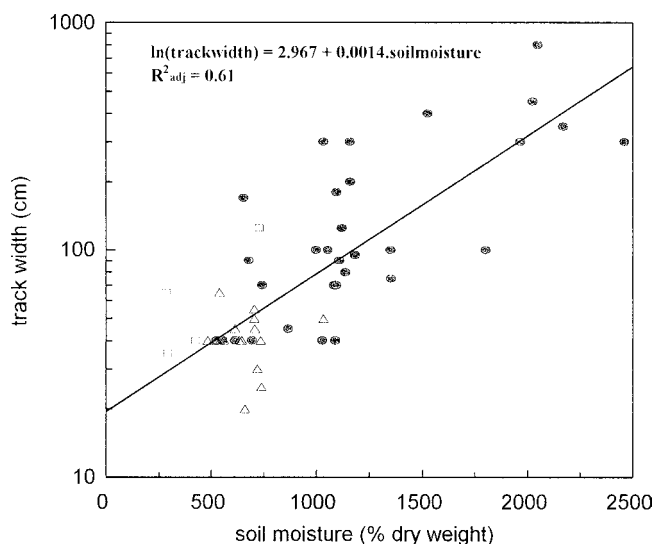


FIGURE 1. Relationship between track width and soil moisture content. Filled circles indicate mire plots, open triangles represent slope plots, and open squares are feldmark plots.

edge of the track and paralleling it lengthwise. At this distance from the track, we saw no signs of disturbance (footprints or damaged plants). In general, a sample site was placed every 100 m along the track, but care was taken to select only sites where the track ran through a homogeneous area, i.e., where the vegetation and site characteristics to the left and the right of the track were the same.

Sites were grouped in three different types of habitat:

1. Mires on peat soil, ranging from very wet to relatively dry. Vegetation with a 20- to 30-cm-high vascular plant stratum dominated by graminoids and a dense bryophyte stratum, usually completely covering the soil (*Juncus scheuchzerioides*–*Blepharidophyllum densifolium* complex; Gremmen, 1981) (30 sites).
2. Lowland slopes, damp mineral soils with an organic top layer. Vegetation consists of a very dense 20- to 40-cm-high vascular stratum, dominated by the small fern *Blechnum penna-marina* and/or the rosaceous dwarf shrub *Acaena magellanica*. The bryophyte stratum usually has low cover (*Acaena magellanica*–*Brachythecium* complex and *Blechnum penna-marina* complex; Gremmen, 1981) (16 sites).
3. Lowland feldmark, areas strongly exposed to the wind on relatively dry mineral soils. Characterized by low plant cover and dominated by the cushion-forming vascular plant *Azorella selago* and cushion-forming mosses. These communities cover over 50% of the lowland areas and dominate the vegetation above 300 m a.s.l. (*Andreaea*–*Racomitrium crispulum* complex; Gremmen, 1981) (4 sites). Low plant cover and dry mineral soils make feldmark areas easy walking, and there is little tendency for people to closely follow the same route and thus create tracks. Hence, only a few sites, where a route crossed a small feldmark area and people tended to walk the same path, are included in our study.

For each site the following characteristics were noted: (1) slope aspect and angle; (2) distance from the weather station; (3) soil type: peat, loamy peat, mineral soil; (4) general plant community type; and (5) track width (defined as the width of the area where clear signs of trampling, e.g., footprints, occurred). For each plot we visually estimated the percentage cover of all species of vascular plants, bryophytes, and lichens as well as the total cover of herb layer, moss layer, rock, and bare

soil. Cover was estimated to the nearest 1% between 0 and 5 and 95 and 100%, otherwise to the nearest 5%. Any cover value >0 and ≤1% was noted as 1%. In the center of each plot, we took a soil sample of known volume to determine soil water content and bulk density.

The number of people that passed over each study site between September 1996 and April 1997 was determined from the logbook recording all field trips on the island. The number of passes ranged from 50 to 381, with an average of 220, which is approximately 1 d⁻¹.

DATA ANALYSIS

We compared the species number, cover of vascular plants and bryophytes and the percentage bare soil, and the cover of individual species between trampled and nontrampled plots using a Wilcoxon signed-ranks test of the hypothesis that the sample means in both groups of plots were equal (Sokal and Rohlf, 1981). We made separate comparisons for the 3 habitat types. The number of sites in feldmark areas was insufficient for a statistical test. Not all species occurred in each pair of plots; thus, the number of pairs in species-level comparisons differed between species and habitats. Species found in fewer than 6 pairs of plots were not tested.

Results

In mire areas, track width ranged from 25 cm to 8 m and increased with soil moisture content (Fig. 1). No significant differences were observed in soil moisture content and soil bulk density between trampled and control plots. Trampling markedly reduced height and cover of both herb and bryophyte strata (Table 1) and resulted in an increase in bare soil. Species number per plot was reduced in trampled plots by ~30%. All trampled mire plots together contained ~13% less species than the mire control plots. Of 13 species that showed a significant impact by trampling, 12 were reduced in cover. Only 1 species, *Juncus scheuchzerioides*, had a significantly higher cover in the trampled plots (Table 1). A comparison of the cover per growth form showed large decreases in the cover of ferns, acrocarpous mosses, and hepatics but no significant change in the cover of graminoids and pleurocarpous mosses (Table 2).

In slope habitats, tracks were narrow (20 to 60 cm). We found no relationship between track width and soil moisture content, but the slope plots fit in with the general relationship between these two variables (Fig. 1). Height and cover of the herb layer, as well as the height of the bryophyte stratum, were considerably reduced by trampling. The cover of the bryophyte layer, however, was not significantly affected (Table 1). Species richness per plot was on average higher in trampled plots, but this difference was not significant. Also, the total number of species in all trampled slope plots was more than 25% higher than in the control plots. Nine species were significantly affected by trampling. Six of these showed an increase in cover in trampled plots, while cover of only 3 species was reduced (Table 1). The large increase in cover of the introduced species *Agrostis stolonifera* and *Sagina procumbens* is noteworthy. Ferns, cushion dicots, and shrubs were largely replaced by graminoid species (Table 2).

In feldmark habitats we had only 4 pairs of plots, too few for significance tests. The data suggest a decrease in height of the herb layer in trampled plots but little change in vegetation cover. The characteristic cushion dicot *Azorella selago* was largely replaced by the introduced grass *Agrostis stolonifera* and the native rush *Juncus scheuchzerioides* (Table 1, Table 2). The species richness per plot in feldmark is considerably lower in trampled plots, while the total number of species in all trampled feldmark plots is slightly lower than in the controls (Table 1).

The number and cover of introduced vascular plant species was larger in trampled plots than in the controls, although the difference was not always significant (Table 1).

TABLE 1

Comparison of characteristics of tracks and untrampled control sites. Significance tests were only performed for species that occurred in more than 6 sites. Mean species cover for each species was calculated using only those pairs of plots where the species occurred in at least 1 plot. Introduced species have been marked with *

	Mires (n = 30)				Slope communities (n = 16)				Feldmark (n = 4)		
	Control	Tracks	Wilcoxon	Nonzero pairs	Control	Tracks	Wilcoxon	Nonzero pairs	Control	Tracks	Nonzero pairs
Track width (cm)	—	171			—	43			—	66	
Soil moisture (% of dry weight)	1208	1192	n.s.		692	728	n.s.		433	390	
Soil bulk (g per soil core)	67.5	69.9	n.s.		82.4	90.3	n.s.		16.4	20.3	
Cover bare ground (%)	0.4	22.3	$P = 0.00$		0	15.1	$P = 0.00$		30.5	37.0	
Cover herb layer (%)	74.1	51.1	$P = 0.00$		96.9	72.1	$P = 0.00$		61.3	61.3	
Height herb layer (cm)	23.5	7.6	$P = 0.00$		31	7.6	$P = 0.00$		18.0	2.8	
Cover moss layer (%)	85.8	50.4	$P = 0.00$		28.5	34.6	n.s.		27.5	27.5	
Height moss layer (cm)	5.2	1.8	$P = 0.00$		5.4	1.5	$P = 0.00$		0.8	0.9	
Total species number	12.8	8.9	$P = 0.00$		7.2	9.7	n.s.		14.8	9.5	
Vascular species number	4.2	3.3	$P = 0.00$		3.5	4	n.s.		5.5	3.8	
Bryophyte species number	8.9	5.4	$P = 0.00$		3.6	5	n.s.		8.3	5.3	
Introduced species number	0.3	1	—	4	0.2	1.3	$P = 0.00$	9	1.5	1.0	2
Total number of species in all plots	47	41			29	37			30	28	
Species cover in %:											
Vascular plants											
<i>Acaena magellanica</i>	4.7	1.3	—	4	23.3	0.6	$P = 0.01$	7	1.0	0.0	1
<i>Agrostis magellanica</i>	35.7	35.8	n.s.	30	1.5	44.5	$P = 0.01$	12	29.5	24.0	4
* <i>Agrostis stolonifera</i>	10.0	10.5		3	10.2	56.0		5	3.0	35.0	2
<i>Azorella selago</i>	1.9	0.2	$P = 0.01$	10	5.8	0.1	$P = 0.01$	8	21.3	0.5	4
<i>Blechnum penna-marina</i>	46.7	8.2	$P = 0.00$	19	87.8	19.9	$P = 0.00$	15	16.5	2.0	2
<i>Juncus scheuchzerioides</i>	2.9	9.3	$P = 0.00$	26	0.3	4.9	$P = 0.03$	7	1.5	30.5	2
<i>Montia fontana</i>	0.3	0.8		4	0.0	1.0	$P = 0.02$	6			
<i>Poa cookii</i>	3.0	0.0		1	11.6	5.5	n.s.	8			
<i>Ranunculus bitermatus</i>	1.0	0.8	n.s.	11	1.0	0		1	1.0	1.5	2
* <i>Sagina procumbens</i>	0.0	2.0		2	0.0	5.4		5	4.0	6.5	2
<i>Ucinia compacta</i>	15.1	1.5	$P = 0.00$	20	6.4	0.6		5			
Mosses											
<i>Brachythecium rutabulum</i>	2.0	0.0		4	2.9	0.6	n.s.	8			
<i>Campylopus arboricola</i>	10.4	2.1	$P = 0.02$	15	0.3	0.7		3	3.0	0.5	2
<i>Campylopus introflexus</i>	1.0	2.9	n.s.	13	0.1	3.2	$P = 0.02$	10	1.0	0.5	2
<i>Distichophyllum fasciculatum</i>	6.0	1.5	n.s.	13	0.0	1.0		2			
<i>Leptodontium proliferum</i>	0.8	0.5		4	0.3	0.9	n.s.	7			
<i>Ptychomnion ringianum</i>	12.2	5.4	n.s.	9							
<i>Racomitrium lanuginosum</i>	15.8	0.8	$P = 0.01$	9	2.5	0.5		2	1.0	0.0	1
<i>Sanionia uncinata</i>	10.2	16.3	n.s.	25	26.4	29.5	n.s.	14	0.5	0.5	2
Hepatics											
<i>Blepharidophyllum densifolium</i>	18.1	0.8	$P = 0.00$	23	0.0	1.0		3			
<i>Clasmatocolea humilis</i>	19.3	29.0	n.s.	25	0.4	11.6	$P = 0.04$	9	13.7	32.7	3
<i>Gymnocoleopsis cylindriciformis</i>	1.0	0.4	$P = 0.01$	14	0.7	0.6	n.s.	11	1.0	0.0	1
<i>Jamesoniella colorata</i>	34.6	2.9	$P = 0.00$	22					1.0	0.5	2
<i>Jensenia piscicolor</i>	0.9	0.3	n.s.	8	0.0	1.0		1	22.5	3.0	2
<i>Lepidozia laevifolia</i>	1.8	1.0	$P = 0.00$	27	0.2	1.2	$P = 0.01$	9	1.0	0.3	3
<i>Leptoscyphus expansus</i>	1.0	0.1	$P = 0.01$	11	1.0	0.3		3			
<i>Lophozia lancistipa</i>	1.3	0.1	$P = 0.01$	12	0.0	1.0		1			
<i>Plagiochila heterodonta</i>	6.6	0.4	$P = 0.01$	10	1.0	0.0		2	2.3	0.3	3

We found no relationship between the number of people that had passed over the track during the year preceding our study and the impact as expressed by changes in cover of bare soil and species number.

Discussion

On Marion Island, tracks were formed by the tendency of people repeatedly visiting the same areas to follow the same route each time. Only recently have people been encouraged to use existing tracks rather than walk through undisturbed areas. In mire areas, wide tracks develop. People appear to avoid trampled muddy areas (cf. Scott and Kirkpatrick,

1994; Leung and Marion, 1996) and walk along the edge of the track. Increased use thus results in a wider zone of disturbance. The width of the track is strongly related to soil moisture content. On the relatively dry slopes the reduction in vascular plant cover resulting from repeated trampling makes walking easier. Narrow tracks develop, and only in the wettest places is there a tendency for tracks to widen, or for parallel tracks to develop. In feldmark areas the low, open vegetation and dry soils make walking easy, and there is less tendency for people to follow a fixed track. On the hard, rocky soil, tracks are difficult to see, making it difficult to follow previous walkers' tracks in any case. Therefore, trampling in feldmark habitats is more diffuse than in mires, and

TABLE 2
Comparison of the cover of plants grouped by growth form

	Mires				Slopes				Feldmark		
	Control n = 30	Tracks	Significance level Wilcoxon	Pairs	Control n = 16	Tracks	Significance level Wilcoxon	Pairs	Control n = 4	Tracks	Pairs
Cushion dicot	1.9	0.2	0.01	9	5.8	0.1	0.01	8	21.3	0.5	4
Fern	46.8	8.2	0.00	18	87.8	19.1	0	15	16.5	2	2
Graminoid	50	45.7	n.s.	30	13.1	60.3	0	15	33.3	58	4
Small herb	0.8	1.5	n.s.	11	0.1	3.7	0.01	10	6.5	8	2
“Shrub”	4.7	1.3		3	23.3	0.6	0.01	7	1	0	1
Acrocarpous mosses	22.6	78	0.00	28	0.8	3.7	0	12	6	2.5	4
Pleurocarpous mosses	12	14.9	n.s.	29	33.1	32.9	n.s.	14	0.5	1	2
Hepatics	69.1	34.2	0.00	28	1.9	11.3	n.s.	12	30.5	27.3	4
Lichens	1.0	1.0	n.s.	6	0.3	1		4	1.3	0.7	3

certainly much more diffuse than in slopes. Hence, the number of people passing over a track is not a good measure of trampling pressure per unit area. This, combined with the possibility that the 8-mo period for which data on track use were available was not representative for overall long-term track use, may explain the lack of a relationship in our study between number of passes over a track and trampling impact.

Reduction of vegetation height and cover and an increase in bare ground by trampling have been observed in many trampling studies (e.g., Sun and Liddle, 1993; Scott and Kirkpatrick, 1994; Monz et al., 1994; Cole, 1995). Most studies also reported a marked decrease in species richness in trampled vegetation (Kuss and Hall, 1991; Liddle, 1991; Sun and Liddle, 1993; Monz et al., 2000). Response to trampling differed between habitats, however (cf. Cole, 1987, 1995; Monz et al., 2000). In general, plant cover and species richness was negatively affected by trampling, but in slope communities this was not the case. In mires, of 13 species significantly affected by trampling only 1 showed a positive response, but in slopes, 6 out of 9 affected species responded positively to trampling. We believe that the differences in impact between habitats are related to differences in soil characteristics, notably soil moisture content (which on Marion Island is generally strongly related to organic matter content), and to differences in the structure of the original vegetation. On organic soils with a high moisture content, a walker's feet tend to sink into the soil, and consequently the structural damage of a single footstep to the above- and below-ground plant structures is considerably greater than on more compact, dry mineral soils. In slope communities the closed cover of *Blechnum* and *Acaena*, which normally outcompete all other species in these habitats, is broken down, and other species, notably graminoids and some bryophytes, are able to reach high cover values. The large number of species occurring in trampled plots in slope habitats may be due partly to the presence of trampling-resistant species. The increase in overall species number in the trampled plots, however, indicates the colonization of trampled sites by species not present in the undisturbed vegetation. This colonization may be caused by a change in light conditions in the trampled plots. Trampling destroys the dense upper stratum of *Blechnum penna-marina* and *Acaena magellanica* and allows more light to reach the surface. Decreased competition for light, and possibly other resources, may allow more species to enter trampled vegetation (Ellenberg, 1982; Sun and Liddle, 1993; Kobayashi et al., 1997).

The resistance of graminoids and the sensitivity of ferns and plants with lignified stems to trampling has been noted by Kuss and Graefe (1985), Cole (1988), and Sun and Liddle (1993). The general sensitivity of bryophytes to trampling also has been noted in several studies (Scott and Kirkpatrick, 1994; Liddle 1997), but most trampling studies have not looked at individual bryophyte species or bryophyte growth forms. Pleurocarpous mosses appear more resistant to trampling than acrocarpous mosses. Our results indicate that even when no significant impact of trampling on total bryophyte cover is found, as in the slope

communities, species composition of the bryophyte layer as well as cover of individual species may be considerably modified.

Tracks have been implicated in the dispersal of introduced species (Scott and Kirkpatrick, 1994; Leung and Marion, 2000). We found a significant increase in the number and cover of introduced species in trampled plots compared to plots with undisturbed vegetation. We found no decrease in the number or the cover of introduced species with increasing distance from the meteorological station. We suspect that the larger number and cover of introduced plants on the trampled plots is due to a more favorable habitat for colonization and growth of these species rather than the effect of people dispersing them along the tracks. This does not mean that humans are not instrumental in the dispersal of introduced species on Marion Island; people have been shown to be vectors in the introduction and dispersal of alien plants and animals on the island (Smith, 1992; Gremmen and Smith, 1999). Rather, the introduced species that we found in our plots are widely spread in the part of the island where we studied the tracks, and people walking around are likely to pick up propagules of these species in any part of the study area.

This study shows that trampling by people has considerable impact. However, effects are very localized, and there are large differences in impact between habitats. Although species loss is much smaller in slope habitats, more importantly, the tracks in these habitats are much narrower than in mires, and thus the area affected is much smaller. Trampling obviously cannot be avoided when people need or want to visit areas away from the meteorological station, but we recommend avoidance of mire areas when possible. Where severe trampling in mire areas can not be avoided, the construction of catwalks should be considered. Certainly when tourism begins to develop on Marion Island, the impact of trampling will be much greater than it is at present, when the tracks are caused only by a few scientists regularly visiting their study sites. At the time of our study, the most intensively used track, running from the meteorological station to Trypot Beach, had fewer than 400 passes over it during one field season, or fewer than 2 passes per day.

Our results are very similar to those found for Macquarie Island by Scott and Kirkpatrick (1994), and similar observations have been made on the upland plateau of Gough Island (Gremmen, unpublished data). Therefore, we believe that our conclusions have some general validity for cold oceanic islands and are useful in planning mitigating measures for human impacts not only on Marion Island but in other subantarctic and cold temperate regions as well.

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References Cited

- Cessford, G., and Dingwall, P. R., 1998: Research on shipborne tourism to the Ross Sea region and the New Zealand sub-Antarctic islands. *Polar Record*, 34(189): 99–106.
- Cole, D. N., 1987: Effects of three seasons of experimental trampling on five montane forest communities and a grassland in western Montana, USA. *Biological Conservation*, 40: 219–244.
- Cole, D. N., 1988: *Disturbance and Recovery of Trampled Montane Grassland and Forests in Montana*. Research Paper INT-389. Ogden, UT: USDA Forest Service, Intermountain Research Station. 37 pp.
- Cole, D. N., 1995: Experimental trampling of vegetation. II. Predictors of resistance and resilience. *Journal of Applied Ecology*, 32: 215–224.
- Cooper, J., and Avery, G. (eds.), 1986: *Historical Sites at the Prince Edward Islands*. South African National Scientific Programmes Report No. 128. Pretoria: CSIR. 82 pp.
- Ellenberg, H., 1982: *Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht*. Stuttgart: Verlag Eugen Ulmer. 989 pp.
- Gremmen, N. J. M., 1981: *The Vegetation of the Prince Edward Islands*. The Hague: Junk. 149 pp.
- Gremmen, N. J. M., and Smith, V. R., 1999: New records of alien vascular plants from Marion and Prince Edward Islands. *Polar Biology*, 21: 401–409.
- Grolle, R., 2002: The Hepaticae and Anthocerotae of the subantarctic and temperate islands in the eastern Southern Hemisphere (90°E to 0°): an annotated catalogue. *Journal of Bryology*, 24: 57–80.
- Heydenrych, R., and Jackson, S., 2000: *Environmental Impact Assessment of Tourism on Marion Island*. Pretoria: South African Department of Environmental Affairs and Tourism. 115 pp.
- Kobayashi, T., Hori, Y., and Nomoto, N., 1997: Effects of trampling and vegetation removal on species diversity and micro-environment under different shade conditions. *Journal of Vegetation Science*, 8: 873–880.
- Kuss, F. R., and Graefe A. R., 1985: Effects of recreation trampling on natural area vegetation. *Journal of Leisure Research*, 17: 165–183.
- Kuss, F. R., and Hall, C. N., 1991: Ground flora trampling studies: five years after closure. *Environmental Management*, 15: 715–727.
- Leung, Y., and Marion, J. L., 1996: Trail degradation as influenced by environmental factors: A state-of-the-knowledge review. *Journal of Soil and Water Conservation*, 51: 130–136.
- Liddle, M. J., 1991: Recreation ecology: effects of trampling on plants and corals. *Trends in Ecology, Evolution and Systematics*, 6: 13–17.
- Liddle, M. J., 1997: *Recreation Ecology: The Ecological Impact of Outdoor Recreation and Ecotourism*. London: Chapman and Hall. 639 pp.
- Monz, C. A., Pokorny, T., Freilich, J., Kehoe, S., and Ayers-Baumeister, D., 2000: The consequences of trampling disturbance in two vegetation types at the Wyoming Nature Conservancy's Sweetwater River Project area. *USDA Forest Service Proceedings RMRS-P-15*, 5: 153–159.
- Monz, C. A., Cole, D. N., Johnson, L.A., and Spildie, D.R., 1994: Vegetation response to trampling in five native plant communities in the Wind River Range, Wyoming, USA. *Bulletin of the Ecological Society of America*, 75: 158.
- Ochyra, R., and Hertel, H., 1990: Contribution to the moss flora of the subantarctic island Marion. *Polish Botanical Studies*, 1: 19–34.
- Øvstedal, D. O., and Gremmen, N. J. M., 2001: The lichens of Marion and Prince Edward Islands. *South African Journal of Botany*, 67: 552–572.
- Schulze, B. R., 1971: The climate of Marion Island. In van Zinderen Bakker, E. M., Winterbottom, J. M., and Dyer, R. A. (eds.), *Marion and Prince Edward Islands*. Cape Town: Balkema, 16–31.
- Scott, J. J., and Kirkpatrick, J. B., 1994: Effects of human trampling on the sub-Antarctic vegetation of Macquarie Island. *Polar Record*, 30 (174): 207–220.
- Smith, V. R., 1992: Terrestrial slug recorded from Marion Island. *Journal of Molluscan Studies*, 58: 50–51.
- Smith, V. R., 2002: Climate change in the sub-Antarctic: an illustration from Marion Island. *Climate Change*, 52: 345–357.
- Sokal R. R., and Rohlf, F. J., 1981: *Biometry*, 2nd ed. San Francisco: Freeman. 859 pp.
- Sun, D., and Liddle, M. J., 1993: A survey of trampling effects on vegetation and soil in eight tropical and subtropical sites. *Environmental Management*, 17: 497–510.

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