Spatiotemporal characteristics and causes of damage to *Azorella macquariensis* cushions

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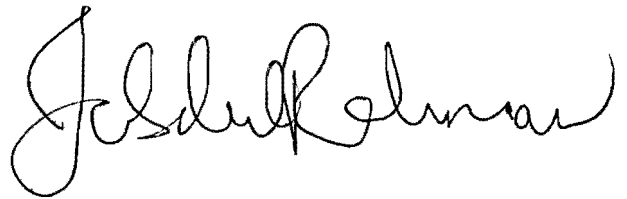
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Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution, and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis.

Signed

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Date

Annotation

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Abstract

Azorella macquariensis is a perennial cushion-forming herb that is endemic to Macquarie Island. During the 2008/09 austral summer, widespread dieback in *A. macquariensis* was observed, and is regarded by many to be a new phenomenon. The dieback is perceived to have spread across the entire island, affecting up to 90 % of cushions in some areas. As a result of this perception the species has been listed as critically endangered under the *Environment Protection and Biodiversity Conservation (EPBC) Act 1999.* Although there have been speculations about potential contributing factors, a definite cause has not been determined. The spatiotemporal characteristics of three dominant damage types affecting the cushion plant were investigated to help determine the cause/s of the putative increasing damage. In the austral summer of 2009/10, data were collected in the course of four studies: a cushion profile study; mapping of the spatial variation of cushion health; monitoring of temporal variation in cushion health; and a study relating soils to health. There was no significant relationship between overall cushion health and environmental variables apart from health decreasing with increasing exposure to strong winds. Type 1 damage was found to be more concentrated on the windward sectors of cushions, was significantly related to cushion exposure, substrate and vegetation community and did not display any major temporal variability. Type 2 damage was found to be more concentrated on the leeward sectors of cushions, was significantly related to cushion exposure, substrate and vegetation community and also did not display any major temporal variability. Type 3 damage was not significantly related to any particular sectors of cushions, nor to the environmental variables with the exception of cushion substrate, and expanded rapidly during the warm season. This suggested that the spatially restricted Type 3 damage might be responsible for the perception of increased dieback. Its cause is uncertain, although many of the symptoms are similar to those of a pathogen. Future monitoring should concentrate on this type of damage.

Acknowledgments

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Chapter 1   Introduction

1.1 Background

In a world of rapid environmental change, species can be imperilled. Although the extinction of species in itself is a natural phenomenon, human disturbance has increased extinction well beyond its natural rate. In the last 200 years alone, hundreds of species have become extinct, and many more are on similar paths (Turner *et al.* 2010). Whether it is change on a global scale or a local scale, species that are most susceptible to environmental change are those which have the lowest range of tolerance to variations in their growing conditions and/or those which are unable to escape from the new, undesirable conditions (Turner *et al.* 2010). The subantarctic islands have both limited ranges of environmental conditions and limited space.

1.1.1 The subantarctic islands

The subantarctic islands comprise several groupings of islands in the Southern Ocean. The exact definition of subantarctic remains contentious. It is commonly agreed that Macquarie Island, South Georgia, the Prince Edward Islands (including Marion and Prince Edward Island), Îles Crozet, Îles Kerguelen, and Heard and McDonald Islands are truly subantarctic (Selkirk *et al.* 1990). Campbell Island, Gough Island and Islas Diego Ramirez remain contentious as subantarctic islands (Shaw 2005). All candidates have latitudes greater than 40°S with Macquarie Island second only to South Georgia as the closest subantarctic island to the South Pole (Shaw 2005).

The climate of the subantarctic islands is heavily influenced by the atmospheric and oceanic circulation patterns. Sometimes referred to as the 'Furious Fifties', the subantarctic region receives constant high winds from a well-defined westerly wind circulation that results from the decay of cyclonic depressions toward the north and south (Selkirk *et al.* 1990). The ocean circulates toward the west at latitudes of less than 60° (Antarctic Circumpolar

Current) and toward the east closer to the Antarctic coast (Antarctic Coastal Current). These currents are primarily driven by gradients in temperature and salinity. The islands are located near the Antarctic Convergence, a dynamic boundary zone where colder oceanic currents from the south mix with warmer currents from the north (Selkirk *et al.* 1990). The convergence of atmospheric as well as oceanographic systems, coupled with the moderating capacity of the surrounding ocean (Selkirk *et al.* 1990), causes the islands to experience a relatively constant cool, wet and windy climate. The only marked seasonal variation is in daylight hours because of the high latitude (Selkirk *et al.* 1990).
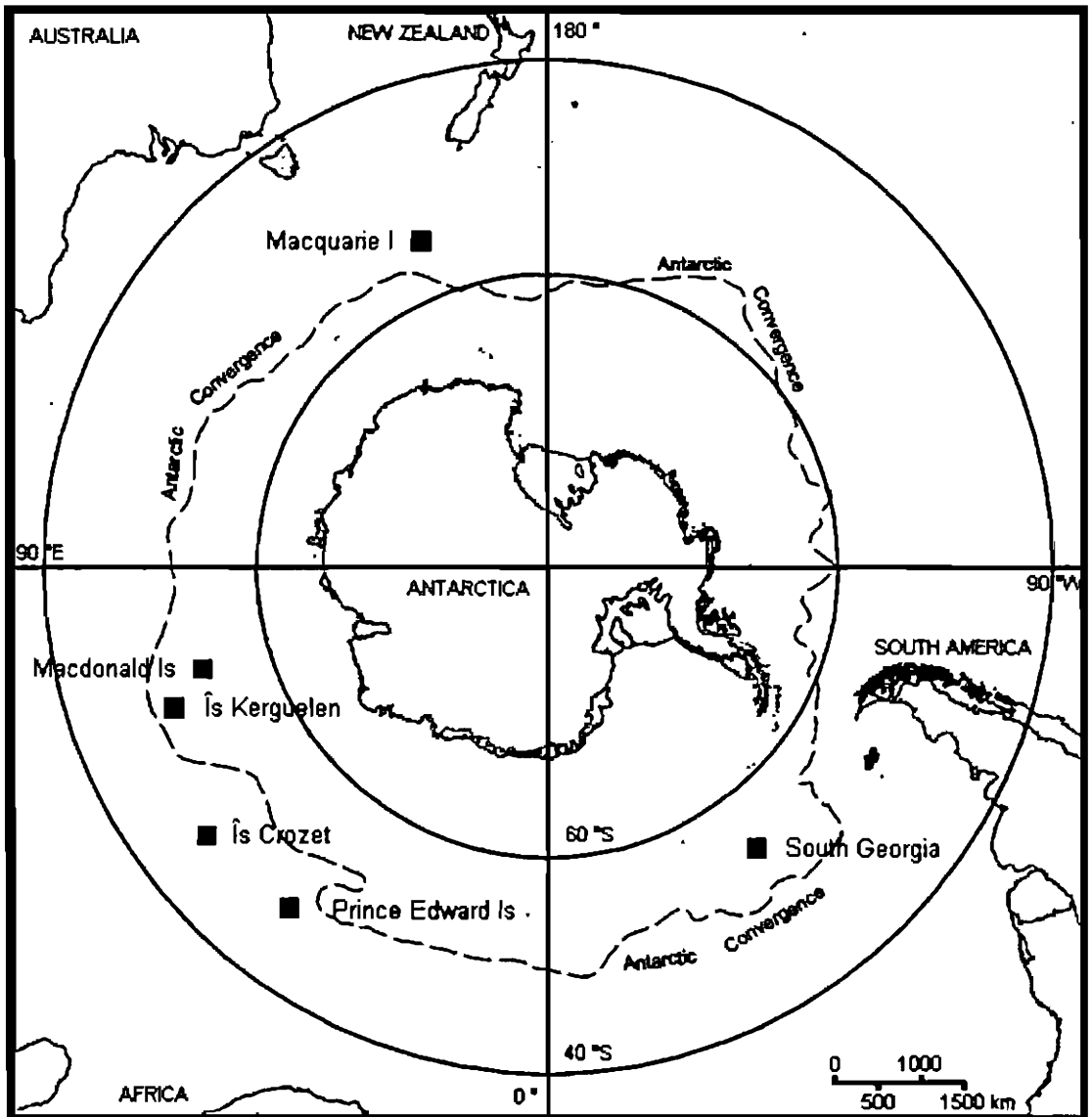
Figure 1.1: Locations of the subantarctic islands and the Antarctic Convergence in the Southern Ocean in relation to Antarctica and adjacent continents. Polar Stereographic Projection, WGS 84. Source: Subantarctic Islands [Black and white] Edition 1, Map no. 13137, Australian Antarctic Division, 2005.

As these subantarctic islands are highly isolated their ecosystems may be particularly susceptible to environmental change. Located between the milder temperate zone and the harsher Antarctic zone, the islands provide habitat for species that cannot tolerate the conditions of either zone (Chown *et al.* 1998).

1.1.2 Macquarie Island

Macquarie Island is situated at 54 ° 30 'S, 158 ° 57 'E, approximately 640 km south-west from the nearest landmass (the Auckland Islands), and 1500 km south-east from Tasmania (Parks and Wildlife Service 2006; Shaw 2005; Figure 1.2). Despite having been previously mapped to the south of the dynamic Antarctic Convergence (Selkirk *et al.* 1990), the island is generally regarded to lie in the warmer waters north of it (Selkirk *et al.* 1990).
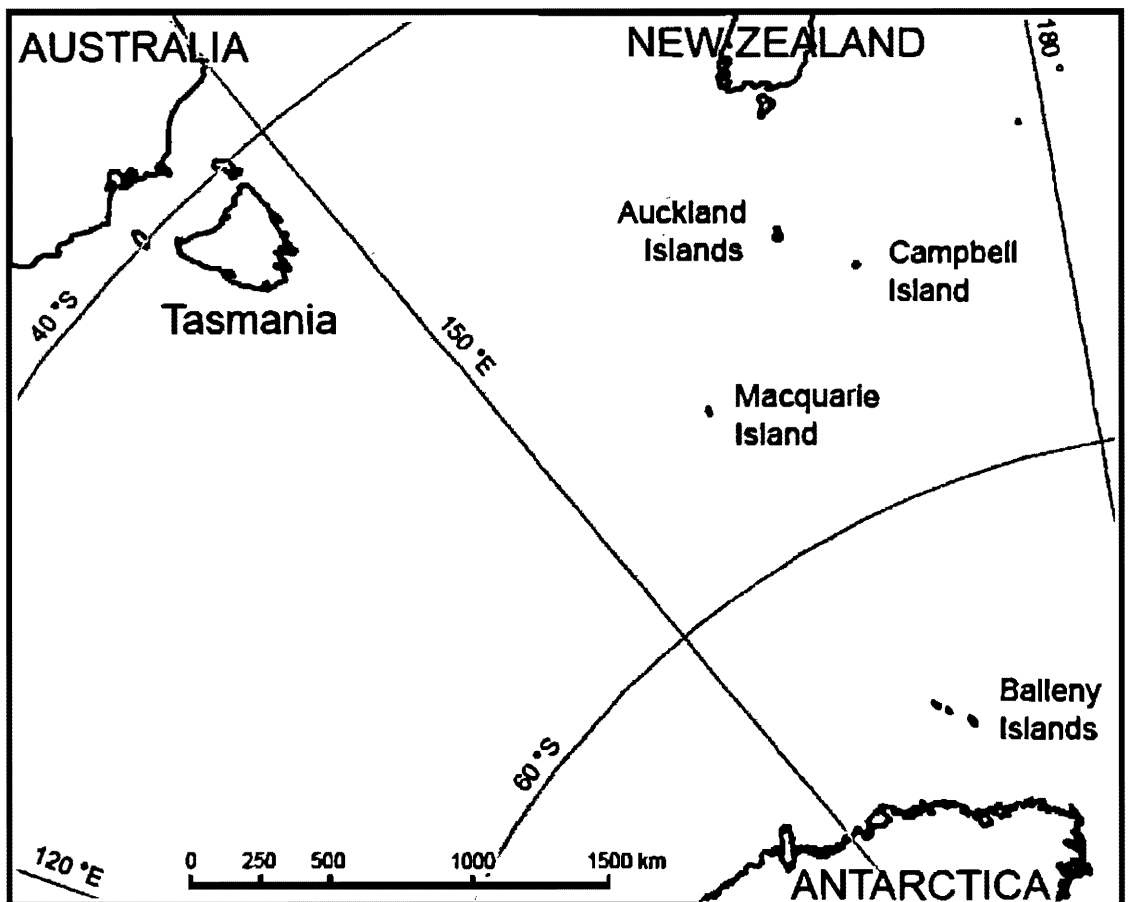
Figure 1.2: The location of Macquarie Island in relation to adjacent terrestrial bodies. Polar Stereographic Projection, WGS 84. Source: Location of Macquarie Island in relation to Australia and Antarctica [Black and white] Edition 1, Map no. 13143, Australian Antarctic Division, 2005.

The island is long and narrow. It is 34 km in length and 5.5 km at its greatest width and extends southwards in a north-north-east to south-south-west orientation (Figure 1.3). The west coast is more rugged than the east. Coastal flats are bounded inland by the steep slopes which, in turn, bound

an undulating plateau with an average altitude of approximately 200 m – 300 m above sea level (Selkirk *et al.* 1990). The southern part of the plateau is the highest region of the island, with an approximate altitude of 300 m and with the island's highest peak, Mt. Hamilton, reaching 433 m (Selkirk *et al.* 1990). The southernmost point of the island is Hurd Point and the northern most point is North Head which forms the tip of Wireless Hill, a flat-topped, elevated mass connected to the bulk of the island to the south by a low-lying isthmus. The Australian National Antarctic Research Expeditions (ANARE) station is located on the isthmus (Figure 1.3).
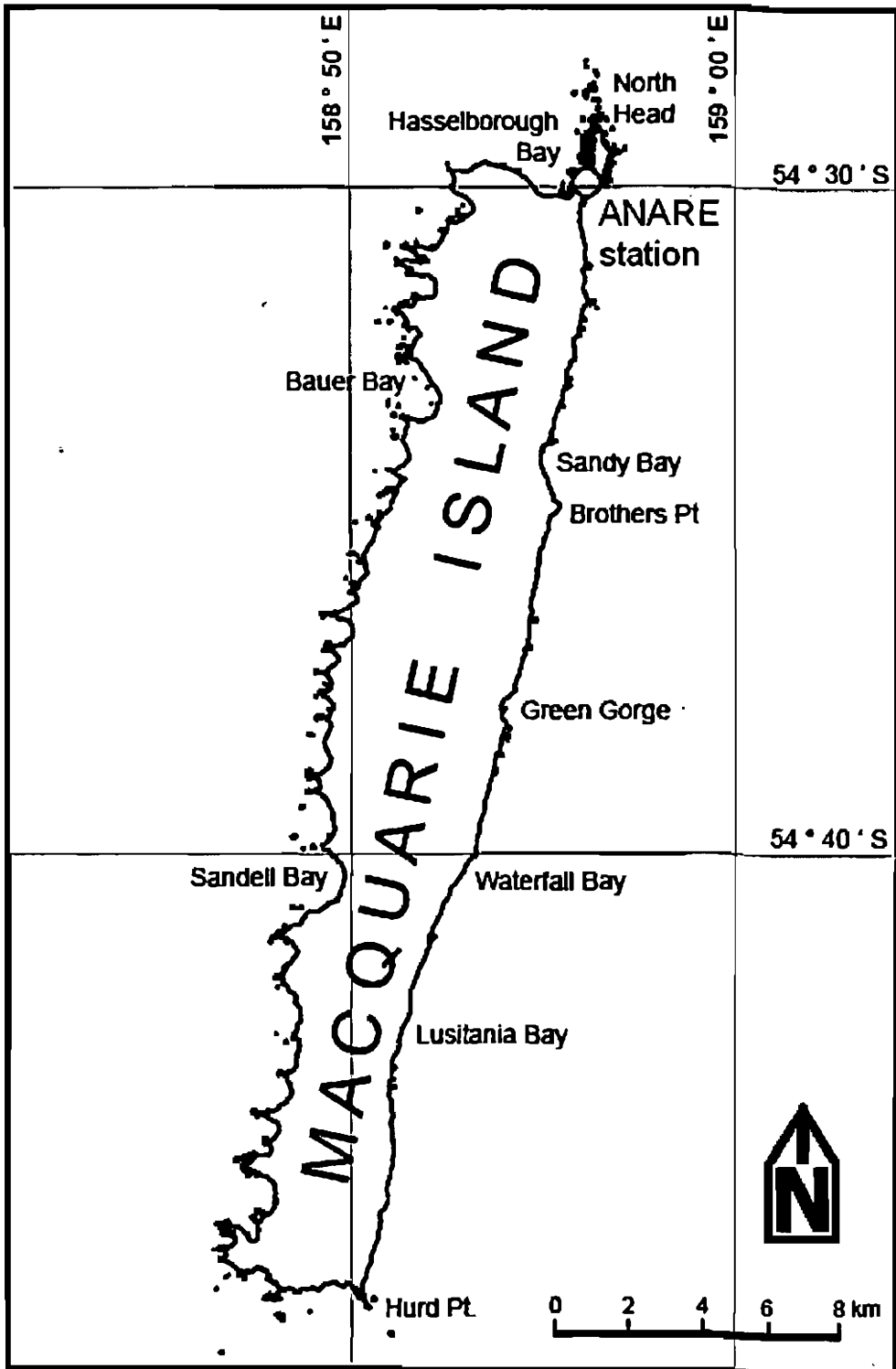
Figure 1.3: Map of Macquarie Island, showing the location of the ANARE station on the isthmus. UTM 57S, WGS 84. Source: Macquarie Island [Black and white] Edition 1, Map no. 13141, Australian Antarctic Division, 2005.

1.1.3 Cushion plants

Cushion plants are named thus because of the uniform growth of close-branching shoots and short internodes that results in the hard and compact hemispherical or subhemispherical shape of the individual plant (Went 1971; Parsons and Gibson 2009; Figure 1.4). However, when individuals combine they can form extensive mats up to more than 4 m in diameter (Taylor 1955b; Rundel and Palma 2000; Erskine 2004; Mortimer *et al.* 2008). There are approximately 338 species of cushion plants worldwide, which are from a wide range of genera, and distributed mainly in alpine, subantarctic and arctic tundra zones (Went 1971; Gibson and Kirkpatrick 1985).

Figure 1.4: A cushion plant (*A. macquariensis*) growing in fjaeldmark on Macquarie Island Photograph by Jared Abdul-Rahman.

The cushion form has been suggested to be a phenotypic response to the harsh environmental conditions in which the species occurs (Went 1971; Billings 1974; Mortimer *et al.* 2008) implying the loss of the cushion form when the stresses of its natural habitat are removed (Hauri and Schröter

1914; Whitehead 1954, 1959; le Roux *et al.* 2005). However, it has also been argued that the cushion formation is a genetic trait and will persist even when the environmental stresses are removed (Rauh 1940; Spomer 1964; Körner 1999).

Streamlined domes and low canopy roughness moderate temperatures and reduce the effects of wind, on evapotranspiration rates (Wilson *et al.* 1987; Smith *et al.* 1995; Körner 1999; Arroyo *et al.* 2003; Nyakatya and McGeoch 2008; Haussmann, Boelhouwers and McGeoch (2009). The accumulation of necromass below the canopy of the cushion plant (Goldstein and Meinzer 1983; Gibson and Kirkpatrick 1992) acts as insulation, further reducing heat and water loss (Ralph 1978; Hedberg and Hedberg 1979; Goldstein and Meinzer 1983).

Cushion plants are long-lived and slow-growing (Gibson 1990; Morris and Doak 1998; Körner 1999; le Roux and McGeoch 2004). This is largely related to nutrition availability and soil stability (Körner 1999). However, plant size is generally not an accurate indicator of plant age because of local environmental variability (le Roux and McGeoch 2004). In areas more exposed to strong winds cushion plants can experience skewed growth resulting in leeward plant migration (Lynch and Kirkpatrick 1995).

Cushion mortality can be caused by several factors. Wind has been highly associated with cushion mortality ranging from localised cushion necrosis on exposed windward sides to total cushion death (Taylor 1955a, 1955b; Lynch and Kirkpatrick 1995). However, although cushion plants benefit from shelter from strong winds, shading from other plant species has also been associated with cushion mortality (Hauri and Schröter 1914). In addition, cushion plants can be damaged and/or killed when used as habitat by burrowing animal species. Burrow-nesting birds and mice on subantarctic islands tend to nest inside and under cushions causing them to disintegrate (Selkirk *et al.* 1990; Phiri *et al.* 2009). Cushion plant mortality is also occasionally caused by herbivory. In the typically harsh environments occupied by cushion plants, the scarcity of vegetation causes the dominant

cushion plant species to become the main food source of herbivores, such as with native herbivore species in the Andes (Rundel and Palma 2000) and introduced herbivore species in the subantarctic (Chapuis et al. 1994, 2004). Human trampling can cause cushion plant mortality (Scott and Kirkpatrick 1994; Whinam and Chilcott 1999, 2003). Cushions have also been exploited for fuel (Rusby 1932; Hodge 1960; Núñez and Grosjean 2003; Kleier and Rundel 2004) and medicinal materials (Muñoz et al. 2004; Madaleno 2006). Little is known about diseases affecting cushion plants (Threatened Species Section 2009).

1.1.4 *Azorella macquariensis*

1.1.4.1 Taxonomy

Azorella macquariensis, in the Apiaceae family, is a perennial herb species which is part of a genus that is mainly concentrated in the Andes of South America (Orchard 1989). *A. macquariensis* was previously considered part of *A. selago*, which is widespread across the subantarctic region and has variable characteristics, but in 1989 it was described as a new species (Orchard 1989).

A. macquariensis was considered a separate species because of its leaves, inflorescence and fruit (Orchard 1989). In comparison to *A. selago*, the leaves of *A. macquariensis* are smaller and have lobes that are fewer and more divided, more acute and bristle-tipped. The wings of the petiole in *A. macquariensis* form a truncate ridge at the base of the lamina, whereas in *A. selago* they form auricles at the base of the lamina. The flowers of *A. macquariensis* are often solitary but are also produced in pairs, whereas in *A. selago* they are often produced in groups of three. *Azorella macquariensis* also differs from *A. selago* in that it has shorter, hidden fruits and deciduous sepals (Orchard 1989).

1.1.4.2   Distribution and habitat

Azorella macquariensis is endemic to Macquarie Island where it mainly dominates fjaeldmark and herbfield on the plateau, extending across more than half the island (Taylor 1955b; Orchard 1989; Selkirk *et al.* 1990). However, it occurs at all altitudes, with individuals recorded on rock stacks at sea level (Taylor 1955b; Shaw 2005; Threatened Species Section 2009; Threatened Species Scientific Committee 2010). Its total extent of occurrence is less than 90 km² (Threatened Species Section 2009).

1.1.4.3   Morphology

In its natural habitat, *A. macquariensis* forms cushions that, when combined with other cushions, can form extensive mats (Orchard 1989; Selkirk *et al.* 1990; Figure 1.5). Individual cushions can be as small as a few centimetres in diameter (Taylor 1955b; Threatened Species Section 2009), which have been referred to as buttons (Taylor 1955b). Mats can have a diameter as large as a few metres (Taylor 1955b; Threatened Species Section 2009).

Figure 1.5: *A. macquariensis* forming a large cushion in the plateau fjaeldmark on Macquarie Island. Scale is indicated by the compass, which is approximately 12.5 cm in length. Photograph by Jared Abdul-Rahman.

1.1.4.4 Life cycle

Flowering mainly occurs from December to February. Flowers are bisexual and have 5 deciduous sepals that are white and approximately 0.5 mm – 0.9 mm but unequal in length, and 5 pale reddish-brown petals that are acute and slightly hooded and 1.5 mm – 2 mm in length (Taylor 1955b; Orchard 1989; Hnatiuk 1993).

Fruiting mainly occurs from January to April. Fruits are yellow-brown and have a body that is 1.3 – 1.7 mm in length and 1 – 1.5 mm in width, hidden amongst the upper leaves (Taylor 1955b; Orchard 1989; Hnatiuk 1993).

In winter, the plant undergoes natural winter senescence/browning. This phenomenon has been described by Taylor (1955b) as leaves dying in the autumn followed by green leaves forming in the spring. Occurring in patches,

leaf death is preceded by a yellow discolouration. Leaf death occurs from March to April and by May there are no remaining green leaves. The forming of new, green leaves occurs from August to September, and by October the old brown leaves are no longer visible. The new leaves grow on the ends of the shoots, adding approximately 6.4 mm to the cushion height and the old brown leaves are hidden below the new dense canopy. The old brown leaves remain relatively undecomposed for several seasons (Taylor 1955b).

1.1.4.5 Ecological significance

A. macquariensis is the only vascular plant species that dominates fjaeldmark communities on Macquarie Island. It is considered to be a major structural component of the community (Shaw 2005; Threatened Species Section 2009). With numerous lateral roots and a tap root that extend several metres deep into the substrate (Taylor 1955a, 1955b), the cushion plant plays a key role in maintaining slope stability (Selkirk and Saffigna 1999). This is not only important for the island's geomorphology, but for its biodiversity as well because the slopes on which the cushion plant occurs provide habitat for burrow-nesting and surface-nesting bird species (Selkirk *et al.* 1990; Threatened Species Section 2009).

As the fjaeldmark community is a stressful environment, the cushion plant also provides shelter for other less tolerant plant species. Vascular and non-vascular plants alike are known to epiphytically colonise parts of cushions (Alliende and Hoffmann 1985; Arroyo *et al.* 2003; Cavieres *et al.* 2005; Shaw 2005; Fajardo *et al.* 2008; Arredondo-Nunez *et al.* 2009).

1.1.4.6 Mortality

Apart from the seasonal death involved in the process of winter browning (Section 1.1.4.4), *A. macquariensis* cushions have been observed to be damaged by wind, rabbits, mice, birds and fungi. Partial mortality of cushions has been observed to be a result of exposure to wind, with total death occurring when wind is extremely strong (Taylor 1955a, 1955b). Rabbits have also been associated with damage to cushions, having been observed

to scratch and dig into cushions (Taylor 1955b; Threatened Species Section 2009), possibly a form of their sexual and/or aggressive behaviours (Southern 1948). Giant petrels have also been associated with damage to *A. macquariensis*, with cushions within the nesting area observed to have been killed by the activities of the birds (Taylor 1955b; Selkirk *et al.* 1990).

During the austral summers of 1986/87 and 1989/90, several cushions were also observed to be affected by fungal rings where leaves in the affected areas were brown, surrounded by a ring of yellow leaves, which appeared to spread radially within and between individual cushions (P. Selkirk pers. comm.; Figure 1.6)

Figure 1.6: *A. macquariensis* cushions with fungal ring observed during the austral summer of 1989/90 on the plateau above Sandell Bay, north of Major Lake. Photograph by Patricia Selkirk.

1.1.5 The *Azorella macquariensis* dieback issue

During the 2008/09 austral summer, widespread dieback in *A. macquariensis*

was observed on Macquarie Island (D. Bergstrom and J. Whinam pers. comm. 2009; Threatened Species Section 2009; Threatened Species Scientific Committee 2010). Preliminary surveys of cushion health reported that dieback symptoms were evident across the entire range of the species distribution, severely affecting up to 90 % of cushions in some areas. By the winter of 2009 cushions on the northern plateau were noted to be worst affected and only patches of cushions on isolated rock stacks and in wet valley bottoms were found to be unaffected (Threatened Species Section 2009). Further monitoring of the dieback during the winter of 2009 was not conducted as it was deemed impossible to differentiate between symptoms of the dieback and winter browning (Threatened Species Section 2009; Threatened Species Scientific Committee 2010).

Typical symptoms of the dieback comprise a brown discolouration of leaves with a distinct boundary between healthy and unhealthy parts of the plant. Often this boundary is marked as an area of yellow leaves stretching across the cushion between brown and green leaves (Figures 1.7 – 1.8).
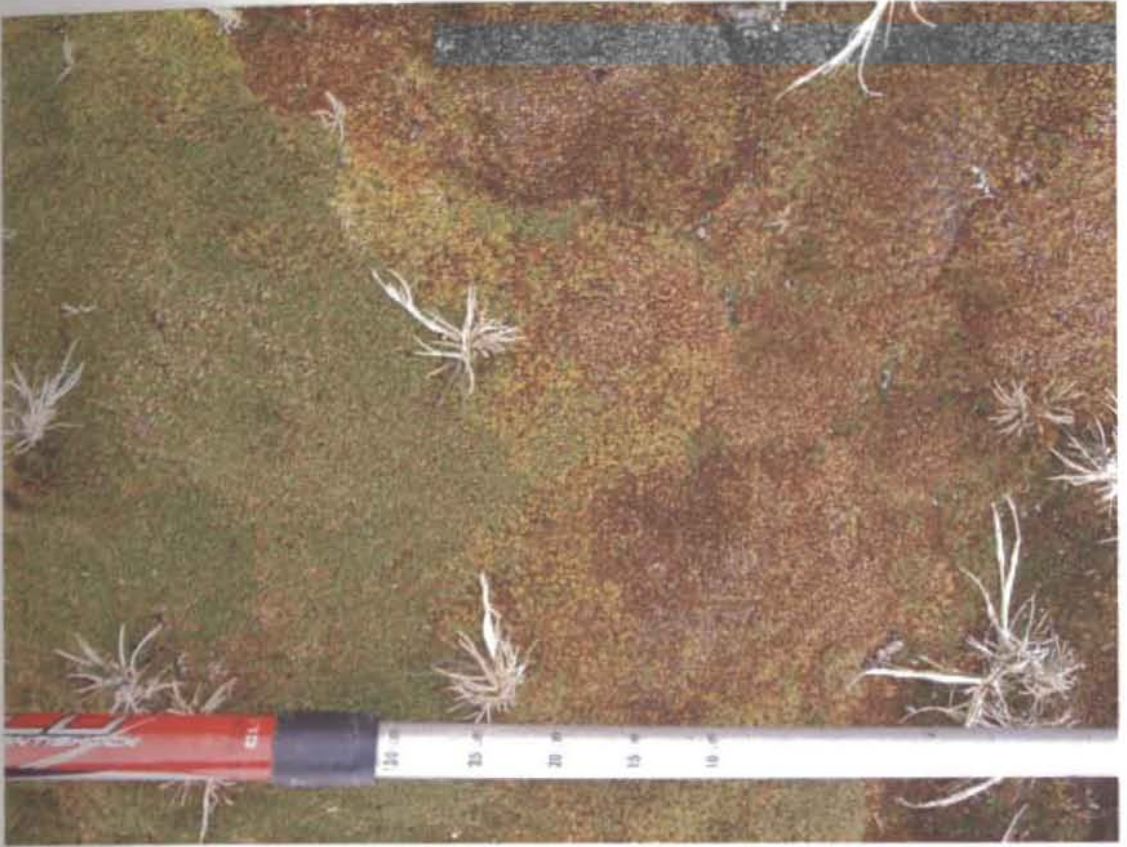
Figure 1.7: Typical symptom of the putative accelerated dieback consisting of an area of brown discoloured leaves outlined by a strip of yellow leaves, on an otherwise green-leaved cushion. Scale is indicated by measurements marked in 5 cm increments on the silver portion of the hiking pole. Photograph by Jared Abdul-Rahman.

The unusually rapid, widespread dieback is regarded by many to be a new phenomenon as it was not noticed in botanical surveys undertaken during the previous summer (Threatened Species Section 2009). Without any apparent barriers to the supposed decline in cushion populations, it has been estimated that the species could become extinct in the wild within a few years (Threatened Species Section 2009). As a result of this perception, the species was listed as endangered under Tasmania's *Threatened Species Protection Act 1995* in late 2009, and as critically endangered under the *Environment Protection and Biodiversity Conservation (EPBC) Act 1999* in August 2010 (Threatened Species Section 2009; Threatened Species Scientific Committee 2010).

Figure 1.8: The range of leaf discolouration from yellow through orange to brown in the symptom of the putative accelerated dieback. Scale is indicated by the hiking pole. Photograph by Jared Abdul-Rahman.

In late 2009, a steering committee was established by the Australian Antarctic Division and the Tasmanian Department of Primary Industries, Parks, Water and Environment to develop a strategy for the conservation of the species. One of the precautionary actions that was decided upon was the establishment of an *ex situ* conservation site on the island, with the assistance of horticultural expertise from the Royal Tasmanian Botanic Gardens, in early 2010 (M. Lang pers. comm. 2010; Figure 1.9). Seeds have also been collected for the Kew Royal Botanic Gardens Millennium Seed Bank and for storage in the Tasmanian Seed Conservation Centre, and plants regarded as healthy have been transported to Hobart and kept in quarantine isolation in order to establish an insurance population for the survival of the species (Threatened Species Section 2009; J. Whinam pers. comm. 2010).

Figure 1.9: *Ex situ* conservation of *A. macquariensis* individuals on Wireless Hill, Macquarie Island in August 2010. The cushions are showing natural winter browning. Photograph by Helen Achurch.

Although there has been speculation about possible contributing factors to the putative dieback, a definite cause has not been determined. The use of the words "infected," "epidemic" and "diseased" in official documentation (Threatened Species Section 2009; Threatened Species Scientific Committee 2010) indicates that the cause of the putative accelerated dieback is widely considered to be pathogen-related. However, testing for pathogens has been negative, showing specimens of fungi and bacterium in collected leaf material only to be saprophytic and showing no signs of other possible pathogens, including *Phytophthora* (Threatened Species Section 2009).

Other potential causes that have been mentioned include rabbits, introduced species in general, and climate change (Threatened Species Section 2009). However, these factors have been considered unlikely to be the direct cause and more likely to have indirectly contributed to the putative accelerated

dieback by enhancing the growth and spread of a pathogen.

As a definite cause has not been determined, a worst-case scenario approach has been taken, implementing biosecurity measures as though the cause of the dieback were a pathogen. Both intra- and inter-island biosecurity risks have been addressed to prevent any further spread of the postulated pathogenic dieback.

1.2 Aims and research questions

This thesis aims to assist current investigations into the putative accelerated dieback by filling gaps in ecological information concerning damage to the cushion plant species, and identifying the damage type/s of most concern. It also aims to provide information regarding dieback and cushion health in general that may assist in current and future management and rehabilitation efforts.

The research questions this thesis will address are:

1. What are the spatiotemporal characteristics of the different damage types on *A. macquariensis*?
2. How are these spatiotemporal characteristics related to cushion and/or environmental variables?
3. What are the causes of these different damage types?
4. Which damage type is likely to be most responsible for the putative accelerated dieback?

1.3 Thesis structure

Chapter 2 presents the methods used in the different investigations into the various aspects of the dieback characteristics. This chapter is divided into site selection, sampling strategies, field data collection, laboratory analyses

and statistical analyses.

Chapter 3 reports the results of investigations described in Chapter 2.

Chapter 4 discusses the implications of the results reported in Chapter 3. This chapter is divided into sections detailing the possible causes of each damage type, the damage type most responsible for the putative accelerated dieback, other possible explanations for the putative accelerated dieback, and recommendations for research, management, rehabilitation and monitoring.

Note: The word 'cushion' in this thesis refers hereafter to *A. macquariensis* unless otherwise specified.

Chapter 2 Methods

2.1 Study sites

2.1.1 Location

The study sites were located on the northern half of the plateau (the northern plateau and the northern half of the central plateau) of Macquarie Island, the altitude of which is generally 200 – 250 m above sea level with some peaks rising to more than 300 m (Selkirk *et al.* 1990). This region was selected because preliminary reports on the status of the putative accelerated dieback indicated that *A. macquariensis* cushions in this region were among the worst-affected on the island (Threatened Species Section 2009; Threatened Species Scientific Committee 2010).

2.1.2 Vegetation

The vegetation of the plateau consists of a wide range of communities, including tall tussock grassland, short grassland, mire, herbfield and fjaeldmark, the distributions of which are mainly related to wind exposure, drainage and soil depth (Selkirk *et al.* 1990). However, the vegetation of the study sites only consisted of two vegetation types, which were herbfield and fjaeldmark (Selkirk *et al.* 1990; Figure 2.1).
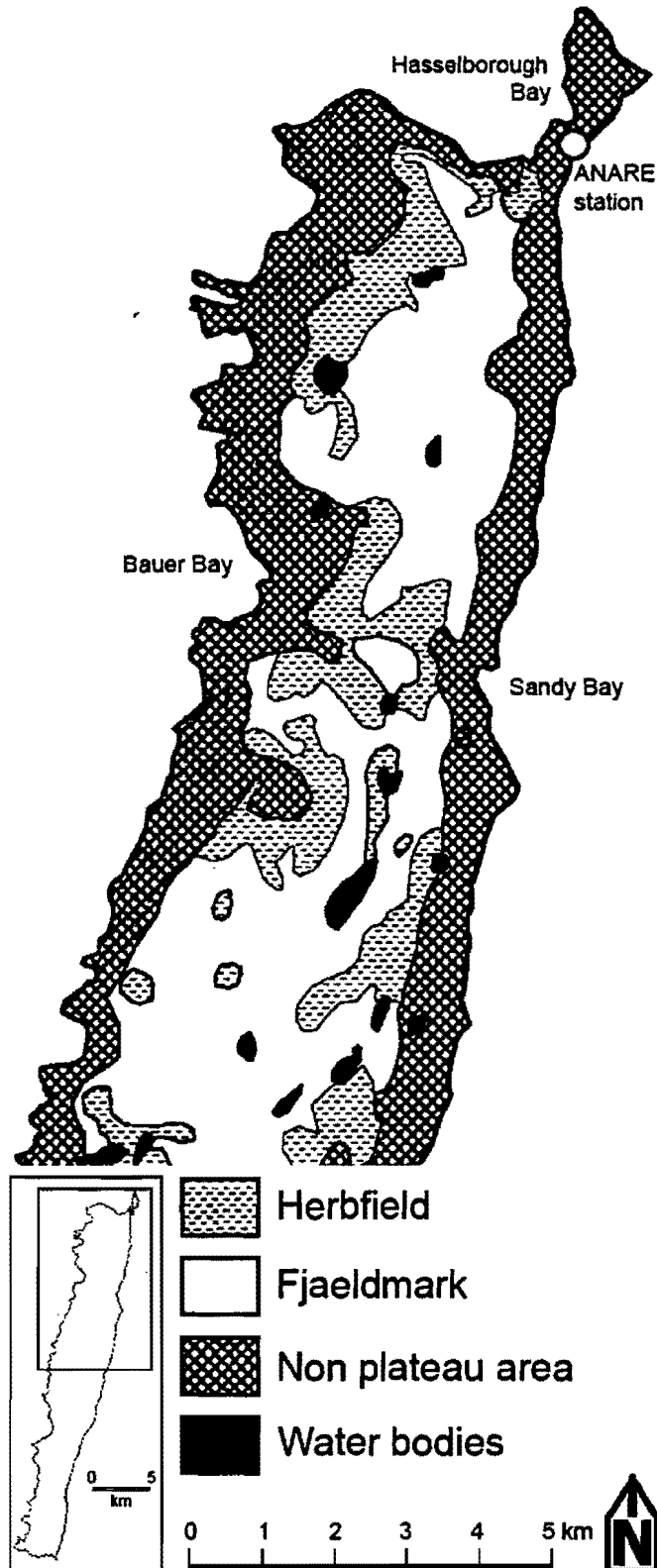
Figure 2.1: The general distribution of vegetation community types on the northern half of the plateau. Sources: Copson *et al.* 1981 and Pye *et al.* 1999.

The herbfield formation has been described as having three major communities, which are dominated by *Acaena* species, by *Pleurophyllum hookeri* and *Stilbocarpa polaris*, and by *A. macquariensis* and *P. hookeri* (Section 1.1.2.3). These herbfield communities are generally located in more sheltered areas of the plateau, with the *A. macquariensis – P. hookeri* community occurring at higher altitudes than the rest (Selkirk *et al.* 1990).

Occupying much of the windswept, higher region of the plateau, and mainly consisting of dwarfed vascular plant species, mosses, lichens and liverworts, the communities that comprise the fjaeldmark formation have been variously described. Taylor (1955b) described two communities, which were dominated by *A. macquariensis* and the bryophyte species *Ditrichum strictum* respectively. Ashton and Gill (1965) described the fjaeldmark as a single vegetation unit, consisting of a complex *A. macquariensis – D. strictum* community, and Selkirk *et al.* (1990) described the bryophyte species *Rhacomitrium crispulum* as more abundant than *D. strictum* and found that fjaeldmark communities occasionally contain minor components of short grassland and/or herbfield species.

As the present study focused only on *A. macquariensis*, the study areas comprised only herbfield and fjaeldmark communities which contained *A. macquariensis*.

2.1.3 Fauna

The animal species which inhabit the plateau are rabbits (*Oryctolagus cuniculus*), rats (*Rattus rattus*), mice (*Mus musculus*) and various bird species. Rabbits are mainly concentrated in herbfield communities, and least concentrated in fjaeldmark communities (Copson *et al.* 1981). Where rabbits are observed in fjaeldmark, it is in areas that are in close proximity to herbfield. However, with a dramatic increase in rabbit populations caused by the eradication of cats (*Felis catus*) on the island (Bergstrom *et al.* 2009) and/or the cessation of effectiveness of the *Myxoma* virus (Scott and

Kirkpatrick 2008), the presence of rabbits in fjaeldmark may have increased. Rats and mice inhabiting the plateau mainly occupy the more densely-vegetated fringes, with hardly any individuals found in the more exposed and scarcely-vegetated fjaeldmark areas (Pye *et al.* 1999).

Skuas (*Catharacta lonnbergi*) have been observed to nest widely over the plateau with a distribution strongly correlated to rabbit distributions. They are thus more concentrated in herbfield communities than fjaeldmark (Jones and Skira 1979; Skira 1984). Burrow-nesting petrels nest in isolated burrows in open patches of ground in both herbfield and fjaeldmark communities, especially in vegetated areas where soil was dry with a moderate to steep slope (Brothers 1984). Giant petrels (*Macronectes giganteus* and *M. halli*) have also been observed to inhabit marginal areas of the plateau adjacent to the upper regions of the steep coastal slopes on which they are most abundant (Taylor 1955b; Selkirk *et al.* 1990).

2.1.4 Climate

The climate of the plateau is more extreme than that at lower altitudes. Temperatures on the island have been observed to have a lapse rate of approximately 1 °C with an increase in altitude of 100 m. Therefore, the plateau is approximately 2 – 3 °C cooler than the meteorological station on the isthmus (Taylor 1955b; Jenkin 1975; Selkirk *et al.* 1990). Applying this lapse rate, in the period 1981 – 2010 the plateau had mean monthly maximum temperatures that varied from approximately 2.9 °C in the winter to 7 °C in the summer, and mean monthly minimum temperatures that varied from approximately -0.6 °C in the winter to 5.4 °C in the summer (Bureau of Meteorology 2010).

Precipitation is also higher on the plateau than at lower altitude. The northern plateau receives up to 42 % more precipitation than on the isthmus (Mallis 1988; Selkirk *et al.* 1990). Accepting this adjustment, the mean monthly rainfall for the driest month, November, is approximately 108 mm and for the

wettest month, March, is approximately 150 mm (1981-2010; Bureau of Meteorology 2010).

Wind speeds on the plateau have been estimated to be approximately 25 – 32 % greater than isthmus wind speeds (Taylor 1955a, 1955b; Jenkin 1975; Selkirk *et al.* 1990). Accepting this adjustment, mean monthly 3 pm wind speed on the plateau is at its lowest in January, at approximately 44 km/h and reaches a peak in May, at approximately 50 km/h (1981 – 2010; Bureau of Meteorology 2010). Similarly, maximum gusts measured for the entire period can be estimated to have reached speeds as high as 226 km/h (Bureau of Meteorology 2010). However, because of the undulating nature of the plateau, wind speeds on the plateau are highly locally variable (Peterson and Scott 1988).

2.1.5 Geology and soils

The geology of the northern plateau consists of five rock types classified as serpentenised peridotite, layered and unlayered gabbro, dolerite dyke swarms, and extrusive volcanics and associated sedimentary rocks consisting mainly of pillow basalts and basalt flows (Selkirk *et al.* 1990). All of the different rock types are included in at least one of the study areas.

The study area contains a range of soil types that have been described as organic loam and dry peat (Taylor 1955b). In the more exposed areas of the fjaeldmark, soils are typically well-drained and often have a surface layer of greyish, undecomposed basalt fragments varying from approximately 0.5 cm to 15 cm in depth. Often the underlying soil is moist, gravelly but highly organic and is of varying depth. However, in some areas where parent rock material has been exposed there is no soil (Taylor 1955b).

2.2 Site selection

2.2.1 Cushion profile study and spatial mapping of cushion health

Ten sites on the northern half of the island's plateau were preselected from existing ecological study sites with populations of A. *macquariensis*. In order to capture the differences between healthy and unhealthy cushions, boundary zones between the different health types were targeted (Figure 2.2).

Figure 2.2: Example of a cushion health boundary zone as seen in the field. Cushions decrease in health condition from the top left to the bottom right of the image. Scale is indicated by the compass in the centre of the image, which is approximately 12.5 cm in length.

Where sites did not include such boundary zones, the boundary zone nearest to the initial site point was selected (Figure 2.3).

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Figure 2.2: Example of a cushion health boundary zone as seen in the field. Cushions decrease in health condition from the top left to the bottom right of the image. Scale is indicated by the compass in the centre of the image, which is approximately 12.5 cm in length.

Where sites did not include such boundary zones, the boundary zone nearest to the initial site point was selected (Figure 2.3).

Figure 2.3: Site locations for the cushion profile study and spatial mapping of cushion health on the northern plateau of Macquarie Island. Topographic contours are shown at 25 m and 50 m intervals. Sources: Macquarie Island [Black and white] Edition 1, Map no. 13141, UTM 57S, WGS 84, (Australian Antarctic Division 2005); and Selkirk et al. 1999; Harris 2001a, 2001b; Brolsma and Harris 2002 (Australian Antarctic Data Centre 2006)

2.2.2 Temporal mapping of cushion health

Thirty-one sites on the northern half of the island's plateau, within 10 – 50 m of walking tracks, were randomly selected using ArcGIS™ ArcMap™ 9 (ESRI 2006). The sites were selected close to tracks to allow easy access for repeat visits, and far enough away from tracks to avoid disturbance by human traffic (Figure 2.4).

At each site, a 1 x 1 m quadrat was placed to the north-west of the site point. Where there were no cushions within the quadrat, the quadrat was relocated to the nearest cushion.
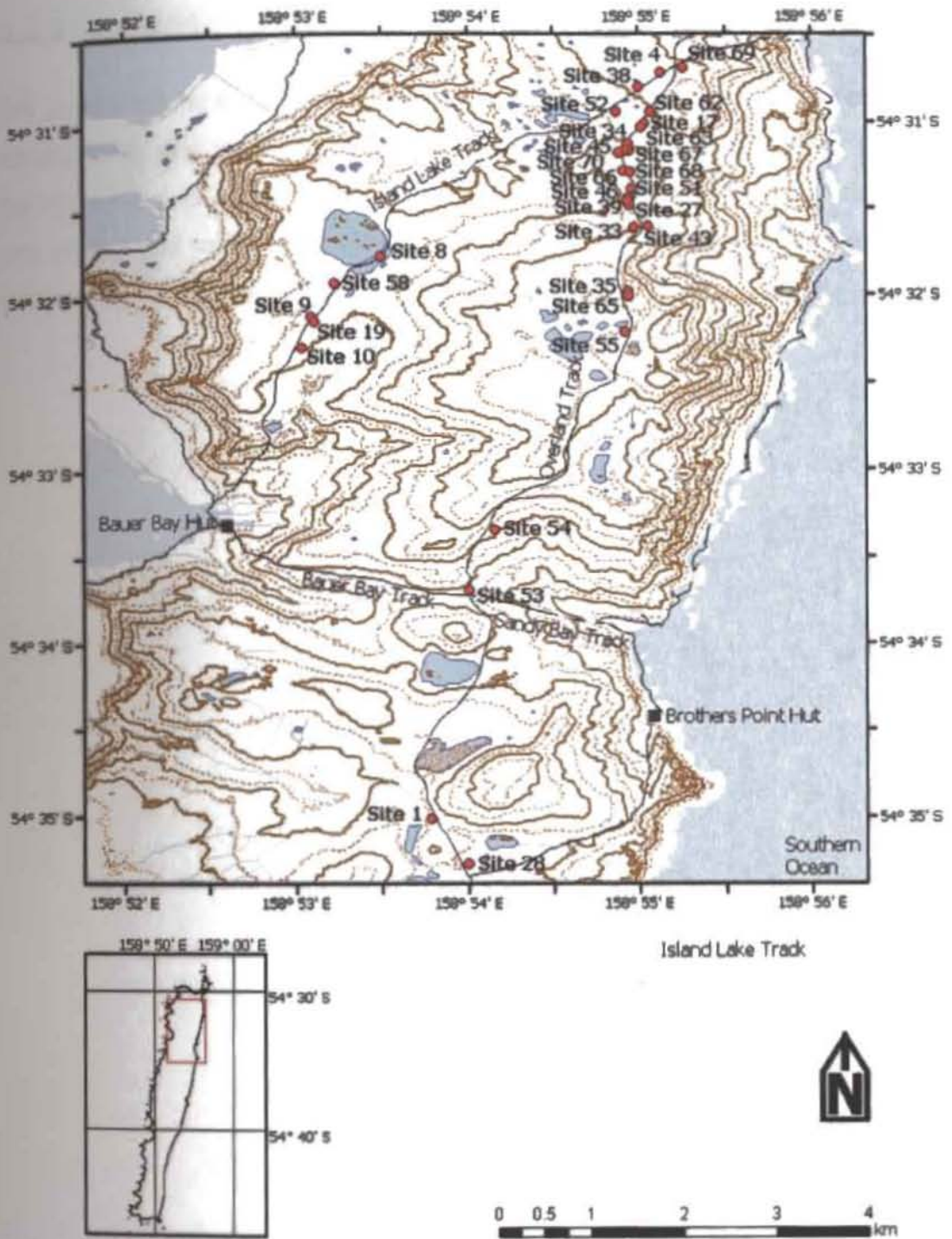
Figure 2.4: Site locations for temporal mapping of cushion health on the northern plateau of Macquarie Island. Topographic contours are shown in 25 m and 50 m intervals. Sources: Macquarie Island [Black and white] Edition 1, Map no. 13141, UTM 57S, WGS 84, (Australian Antarctic Division 2005); and Selkirk *et al.* 1999; Harris 2001a, 2001b; Brolsma and Harris 2002 (Australian Antarctic Data Centre 2006)

2.2.3 Cushion soils study

Six peak sites on the northern half of the island were selected based on peak accessibility and the presence of cushions. Eleven valley sites were chosen by following a randomly selected convex slope down from the peak sites until reaching a flat in the valley below. This was repeated for every peak site except site 13. There were 17 sites in total (Figure 2.5).
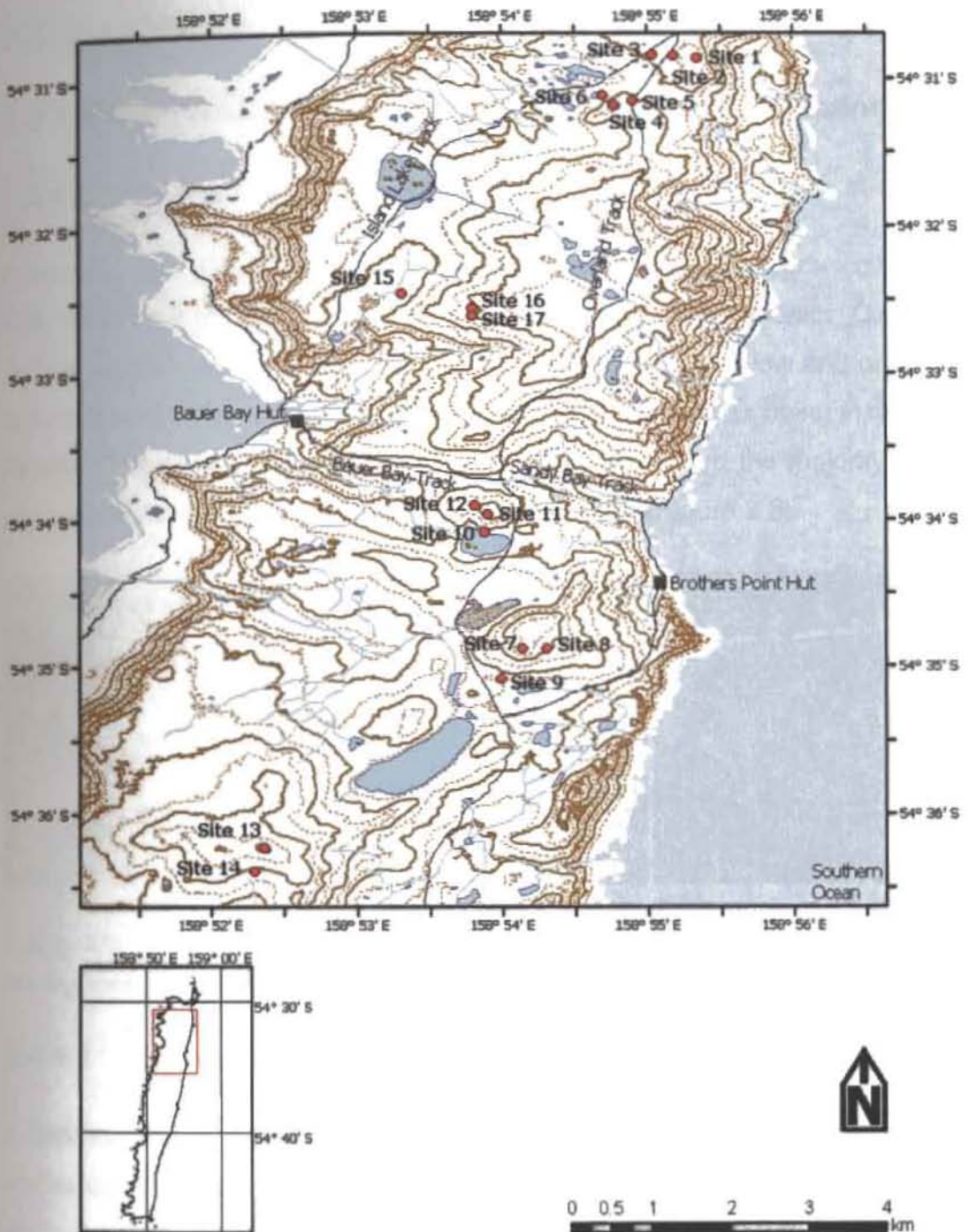
Figure 2.5: Site locations for the cushion soils study on the northern plateau of Macquarie Island. Topographic contours are shown at 25 m and 50 m intervals. Sources: Macquarie Island [Black and white] Edition 1, Map no. 13141, UTM 57S, WGS 84, (Australian Antarctic Division 2005); and Selkirk et al. 1999; Harris 2001a, 2001b; Brolsma and Harris 2002 (Australian Antarctic Data Centre 2006)

2.3 Sampling strategies

2.3.1 Definitions of environmental and damage classifications

2.3.1.1 Cushion health classes

Cushions with green leaves forming the majority of the surface cover and with nil to minor damage were classed as being in good health. Cushions with a surface cover comprising a mixture of green and yellow and/or brown leaves and with minor to moderate damage were classed as being in medium health. Cushions with brown and/or dead leaves forming the majority of the surface cover were classed as being in poor health (Figure 2.6).
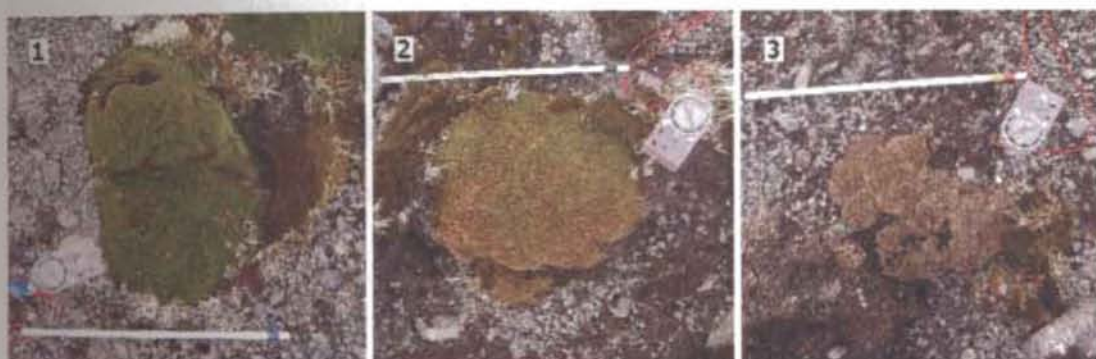
Figure 2.6: Classification of cushions by health (1 = good, 2 = medium, 3 = poor). Photographs by Jared Abdul-Rahman.

2.3.1.2 Cushion damage types

Classification of different damage types was based on cushion surface variables (Figure 2.7). Type 1 damage describes leaves on the cushion surface being absent and replaced by a smooth black or grey layer. Type 2 damage describes small patches or streaks of leaves with their tips removed and their shoots exposed. Type 3 damage describes intact leaves with yellow and/or brown discolouration.

A. Type 1 damage   B. Type 2 damage   C. Type 3 damage
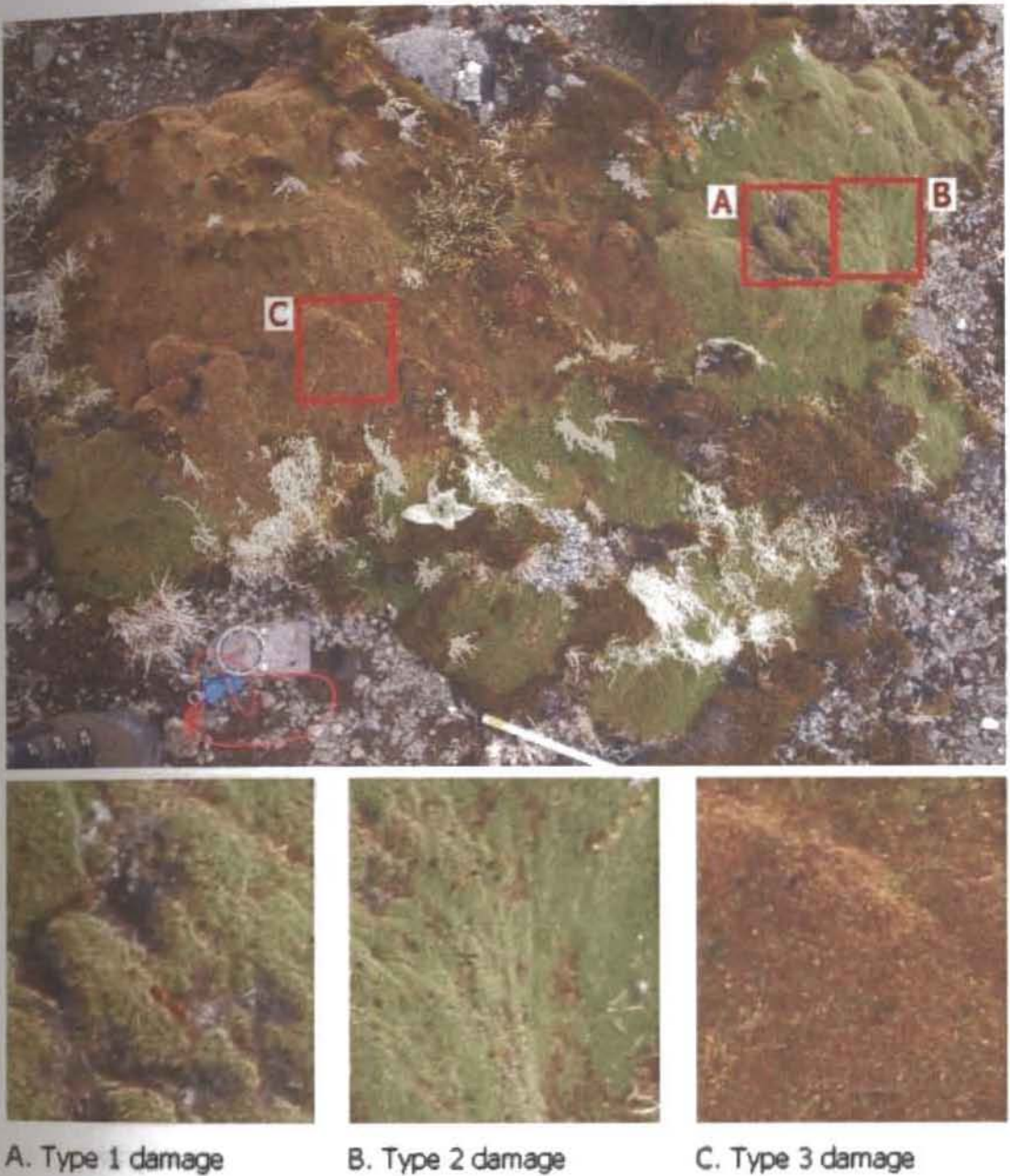
Figure 2.7: Examples of the identified cushion damage types 1, 2 and 3. Detailed examples of each damage type are shown in the three smaller images, each corresponding to a different area of the cushion in the large image as marked in red. Scale is indicated by the compass in the bottom left of the image, which is approximately 12.5 cm in length. Photograph by Jared Abdul-Rahman.

2.3.1.3   Cushion size

Cushions were classified by size to maintain consistency for comparison between cushions. Cushions with a diameter of less than 31 cm were classed as small. Cushions with a diameter of 31 – 70 cm were classed as

medium. Cushions with a diameter of greater than 70 cm were classed as large.

2.3.1.4   Cushion exposure

Cushion exposure was classified based on the prevailing wind patterns given by meteorological data (Bureau of Meteorology 2009), and the dominant wind directions identified according to methods discussed in Section 2.3.1.7. Cushions were classed as sheltered if more than 50 % of their windward side was completely protected from the direct force of the wind. Cushions were classed as intermediate if more than 50 % of their windward side was partially protected from the direct force of the wind. Cushions were classed as exposed if more than 50 % of their windward side was completely unprotected from the direct force of the wind. Protection from wind was determined by identifying obstacles that reduce the impact of the wind against the cushion surface such as rocks, surrounding or epiphytic vegetation, or geomorphological features.

2.3.1.5   Cushion substrate type

Cushion substrate types were classified based on the methods of McDonald *et al.* (1990). Cushions observed to be growing on an approximately equal combination of mossbed organic material and particles < 2 mm in diameter were classed as having a substrate of mossbed/soil. Cushions observed to be growing only on particles < 2 mm in diameter were classed as having a substrate of soil. Cushions observed to be growing on an approximately equal combination of particles < 2 mm and > 2 mm in diameter were classed as having a substrate of soil/gravel. Cushions observed to be growing only on particles > 2 mm were classed as having a substrate of gravel.

2.3.1.6   Vegetation community type

Vegetation community type was classified structurally based on Taylor (1955b), Smith (1984) and Selkirk *et al.* (1990), using methods from Beadle and Costin (1952), Specht (1970) and Kirkpatrick (1997). Areas with

vegetation mainly comprising bryophytes, cushions and lichens and with a ground cover consisting mainly of exposed gravel and aeolian sediments were classified as fjaeldmark. Areas with vegetation mainly comprising herbs, cushions and sedges and with a ground cover consisting mainly of vegetation were classified as herbfield.

2.3.1.7 Dominant wind direction

Dominant wind direction was identified based on the damage to, and orientations of, vegetation surrounding the target cushion, as in Noguchi (1979), Robertson (1987) and Wooldridge et al. (1996), who suggest that wind direction and speed can be determined by plant damage and deformation caused by prevailing winds, with reasonable agreement to instrumental observations. Where there was no clear visible evidence of one dominant wind direction, an average of the various possible orientations was recorded.

2.3.2 Cushion profile study

Within each of the 10 sites, 3 cushions were selected on the basis of health and size. Selected cushions were each of a different health class and each was between 30 cm and 80 cm in diameter. Size was used as selection criteria to ensure that cushion depth across the whole cushion could be measured once the profiling frame was assembled in position over the cushion. The profiling frame was 1 m in length, and had an adjustable height up to 50 cm. It also had an attached spirit level to ensure it was assembled horizontally.

Prior to assembling the profiling frame, the diameter of the cushion was measured on its longest diameter. The cushion's longest diameter, or primary axis, and the diameter perpendicular to this were used as axes for the profiling transects over the cushion. The longest diameter was used as

Transect 1 and perpendicular diameter was used as Transect 2 (Figure 2.8).
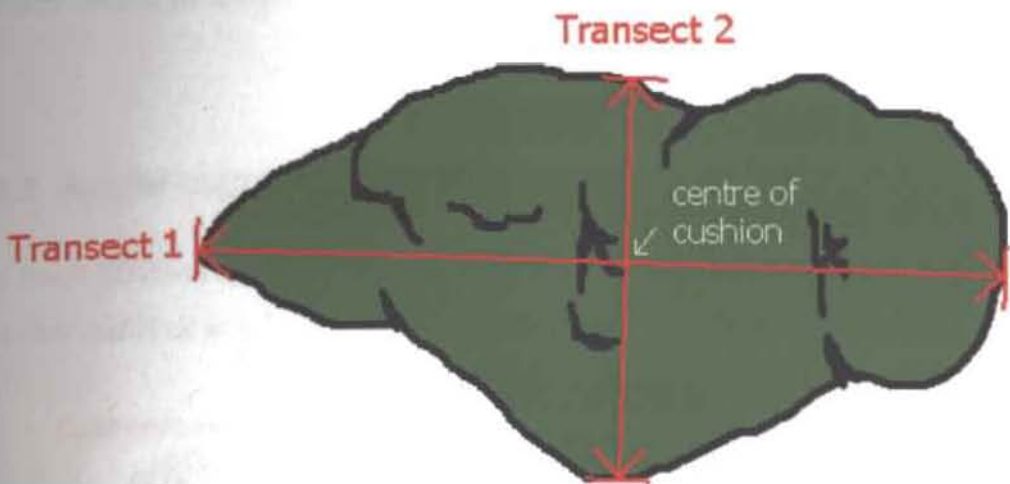
Figure 2.8: The two profiling transects along the surface of a cushion. Transect 1 followed the cushion's diameter at its longest. Transect 2 followed the cushion's diameter perpendicular to the longest diameter.

Transect direction was measured from the relatively windward end to the relatively leeward end, based on the dominant wind direction as determined at the cushion. This is based on the evidence that cushions grow and migrate downwind (Taylor 1955a, 1955b; Lynch and Kirkpatrick 1995; Haussmann, McGeoch and Boelhouwers 2009). Cushions with a Transect 1 direction ranging from 338° – 22° were classified as having a south – north orientation. Cushions with a Transect 1 direction ranging from 23° – 67° were classified as having a south-west – north-east orientation. Cushions with a Transect 1 direction ranging from 68° – 112° were classified as having a west – east orientation. Cushions with a Transect 1 direction ranging from 113° – 157° were classified as having a south-east – north-west orientation.

Cushion depth was measured by inserting a small probe until the change in consistency between cushion and soil material was detected. These distances were measured along both axes from the windward side to the leeward side of the cushion.

At individual point level, the presence of Type 1 and Type 2 damage was recorded as a yes/no response. Type 3 damage was recorded as cushion surface health as indicated by the colour of the leaves (yellow, brown).

2.3.3 Spatial mapping of cushion health

For each cushion selected for profiling, the nearest cushion in the direct line of every cardinal and intermediate direction was identified (Figure 2.9).
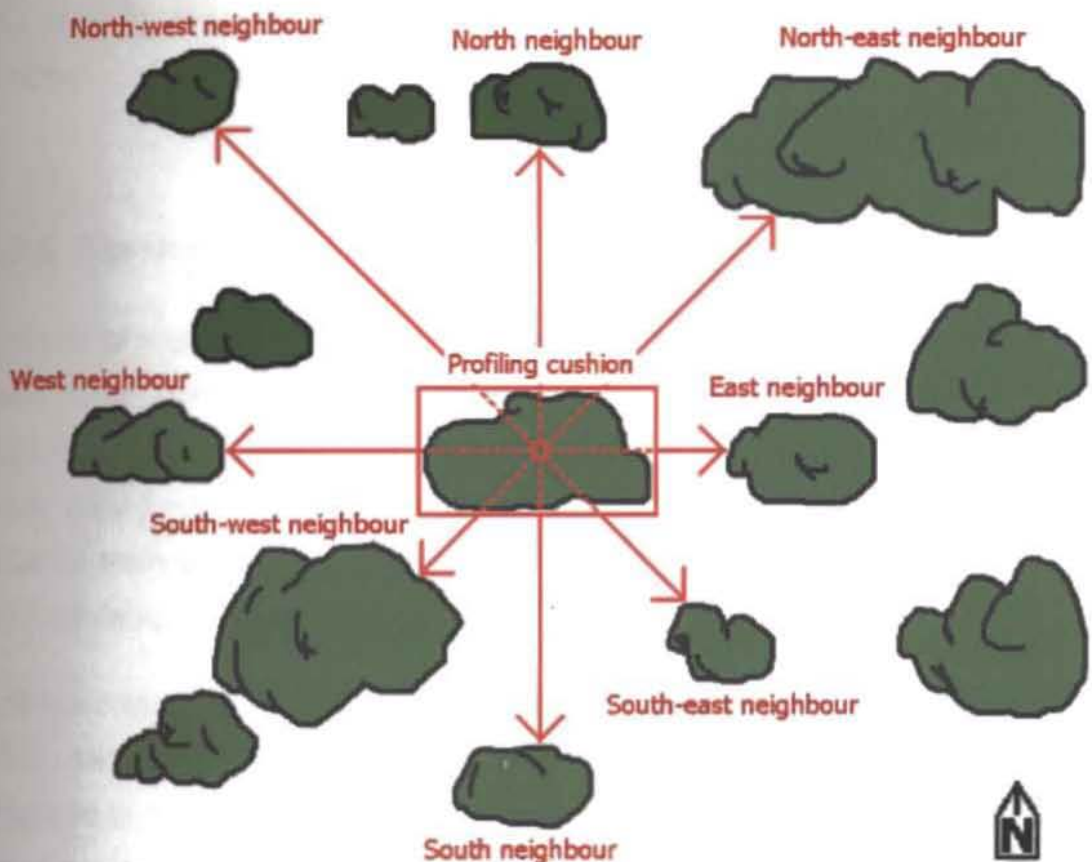
Figure 2.9: Selecting the nearest neighbouring cushion in each of the 8 directions from the profiling cushion.

Slope between the profiling cushion and each neighbour was measured using a handheld clinometer, and distance was measured using a measuring tape.

2.3.4 Temporal mapping of cushion health

Close-range vertical photography was conducted based on the methods described in Bennett *et al.* (2000). The camera was mounted onto a tripod, pointing downward. The tripod was used to position the camera approximately 2 m above the ground for sufficient distance to capture the entire quadrat within the frame. The tripod was positioned in such a manner that, when raised, its shadow would not be cast into the area of the quadrat, obscuring the features within it. The camera was always oriented with its top towards the most northerly side of the quadrat. Once the camera was raised into position using the tripod, photographs were captured using the self-timer function.

2.3.5 Cushion soils study

Soil pits of approximately 50 cm x 50 cm were excavated to the depth of the solid parent material beside cushions to avoid damage to the cushions and their root systems. Once data were recorded and samples collected, soil pits were refilled with their original material. Where possible, the layer of surface organic material was excavated and replaced as one piece, to reduce the environmental impact of the soil pit.

Soil horizons, as defined by the Australian soil classification (McDonald *et al.*, 1990; McKenzie *et al.*, 2002; Isbell 2002), were differentiated by perceptible changes in colour, texture, structure, and/or root depth. Organic-rich horizons were designated as O and P horizons and mineral horizons were classified according to the guidelines described by McDonald *et al.* (1990).

2.4 Field data collection

2.4.1 Cushion profile study

Health, size, exposure, substrate and vegetation community were recorded for each cushion. Presence and type of damage were also recorded. The presence of faunal activity as evidenced by scats, burrowing and/or grazing was recorded.

The directions of the two axes of the cushion to be used as the profiling transects were measured. Cushion surface and sub-surface soil topography along Transects 1 and 2 were measured using the cushion profiling frame. At intervals of 5 cm, vertical distance between the profiling frame (A) and the cushion surface (B), and between the cushion surface and the underlying soil surface (C) were measured (Figure 2.10).
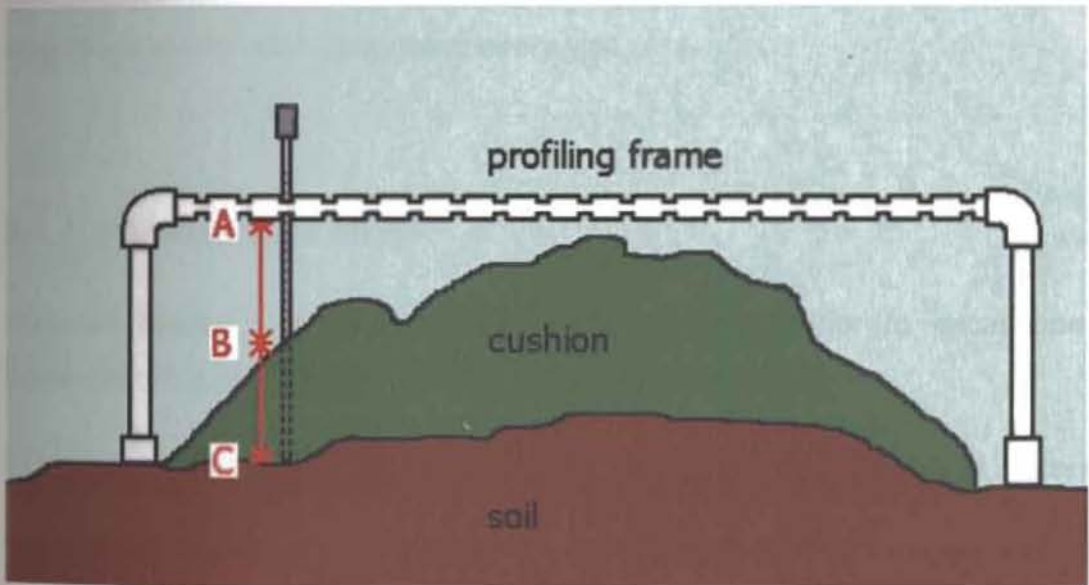
Figure 2.10: Measuring cushion surface and sub-surface topography using the profiling frame (A = profiling frame, B = cushion surface, C = underlying soil surface).

Health variables and damage variables were also recorded at each probe point on the cushion surface.

2.4.2 Cushion health spatial mapping

Distance was measured between the centre of the profiling cushion and the centres of its neighbour cushions. This was repeated for each of the 3 profiling cushions. The health of each cushion was recorded.

Slope, distance and direction were then measured between each of the profiling cushions. Every profiling cushion and neighbour cushion was photographed for laboratory analysis.

2.4.3 Cushion health temporal mapping

Repeat photographs were taken of the 1 m x 1 m quadrat at each site (Figure 3) at intervals of approximately 3 weeks between 30 October 2009 and 24 March 2010. Cushion health, damage occurrence and type of damage were also recorded for each quadrat at every visit.

2.4.4 Cushion soils study

Cushion health, size and exposure were recorded prior to excavation. Vegetation community type and substrate were also recorded.

After digging, total soil depth from soil surface to underlying solid parent material was recorded. The depth and thickness of each horizon was also recorded.

Soil samples were collected from each discernible horizon, double-bagged in zip-lock plastic bags. Samples were stored in a drum and refrigerated below 4 °C for transport to Hobart for laboratory analysis.

2.5 Laboratory analysis

2.5.1 Photograph interpretation

2.5.1.1   Spatial mapping of cushion health

The following data were extracted from the photographs of the 270 cushions from the spatial mapping sites: percentage cushion damage by type, estimated by eye with the use of an overlaid grid to the nearest percent; cushion size; cushion exposure; substrate; vegetation community type; and dominant wind direction.

2.5.1.2   Temporal mapping of cushion health

Photographs of the 31 cushions from the temporal mapping sites were used to identify temporal changes in cushion damage. Areas of cushion damage were marked in layers overlaid onto the images from each visit, identifying damage types 1, 2, and 3. Changes in cushion colour across the different stages of summer greening/winter browning were also identified and recorded.

2.5.2 Soils analyses

All samples were weighed and subsequently air dried as soon as possible after arrival in Hobart. Soils were air-dried in a laboratory fume cupboard with forced air of less than 20°C passing over the samples until constant weight was achieved. The samples were then passed through a 2 mm sieve prior to analysis for organic matter and pH. Large roots were withheld. Subsets of soil samples for analysis were divided using the soil homogenising technique described by Rayment and Higginson (1992).

2.5.2.1   Soil moisture

A subset of the air-dried soils was placed in an oven set at 105 °C for 24 hours. The percent gravimetric water content for each soil sample was

then calculated by dividing the mass of the water lost during oven drying by the dry mass of the soil after oven drying and multiplying by 100 (Rayment and Higginson 1992).

2.5.2.2 Gravel content

Gravel was considered as particles with a diameter greater than 2 mm (McDonald *et al.* 1990). Gravel content for each soil sample was determined on air-dried soil. The total soil sample was weighed and passed through a 2 mm sieve. The mass of the sample remaining in the sieve was obtained and expressed as a percent of the total air-dried soil mass.

2.5.2.3 Organic matter

Organic matter was measured as a percentage weight loss after fired oven-dried soil (loss on ignition). Moisture was removed from the samples by oven-drying at 105°C until the weight was constant (usually within 24 hours). The samples were then immediately processed and fired at 550°C for 6 hours. Previous research has found firing at 550°C for 6 hours to give the most easily replicated results (Ball 1964, Heiri *et al.* 2001, Isbell 2002, Boyle 2004).

2.5.2.4 pH

The pH of samples was determined following the directions and methods of Rayment and Higginson (1992). The soil pH procedure was performed on air-dried samples less than 2 mm in diameter. The sample was mixed in a ratio of 1 part soil to 5 parts distilled water and shaken before a pH reading was taken using a standard pH probe unit.

2.6 Statistical analysis

All analyses were conducted in Minitab® 15 (Minitab Inc. 2006), apart from the analysis of cushion health in relation to elevation and direction, which

was conducted in R 2.10.1 (R Development Core Team 2009). Relationships were considered to be statistically significant if $P \leq 0.05$. Tukey's Honestly Significant Difference (HSD) tests were conducted with all analyses of variance (ANOVA) involving more than two classes to identify where significant differences occurred.

2.6.1 Cushion profile study

At overall cushion level, analyses of variance (ANOVA) were performed on mean maximum cushion depth to determine if there was a significant relationship between cushion depth and site, vegetation community, cushion size, cushion exposure and cushion substrate. ANOVAs were also performed on mean maximum cushion depth between cushion health classes, and between sites by cushion health class.

At individual point level, ANOVAs were performed on cushion depth to determine if there was any significant difference between the presence and absence of each cushion surface variable, and between the different cushion surface variables.

Mean maximum cushion depth was also analysed using ANOVAs to test between the presence and absence of damage in general as well as more specifically for damage types 1 and 2. At individual point level, ANOVAs were performed to identify any variation in cushion depth between the presence and the absence of damage in general and of damage types 1 and 2.

2.6.2 Spatial mapping of cushion health

Kruskal's non-metric, multidimensional scaling (NMDS) was performed on the Euclidean distance matrix of the individual distances (m) between sample sites using the MASS package (Venables and Ripley 2005) in R 2.10.1. (R Development Core Team 2009). To ensure that the scaling did not

converge to a local minimum, the NMDS was performed from 100 random starts (10,000 iterations) before a stable solution was accepted.

Smooth surfaces for health, measured on an ordinal scale with 1 = poor health, 2 = medium health and 3 = good health, and elevation (m above sea level) were fitted using thinplate spline fitting. The fitted values were interpolated into a regular grid using the vegan package (Oksanen *et al.* 2010) in R 2.10.1. (R Development Core Team 2009). These were plotted as contours on the NMDS plot.

Chi-square analyses were conducted to determine consistency of any patterns relating to direction or elevation between sites and to determine any significant differences in cushion health between classes of each of vegetation community, cushion size, cushion exposure and cushion substrate.

The differences in percentage damage between damage types 1, 2 and 3 at the cushion level were analysed using ANOVA. ANOVAs were also conducted to determine any significant differences in total percentage cushion damage and in damage types 1, 2 and 3 between sites.

Pearson's product moment correlation coefficient was used to determine any relationships between the percentages of the damage types, including total damage.

ANOVAs were conducted relating each of the percentages for total damage and types 1, 2 and 3 to cushion health classes, vegetation community types, cushion size classes, cushion substrate classes, and cushion exposure classes. General linear models were performed to predict percentage total damage and each of the damage types using vegetation community, cushion size, cushion exposure, cushion substrate, and site. Site was incorporated into each of the models as a random variable.

Chi-square analyses were conducted to identify any significant differences between concentrated and unconcentrated damage, and between directional

and centre damage for concentrated damage recorded for each of the damage types.

2.6.3 Cushion soils study

The cushion health classes of poor and medium were combined in order to create a binary format (unhealthy or unhealthy) for cushion health data.

ANOVA was used to relate horizon thickness to the seven horizon classes. The hypothesis that horizon thickness would be significantly less where cushions were unhealthy was tested using the one-tailed t-test. Total depth, number of horizons and topographic position were also analysed for significant differences that occurred between cushion health classes (ANOVA).

Horizons were divided into three classes based on position within soil profile (top, middle, bottom). For each of these horizon classes, ANOVAs were used to determine if each of thickness, percentage organic matter and soil pH varied between each of the cushion health classes and the two vegetation types.

Chapter 3   Results

3.1 Cushion profile study

With a mean of 10.2 cm (SD = 4.5) and mode of 10 cm (n = 48), cushion depth ranged from 1 cm to 26.5 cm (Figure 3.1). Cushion depth varied between sites (F = 29.79, P < 0.001). The thickest cushions were measured at site 3 and the thinnest cushions at site 10. Most pairs of sites differed in cushion depth (Table 3.1).
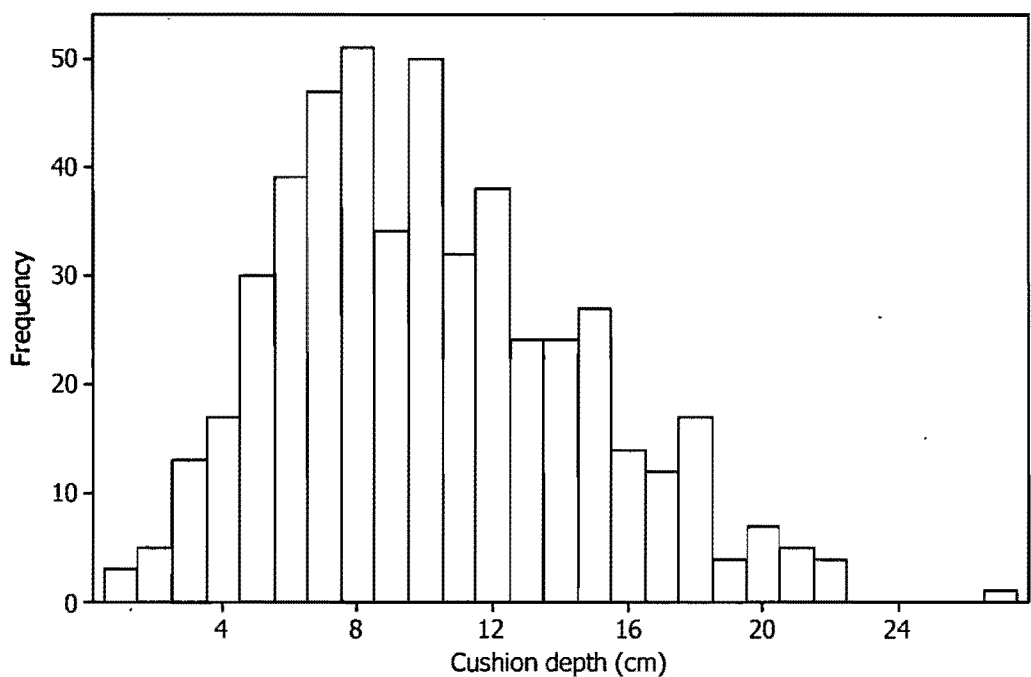
Figure 3.1: Pooled cushion depth frequencies from the 30 cushions.

Table 3.1: Means and standard deviations ( ) for cushion depths between sites (ANOVA). Sites with the same letter are statistically identical at P > 0.05 using Tukey's test

Site	Cushion depth (cm)	
1	12.93ab	(3.9)
2	11.71b	(3)
3	14.68a	(3.7)
4	9.06c	(3)
5	7.73cd	(2.7)
6	8.72cd	(4.4)
7	7.54cd	(5.6)
8	11.9b	(4.5)
9	7.93cd	(2.2)
10	6.43d	(2)

Cushion depths also varied significantly with vegetation community, cushion size, exposure and substrate (Table 3.2). Herbfield had deeper cushions than fjaeldmark. Large cushions were deeper than both small and medium cushions. Cushions of intermediate exposure were deeper than sheltered or exposed cushions. The cushions were deepest on soil.

Table 3.2: Cushion vegetation community type, size, exposure, and substrate variables related to cushion depth means and standard deviations ( ) (ANOVA). Means in rows with the same letter are statistically identical at P > 0.05 using Tukey's test

	Cushion depth (cm)				F	P
	Herbfield		Fjaeldmark			
Veg type	11.13a (4.2)		9.19b (4.6)		24.16	<0.001
	Small	Medium	Large			
Size	9.28b (4.7)	10.08b (4.5)	12.28a (3.9)		4.42	0.013
	Sheltered	Intermediate	Exposed			
Exposure	6.4b (5.6)	11.21a (4.2)	8.06b (4)		35.21	<0.001
	Mossbed/ soil	Soil	Soil/ gravel	Gravel		
Substrate	7.65d (2.4)	13.69a (3.8)	11.06b (3.9)	9.16c (4.7)	42.22	<0.001

Cushion depth did not vary between overall cushion health classes (ANOVA, F = 0.03, P = 0.97; Table 3.3). However, there was a significant difference in cushion depth means by site within the poor and good health classes (Table 3.4). For the poor health class, there were differences between sites 2 and 5, and 5 and 10. For the good health class, although the Tukey's test did not identify any differences between sites at 95% simultaneous confidence intervals, sites 7 and 10 were the extremes.

Table 3.3: Overall cushion health classes related to means and standard deviations ( ) of cushion depth (ANOVA)

Cushion health	Cushion depth (cm)	
Poor	10.08	(4.3)
Medium	10.18	(4)
Good	10.2	(5.2)

Table 3.4: Differences in cushion depth means (cm) and standard deviations ( ) between sites for each of the health classes (ANOVA). Means in columns with the same letter are statistically identical at P > 0.05 using Tukey's test

Cushion health class

Site	Poor		Medium		Good	
1	11.06ab	(3.2)	10.43a	(5.6)	11.7a	(5.1)
2	8.55b	(4.2)	11.03a	(4.1)	9.21a	(3.6)
3	9.32ab	(3.3)	9.22a	(5.3)	9.58a	(3.7)
4	10.11ab	(5)	10.16a	(4.7)	9.87a	(4.6)
5	14.6a	(4.2)	11.75a	(6.8)	12.46a	(4.3)
6	10ab	(4.5)	12.31a	(4.4)	11.78a	(3.4)
7	11.13ab	(3.8)	11.77a	(3.7)	12.08a	(5)
8	11.14ab	(4.4)	8.94a	(3.4)	8.39a	(4)
9	9.61ab	(4.2)	8.41a	(4)	9.25a	(3.3)
10	7.47b	(2.9)	8.98a	(3.8)	7.83a	(5.2)
F	2.65		1.42		2.25	
P	0.007		0.184		0.022	

There was also variation in cushion depth with cushion surface health variables at the individual point level. The only cushion surface health type that had a significant relationship with cushion depth in the pooled data was brown (Table 3.5). Where the cushion surface was brown, cushion depth was less than where the cushion surface was not brown.

Table 3.5: Occurrence of cushion surface health variables at individual point level related to means and standard deviations ( ) of cushion depth (ANOVA)

Cushion surface type	Cushion depth (cm)					F	P
	Yes		No				
Dead	10.4	(4.6)	10.05	(4.5)		0.45	0.502
Brown	9.04	(3.7)	10.57	(4.8)		11.67	0.001
Yellow	9.67	(4.2)	10.18	(4.6)		0.59	0.442
Green	10.21	(4.6)	9.9	(4.3)		0.47	0.493

There was a significant difference in cushion depth means between cushion surface health variables (ANOVA, F = 2.82, P = 0.038). These differences occurred between brown and dead, and between brown and green (Table 6). Where cushion surface was brown, cushion depth was significantly less in comparison to dead and to green.

Table 3.6: Cushion surface health variables at individual point level related to means and standard deviations ( ) of cushion depth (ANOVA). Means with the same letter are statistically identical at P > 0.05 using Tukey's test

Cushion surface type	Cushion depth (cm)	
Dead	10.4a	(4.6)
Brown	9.04b	(3.7)
Yellow	9.67ab	(4.2)
Green	10.21a	(4.6)

Cushion damage at the overall cushion level was also found to be significantly related to cushion depth (ANOVA, F = 6.44, P = 0.011; Table 3.7). Cushions with damage had more overall cushion depth than cushions without damage.

Table 3.7: Overall occurrence of cushion damage related to means and standard deviations ( ) of cushion depth (ANOVA)

Damage	Cushion depth (cm)	
No	8.88	(3.9)
Yes	10.36	(4.6)

Type 1 and Type 2 damage at the overall cushion level were significantly related to cushion depth (Table 3.8). Cushions with Type 1 damage had less overall cushion depth than cushions without Type 1 damage. For cushions with Type 2 damage it was the opposite, with cushions displaying Type 2 damage having more overall cushion depth than cushions without Type 2 damage.

Table 3.8: Occurrence of cushion damage types at overall cushion level related to means and standard deviations ( ) of cushion depth (ANOVA)

	Cushion depth (cm)					
Damage type	No		Yes		F	P
Type 1	11.31	(4.6)	9.16	(4.2)	30.19	<0.001
Type 2	8.82	(4.2)	11.73	(4.4)	57.33	<0.001

Damage was also significantly related to cushion depth at individual point level (ANOVA, F = 19, P < 0.001; Table 3.9). Where there was cushion damage, cushion depth was more than where there was no cushion damage.

Table 3.9: Occurrence of cushion damage related to means and standard deviations ( ) of cushion depth (ANOVA)

Damage	Cushion depth (cm)	
No	9.8	(4.4)
Yes	12.26	(4.7)

In analysing the different types of damage at individual point level, Type 1 damage appeared to have mainly occurred where cushion depth ranged from 5 – 13.5 cm. This was also where cushion depth in general was most frequent (Figure 3.2). This combination of cushion depths corresponded to two distinct areas on the cushion surface, where the distance from the profiling frame to the cushion surface was 0 – 4 cm and 16 cm (Figure 3.3).

Type 2 damage appeared to have occurred where cushion depth ranged from 6 – 22 cm (Figure 3.4). This combination of cushion depths corresponded to two distinct areas on the cushion surface where the distance from the profiling frame to the cushion surface was 0 – 10 cm (Figure 3.5).
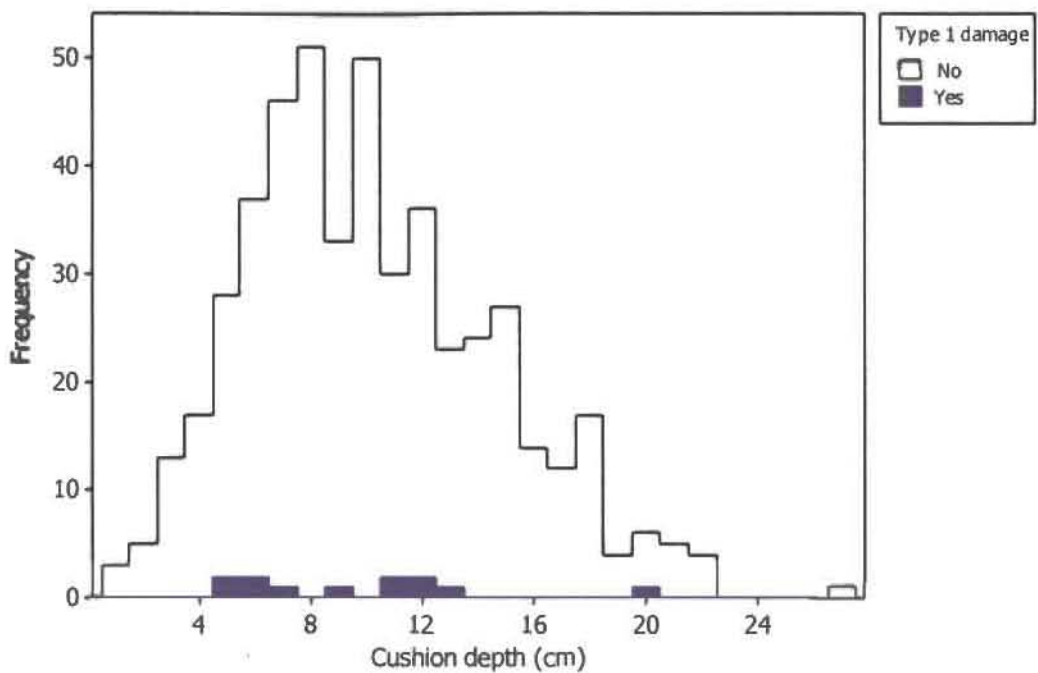
Figure 3.2: Frequencies of cushion depths where Type 1 damage did and did not occur.
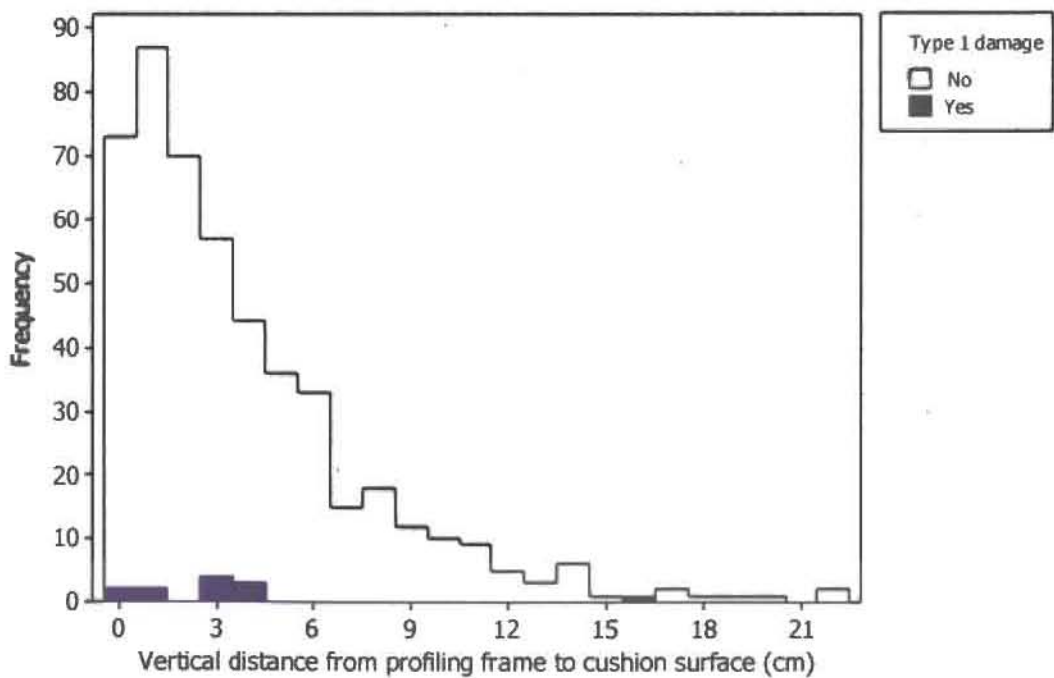
Figure 3.3: Frequencies of distances between profiling frame and cushion surface where Type 1 damage did and did not occur.
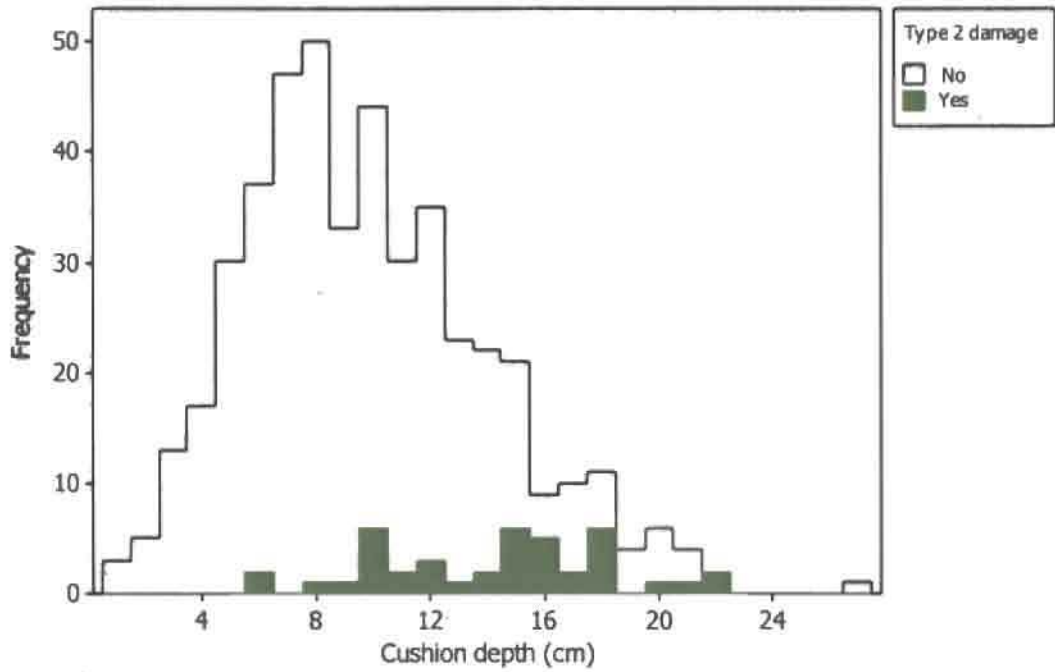
Figure 3.4: Frequencies of cushion depths where Type 2 damage did and did not occur.
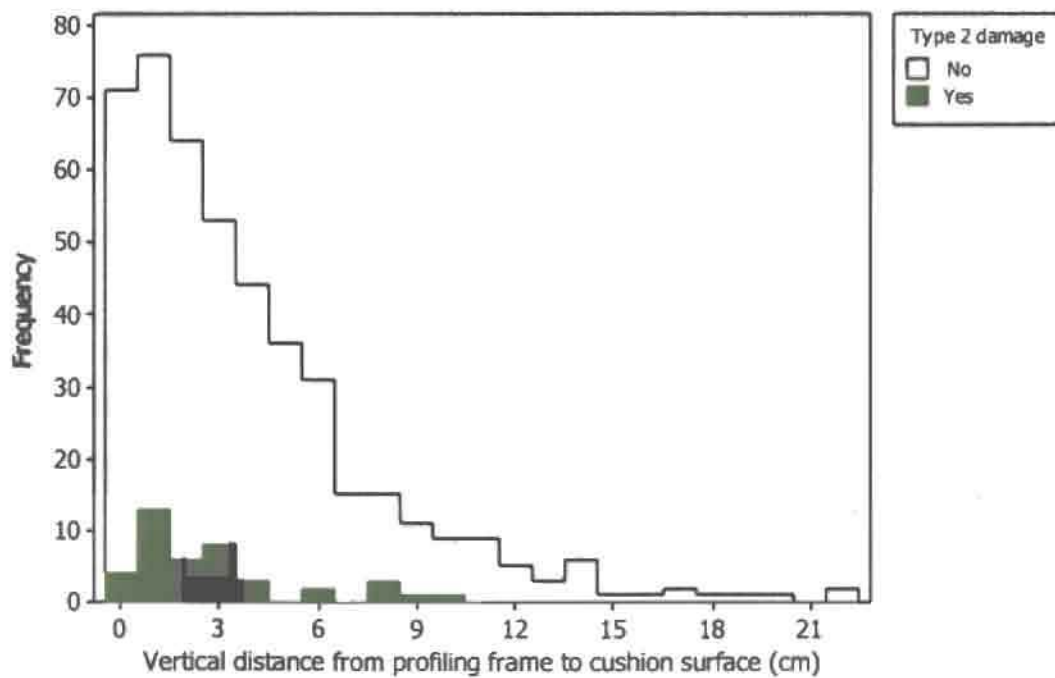
Figure 3.5: Frequencies of distances between profiling frame and cushion surface where Type 2 damage did and did not occur.

However, only Type 2 damage showed any relationship with cushion depth at individual point level (Table 3.10). Where Type 2 damage occurred, cushion depth was significantly more than where Type 2 damage did not occur.

Table 3.10: Occurrence of cushion damage types related to means and standard deviations ( ) of cushion depth at individual point level (ANOVA)

	Cushion depth (cm)				
Damage type	No		Yes		F	P
Type 1	10.17	(4.5)	9.75	(4.4)	0.1	0.752
Type 2	9.79	(4.4)	14.27	(4)	40.21	<0.001
Other	10.18	(4.5)	9.5	(4.2)	0.42	0.518

3.2 Spatial mapping of cushion health

3.2.1 Variation in cushion health within and between sites

At all sites except 1 and 8 there was strong directional variation in cushion health (Table 3.11). All sites showed one area of poor health concentration, except for sites 4 and 6 where there were two areas.

However, there was no consistency between sites in the compass directions of health classes (Chi², P > 0.05). Cushions in good health were located towards the west in sites 2, 3, 4 5 and 7 (NW = 3, SW = 2), and towards the east in sites 6 and 10 (NE = 1, SE = 1). Sites 1, 8 and 9 did not show any unidirectional pattern in cushion health.

Table 3.11: The R^2, F and P values for cushion health fitted as a linear vector to cushion geocoordinates within sites

	Vector	
Site	R^2	P
1	0.02	0.774
2	0.65	< 0.001
3	0.33	0.006
4	0.21	0.042
5	0.81	< 0.001
6	0.24	0.036
7	0.58	< 0.001
8	0.05	0.535
9	0.7	< 0.001
10	0.47	0.003

The health classes of cushions were strongly related to elevation within all sites. However, there was no consistency in the topographic location of cushions in good health (Chi^2, P > 0.05), which were clearly located upslope in sites 3, 5, 9 and 10 (Figure 3.5), and downslope in sites 4, 6, 7 and 8 (Figure 3.6). Sites 1 and 2 had significant, but less clear, elevation patterns in cushion health (Figure 3.7).
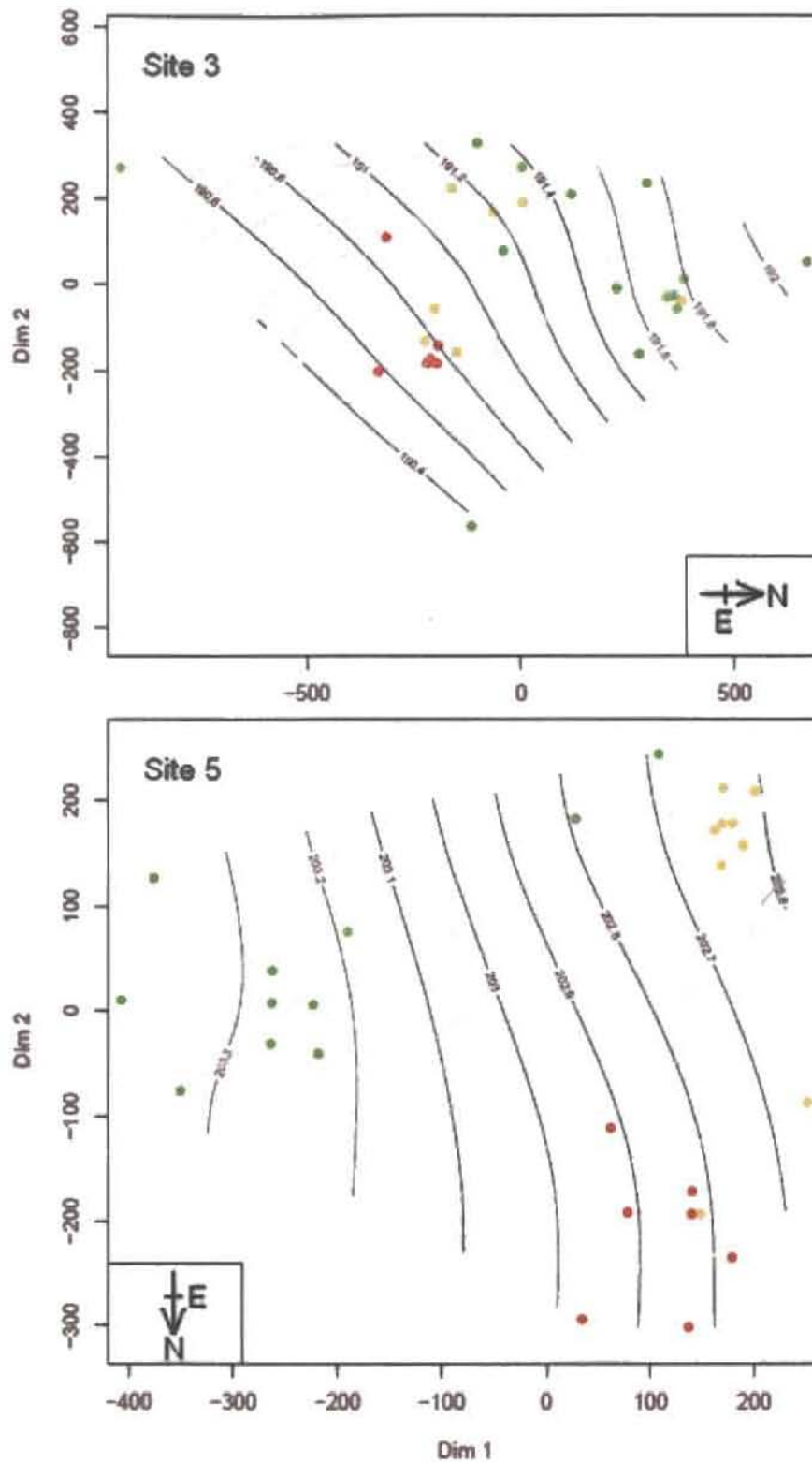
Figure 3.5a: Trend surface for cushion health (blue) and elevation contours (black) for sites 3 and 5, where cushions in good health were located upslope from cushions in poor health (•
= good (3); • = medium (2); • = poor (1)). Elevation is shown in metres.
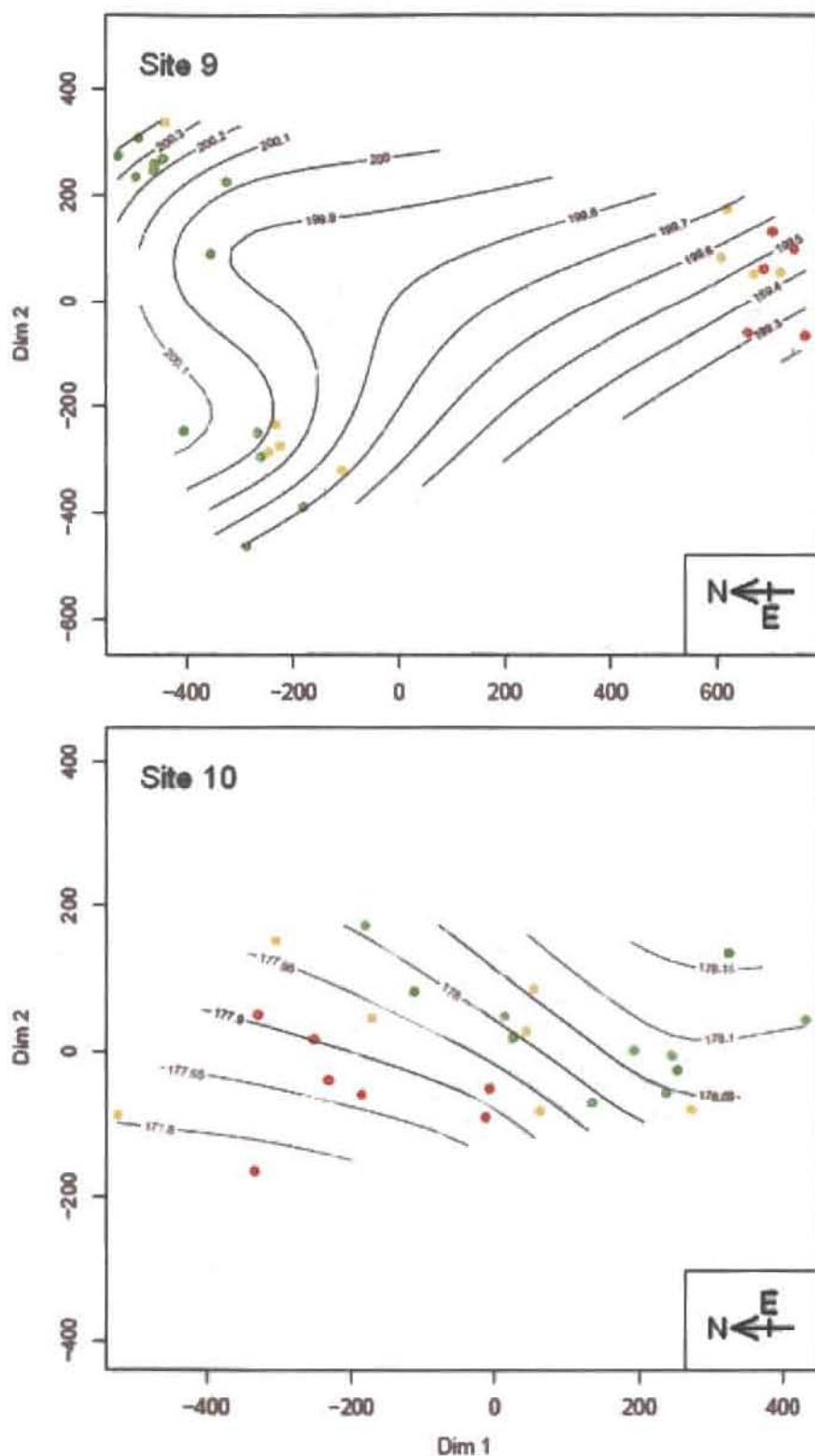
Figure 3.5b: Trend surface for cushion health (blue) and elevation contours (black) for sites 9 and 10, where cushions in good health were located upslope from cushions in poor health (● = good (3); ● = medium (2); ● = poor (1)). Elevation is shown in metres.
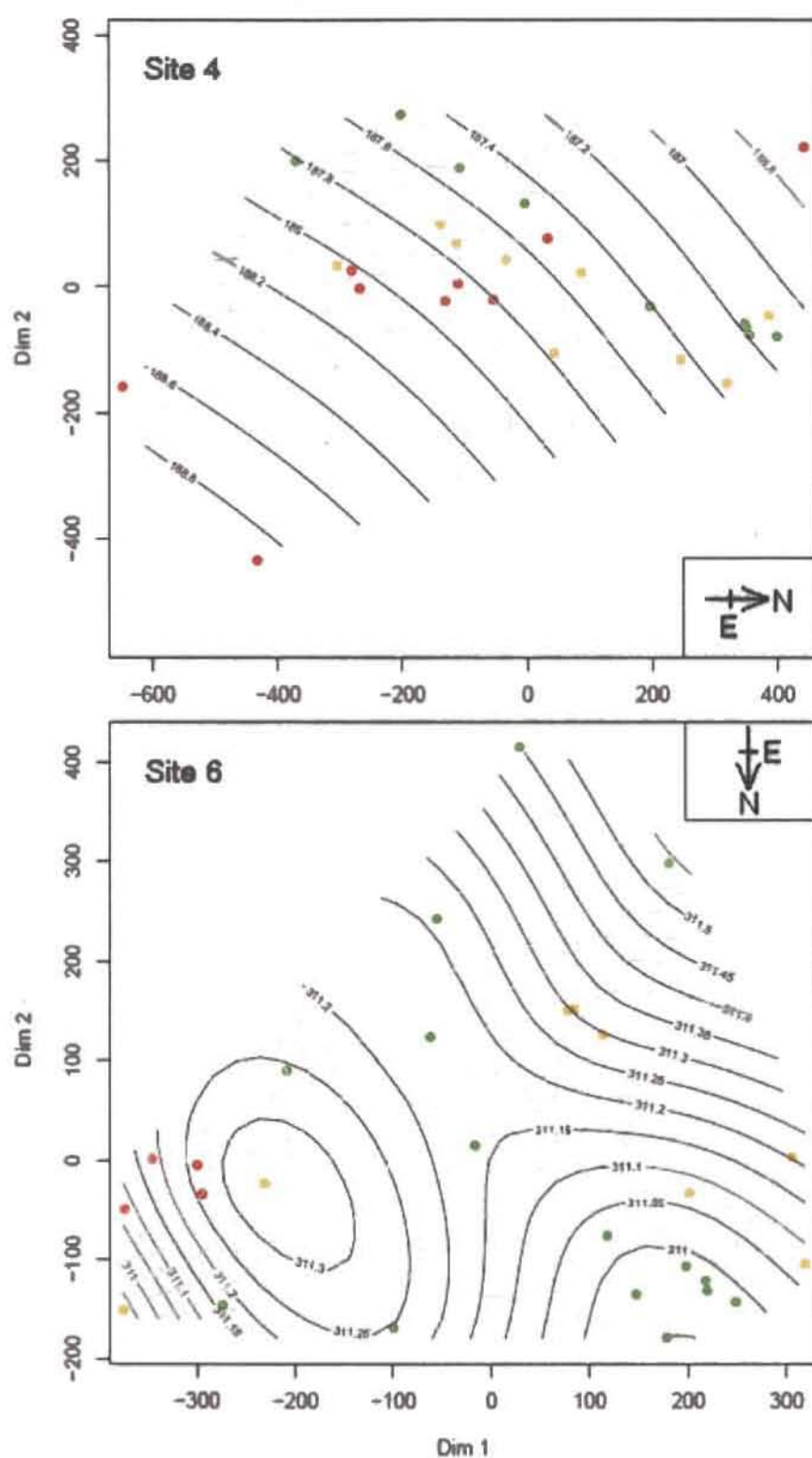
Figure 3.6a: Trend surfaces for cushion health (blue) and elevation contours (black) for sites 4 and 6, where cushions in good health were located downslope from cushions in poor health (● = good (3); ● = medium (2); ● = poor (1)). Elevation is shown in metres.
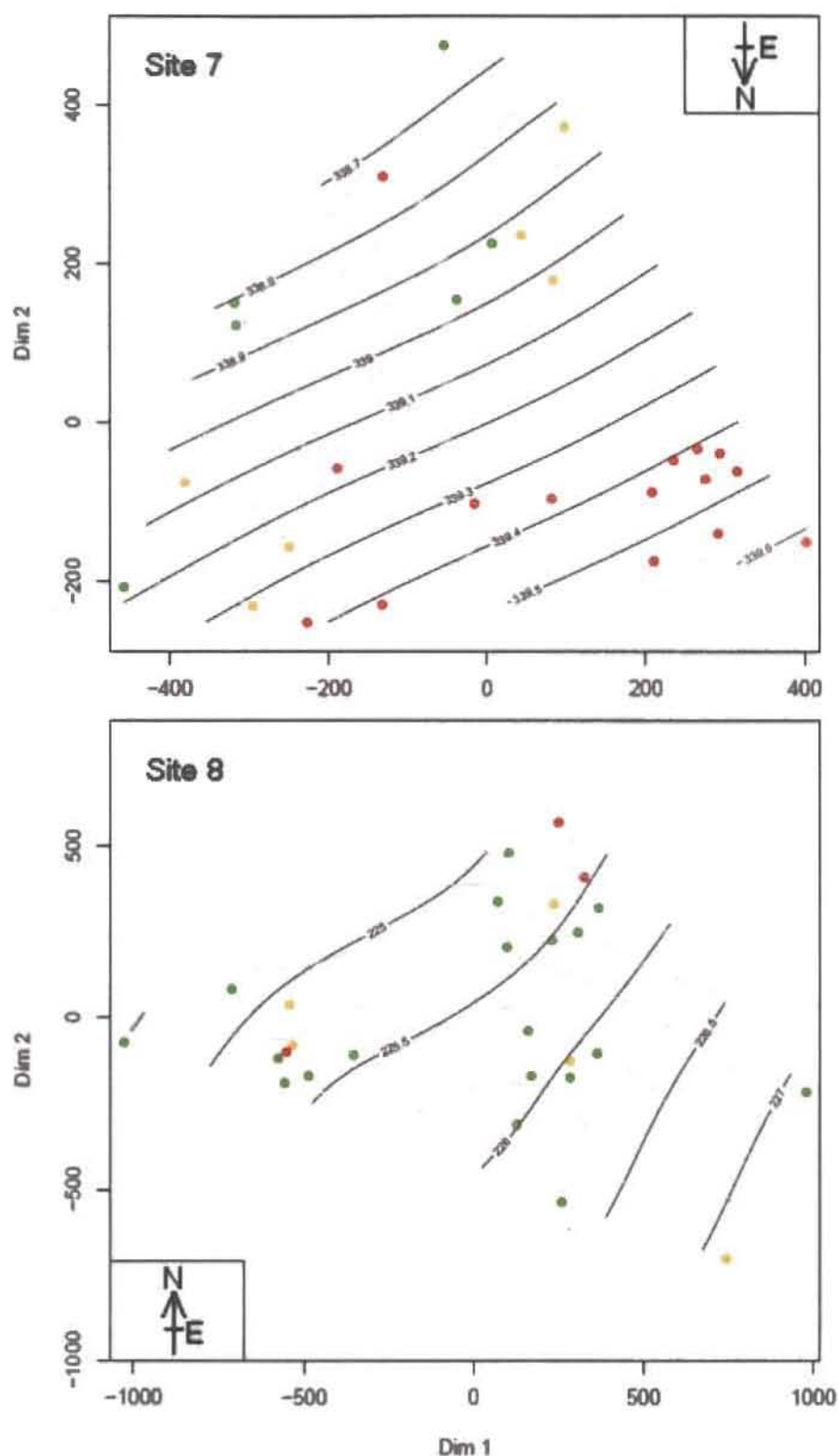
Figure 3.6b: Trend surfaces for cushion health (blue) and elevation contours (black) for sites 7 and 8, where cushions in good health were located downslope from cushions in poor health (● = good (3); ● = medium (2); ● = poor (1)). Elevation is shown in metres.
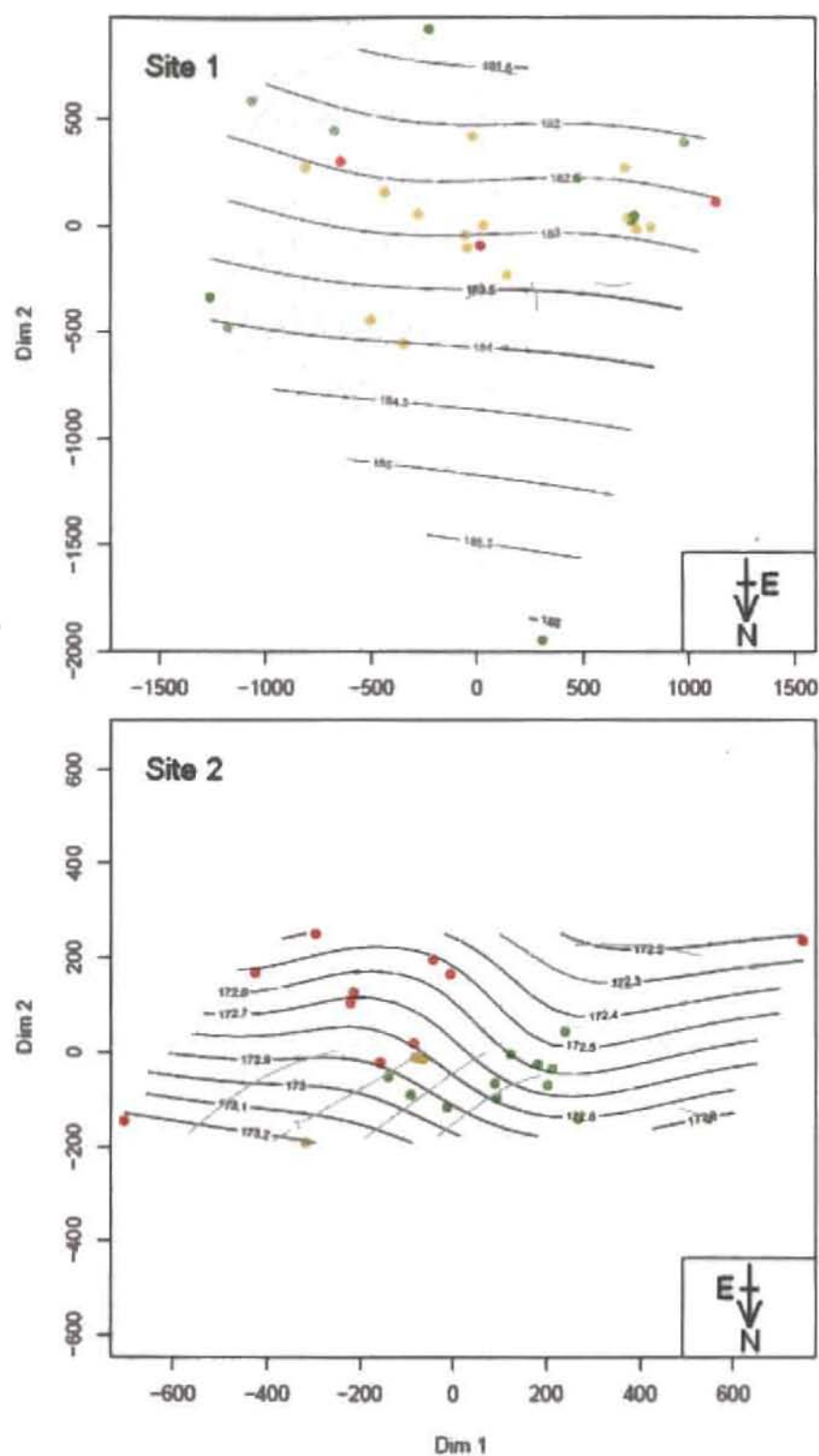
Figure 3.7: Trend surfaces for cushion health (blue) and elevation contours (black) for sites 1 and 2 (● = good (3); ● = medium (2); ● = poor (1)). Elevation is shown in metres.

Cushion health was not found to have any significant relationship with vegetation community, cushion size, or cushion substrate. However, it did have a significant relationship with wind exposure (Table 3.12).

Table 3.12: Chi-square analysis of cushion health between the different variables of vegetation community, cushion size, cushion substrate, and cushion exposure

	Cushion health class					
	Poor	Medium	Good	Chi²	df	P
Veg type						
Herbfield	30	40	73	5.41	2	0.067
Fjaeldmark	39	40	48			
Cushion size						
Small	27	44	50	8	4	0.092
Medium	30	29	45			
Large	12	7	26			
Cushion substrate						
Mossbed/soil	14	26	44	12.01	6	0.062
Soil	9	11	19			
Soil/gravel	15	6	12			
Gravel	13	37	46			
Cushion exposure						
Sheltered	2	4	27	24.28	4	< 0.001
Intermediate	49	64	77			
Exposed	18	12	17			

3.2.2 Variation in cushion damage within and between sites

With a mean of 43.75 % (SD = 34) and mode of 0 (n = 19), cushion damage ranged from 0 % to 100 %, with cushions tending to be either largely damaged or largely undamaged (Figure 3.8). The site with the highest pooled damage percentage was site 7 and the lowest was site 8 (Table 15).
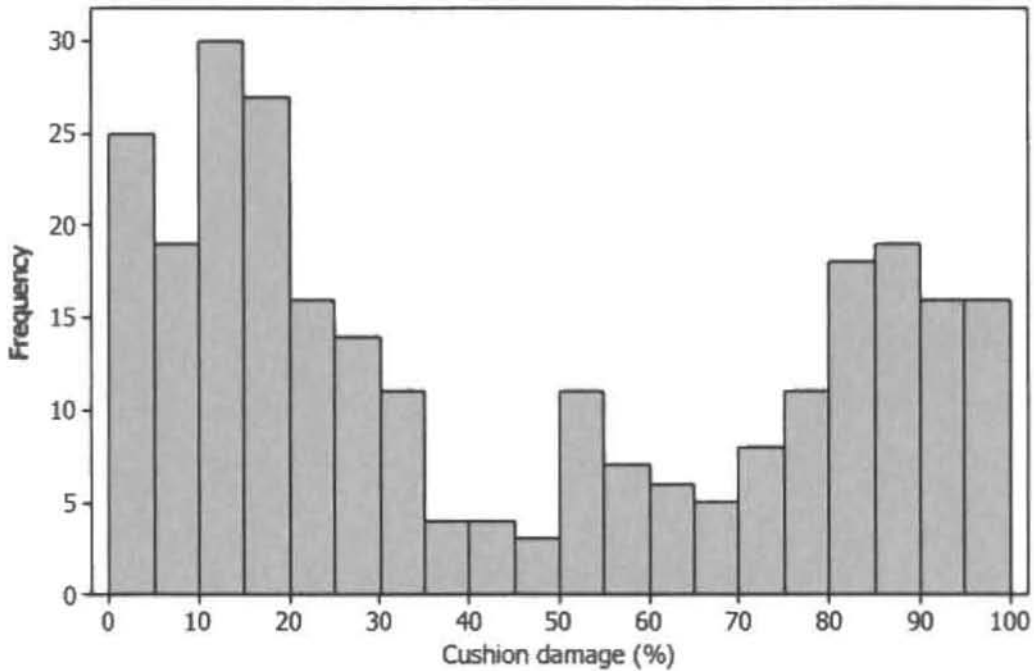
Figure 3.8: Pooled cushion damage percentage frequencies from the 270 cushions.

There was a significant difference in percentage damage between sites (F = 4.36, P < 0.001). Significant differences occurred between site 1 and 4, 7; site 2 and 8; site 4 and 1, 8; site 5 and 8; site 7 and 1, 8; site 8 and 2, 4, 5, 7, 10; site 10 and 8 (Table 3.13).

Table 3.13: Means and standard deviations ( ) for cushion percentage damage between sites (ANOVA). Sites with the same letter next to the damage value are statistically identical at P > 0.05 using Tukey's test

Site	Damage (%)	
1	27.18bc	(22.8)
2	53.63ab	(38.3)
3	42.21abc	(32.4)
4	55.79a	(30.6)
5	47.51ab	(34.2)
6	34.41abc	(28.7)
7	57.47a	(33.5)
8	19.5c	(20.8)
9	45.74abc	(40.6)
10	54.09ab	(34.9)

There was a significant difference between percentage damage for each of the damage types in the pooled data (ANOVA, $F = 97.77$, $P < 0.001$; Table 3.14). Type 1 had the highest percentage, and Type 2 had the lowest.

Table 3.14: Differences between means and standard deviations ( ) of cushion damage type percentages (ANOVA). Means with the same letter are statistically identical at P > 0.05 using Tukey's test

Damage type	Percentage of cushion surface	
Type 1	28.19b	(27.2)
Type 2	3.23c	(7.6)
Type 3	11.63a	(23.3)

The site with the highest percentage of Type 1 damage was site 7, and the lowest damage was at site 2. The site with the highest percentage of Type 2

damage was site 1, and the lowest damage was at site 6. The site with the highest percentage of Type 3 damage was site 2 and the equal lowest were sites 1 and 8 (Figure 3.9).
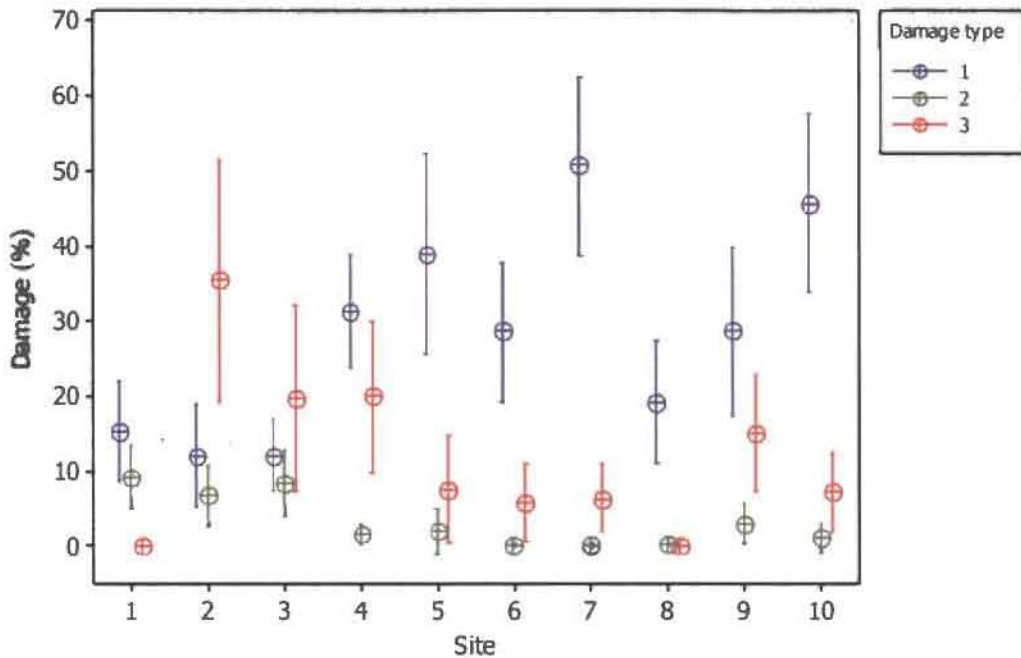
Figure 3.9: Cushion percentage damage means and 95% confidence intervals by type and site.

The significant differences in Type 1 damage occurred between site 1 and 5, 7, 10; site 2 and 5, 7, 10; site 3 and 5, 7, 10; site 5 and 1, 2, 3; site 6 and 7; site 7 and 1, 2, 3, 6, 8, 9; site 8 and 7, 10; site 9 and 7; site 10 and 1, 2, 3, 8.

The significant differences in Type 2 damage occurred between site 1 and 4, 5, 6, 7, 8, 9, 10; site 2 and 6, 7, 8; site 3 and 4, 5, 6, 7, 8, 10; site 4 and 1, 3; site 5 and 1, 3; site 6 and 1, 2, 3; site 7 and 1, 2, 3; site 8 and 1, 2, 3; site 9 and 1; site 10 and 1, 3.

The significant differences in Type 3 damage occurred between site 1 and 2, 3, 4; site 2 and 1, 5, 6, 7, 8, 9, 10; site 3 and 1, 8; site 4 and 1, 8; site 5 and 2; site 6 and 2; site 7 and 2; site 8 and 2, 3, 4; site 9 and 2; site 10 and 2.

Type 1 damage had a negative correlation with Type 2 damage ($r = -0.264$, P < 0.001). There were no other significant correlations between damage types. Type 1 and Type 3 damage decreased as cushion health increased. However, Type 2 damage increased with cushion health (Table 3.15).

Table 3.15: Relationship between damage types and health (ANOVA) showing percentage damage means, standard deviations ( ), F and P values. Means with the same letter are statistically identical at $P > 0.05$ using Tukey's test

| | Cushion health class | | | | |
Damage	Poor	Medium	Good	F	P
Total	82.93a (17.2)	54.51b (26.5)	14.3c (11.2)	325.14	<0.001
Type 1	53.44a (31.5)	35.07b (19.9)	9.25c (8.6)	113.26	<0.001
Type 2	1.44c (5.6)	2.71b (7)	4.59a (8.7)	4.12	0.017
Type 3	26.84a (32.3)	15b (22.6)	0.73c (4.7)	36.55	<0.001

There were no significant differences in total damage between substrate classes (Table 3.16). Type 1 damage was lowest on soil, whereas damage types 2 and 3 showed the reverse pattern (Table 3.16).

Table 3.16: The relationship between substrate and cushion damage percentage means and standard deviations ( ) (ANOVA). Means with the same letter are statistically identical at P > 0.05 using Tukey's test

	Cushion substrate class					
Damage	Mossbed/soil	Soil	Soil/gravel	Gravel	F	P
Total	38.32a (35)	44.61a (34.5)	55.54a (36.7)	44.05a (31.7)	2.07	0.104
Type 1	27.77a (28.9)	10.42b (10.7)	33.11a (32.7)	33.17a (25.8)	7.74	<0.001
Type 2	2.93b (8.3)	7.28a (9.9)	4.64ab (9.4)	1.66b (4.6)	6.05	0.001
Type 3	8.13b (16.7)	25.31a (35)	16.56ab (32)	8.11b (16.9)	6.93	<0.001

There were no significant differences in percentage damage in total and for any damage type between cushion size classes, but there were strong differences between cushion exposure classes. For Type 1 and total damage, exposed cushions had the highest damage (Table 3.17). For Type 2 damage, sheltered cushions had the highest damage. There was no relationship between Type 3 damage and cushion exposure (Table 3.17).

Table 3.17: The relationship between cushion exposure and cushion damage percentage means and standard deviations ( ) (ANOVA). Means with the same letter are statistically identical at P > 0.05 using Tukey's test

	Cushion exposure class				
Damage type	Sheltered	Intermediate	Exposed	F	P
Total	15.95b (25.7)	46.73a (33.3)	51.25a (33.1)	14.19	<0.001
Type 1	3.59b (7.2)	30.8a (27)	34.92a (28)	17.83	<0.001
Type 2	7.47b (14.3)	2.62a (6.1)	2.71a (5.5)	6.05	0.003
Type 3	4.59a (18.4)	13.08a (23.4)	10.7a (25)	1.94	0.146

Total damage and Type 3 damage did not differ between vegetation communities (Table 3.18). Type 1 damage was most prominent in fjaeldmark while Type 2 damage was most prominent in herbfield (Table 3.18).

Table 3.18: The relationship between vegetation community type and percentage cushion damage means and standard deviations ( ) (ANOVA). Means with the same letter are statistically identical at P > 0.05 using Tukey's test

	Vegetation community type				
Damage type	Herbfield		Fjaeldmark		F	P
Total	40.43a	(34.8)	47.49a	(32.7)	2.93	0.088
Type 1	22.01b	(25.7)	35.15a	(27.2)	16.63	<0.001
Type 2	4.37a	(9.2)	1.94b	(5)	7.04	0.008
Type 3	13.97a	(26.6)	9a	(18.6)	3.09	0.080

The general linear model that best explained total damage incorporated site and cushion exposure (Table 3.19). The best model for Type 1 damage incorporated site, substrate, cushion exposure, and vegetation community type (Table 3.19). The best model for Type 2 damage incorporated site and cushion exposure (Table 3.19). The best model for Type 3 damage only incorporated site (Table 3.19).

Table 3.19: General linear models for damage incorporating environmental fixed variables and site as a random variable

Damage type	Source	df	Seq. SS	F	P
Total	Site	9	38062.3	4.5	<0.001
	Cushion Exposure	2	29840.8	14.45	<0.001
	R^2 = 18.54 %				
Type 1	Site	9	46316.9	7.96	<0.001
	Substrate	3	5011.9	2.72	0.045
	Cushion Exposure	2	21887.1	20.39	<0.001
	Vegetation Type	1	2254.6	4.65	0.032
	R^2 = 34.34 %				
Type 2	Site	9	2949.8	6.36	<0.001
	Cushion Exposure	2	435.6	4.6	0.011
	R^2 = 18.37 %				
Type 3	Site	9	28779.4	7.13	<0.001
	R^2 = 17.02 %				

3.2.3 Variation in cushion damage within cushions

There was a significant difference in the degree of concentration of damage between damage types. Types 1 and 2 damage were more concentrated, mainly affecting particular sectors of the cushion. However, Type 3 damage was less concentrated, affecting the whole cushion when it did occur (Table 3.20).

Table 3.20: Chi-square analysis of concentrated and unconcentrated damage by damage type

	Damage type					
Concentrated	Type 1	Type 2	Type 3	Chi²	df	P
No	11	34	52	139.2	2	<0.001
Yes	223	46	21			

Type 1 damage occurred most frequently on the south-west sector of the cushion. This was followed by the centre of the cushion (Figures 3.10 – 3.11). Type 2 damage occurred most frequently in the centre of the cushion. This was followed by the north sector (Figures 3.12 – 3.13). Type 3 damage occurred most frequently on the south-west sector of the cushion. This was followed by the east sector (Figures 3.14 – 3.15).
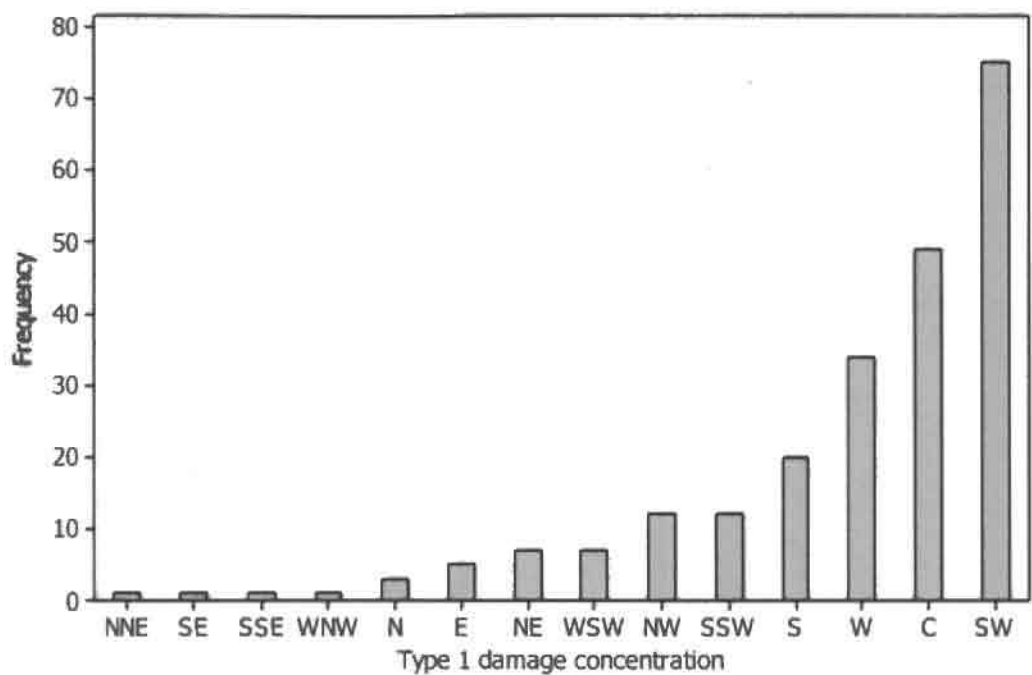
Figure 3.10: Frequencies for the different sectors of the Type 1 damage concentrations, sorted by ascending frequencies (C = centre).
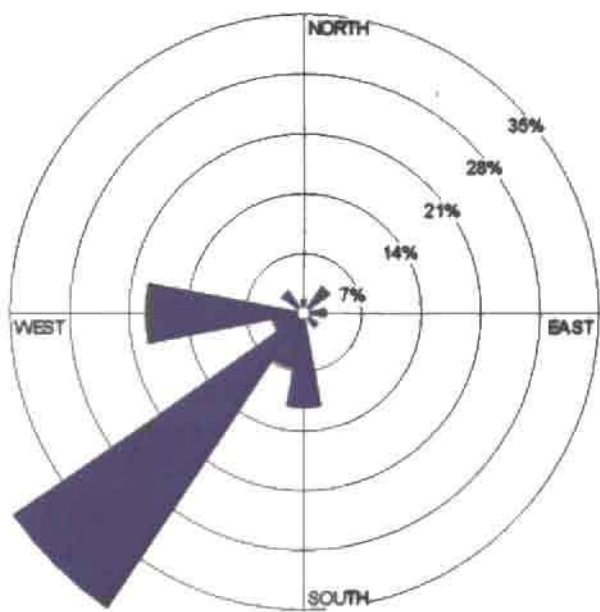
Figure 3.11: Directional concentrations of Type 1 damage, shown as percent of combined total of directional damage.
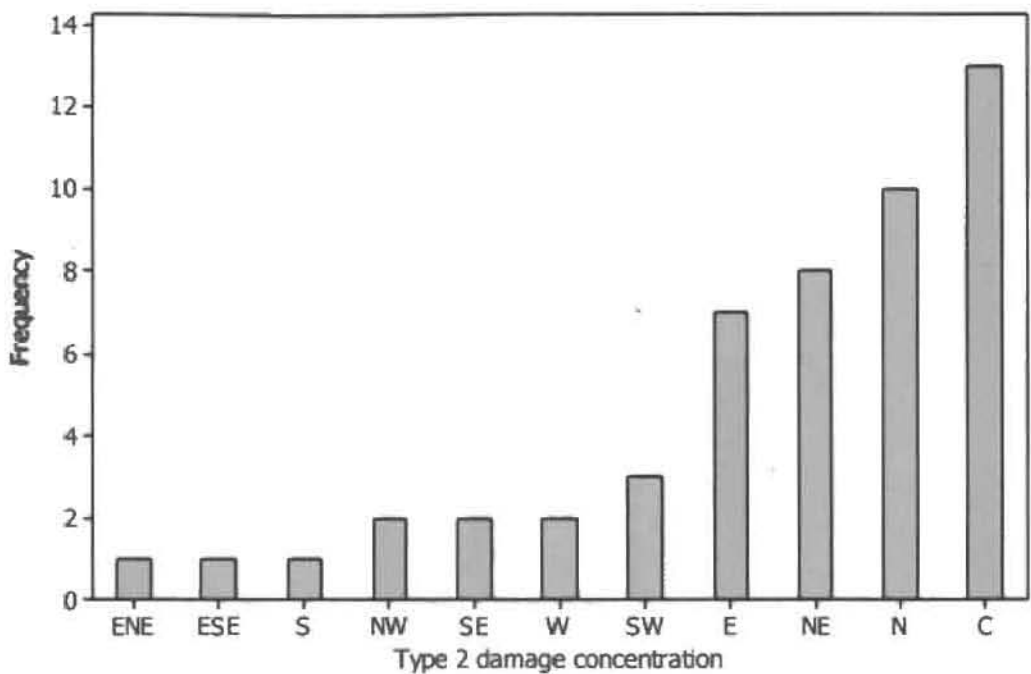
Figure 3.12: Frequencies for the different sectors of the Type 2 damage concentrations, sorted by ascending frequencies (C = centre).
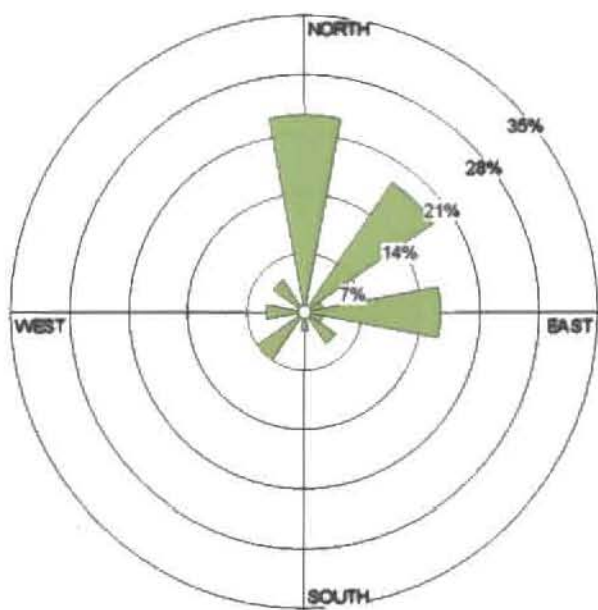
Figure 3.13: Directional concentrations of Type 2 damage, shown as percent of combined total of directional damage.
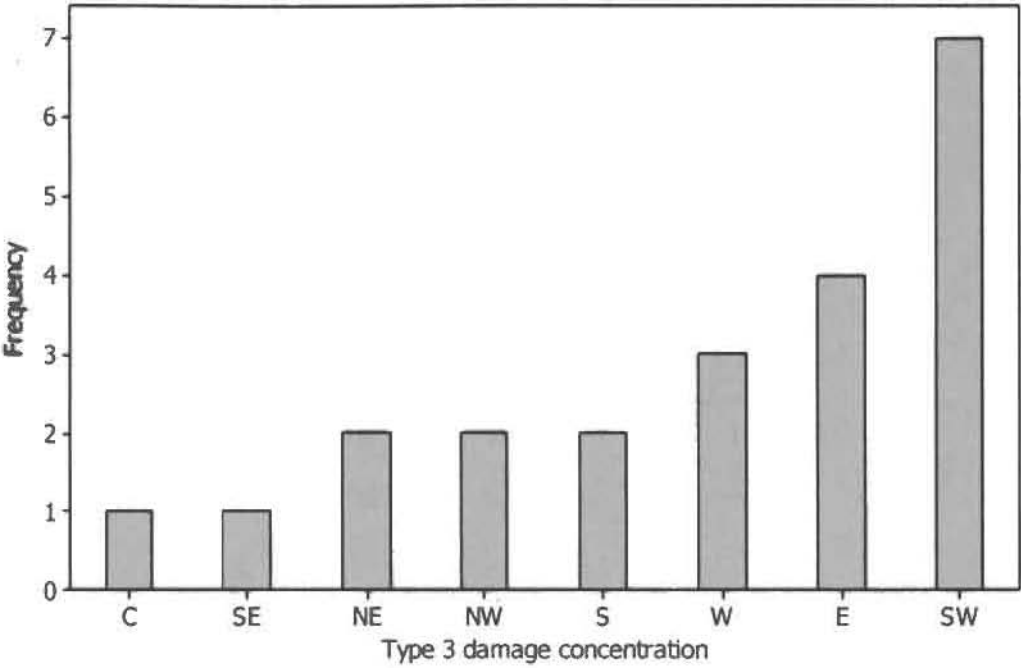
Figure 3.14: Frequencies for the different areas of Type 3 damage concentrations, sorted by ascending frequencies (C = centre).
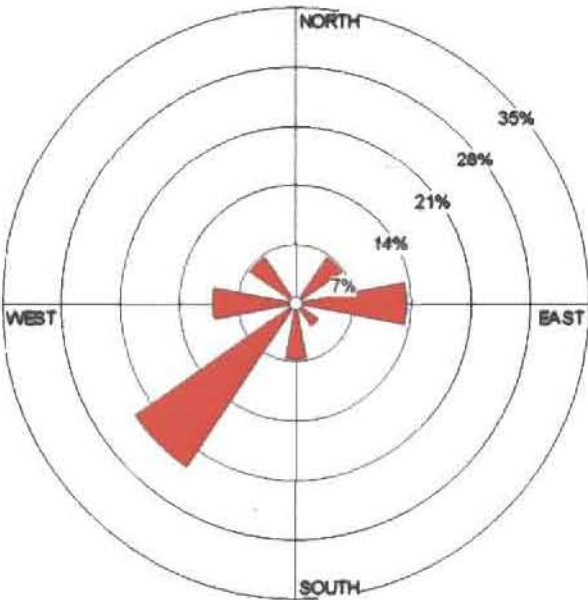
Figure 3.15: Directional concentrations of Type 3 damage, shown as percent of combined total of directional damage.

Types 1 and 3 damage occurred more frequently in areas other than the centre of the cushion. There was no significant difference between centre and directional damage for Type 2 (Table 3.21).

Table 3.21: Chi-square analysis between centre-concentrated and not centre-concentrated damage by damage type

	Damage type					
Concentration	Type 1	Type 2	Type 3	Chi²	df	P
Centre	49	13	1	16	2	<0.001
Directional	185	67	72			

3.2.4 Dominant wind directions

Dominant wind directions, as judged from evidence on the photographs, ranged from south, clockwise to north-west. The direction with the highest frequency was west-south-west, followed by south-west. The directions with zero frequency were north to southeast clockwise (Figures 3.16 – 3.17).
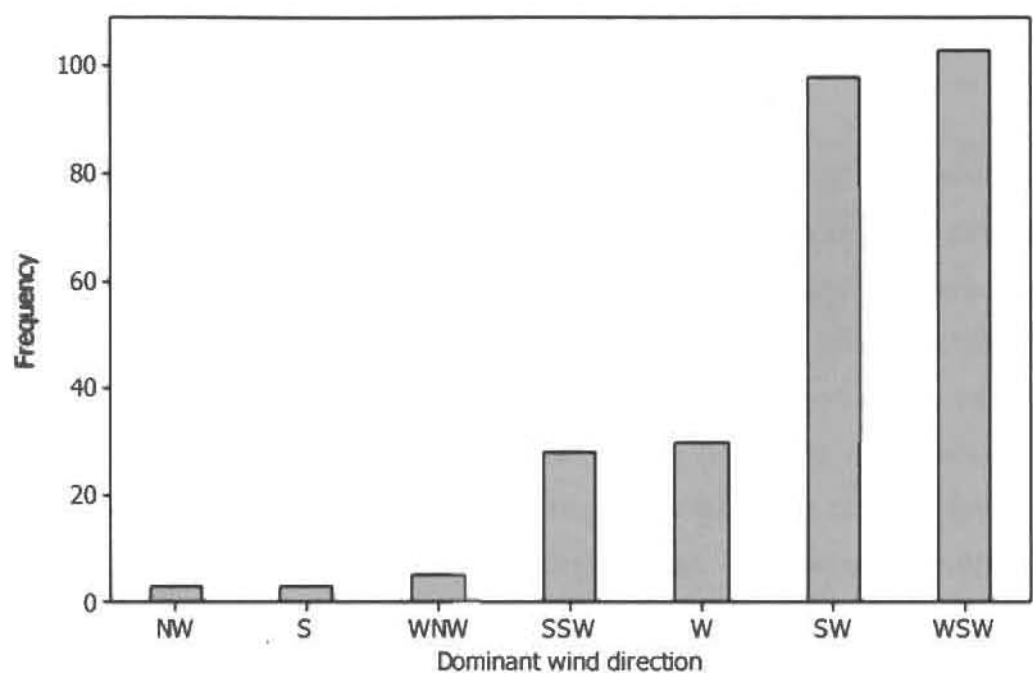
Figure 3.16: Pooled dominant wind directions for the 270 cushions, sorted by ascending frequencies.
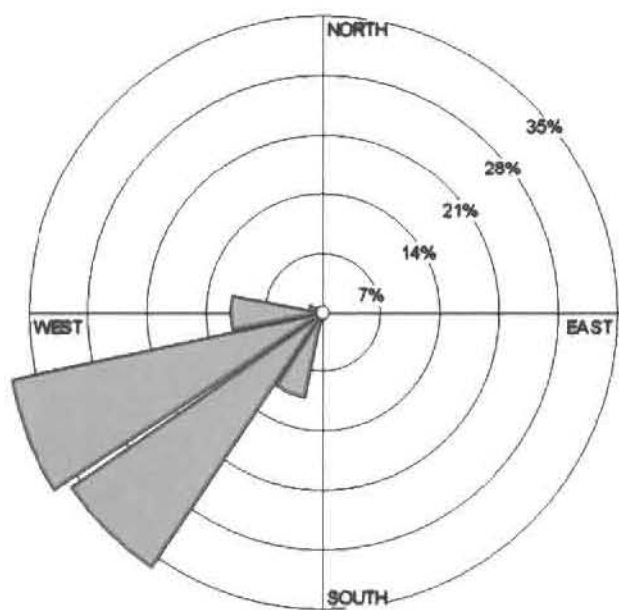
Figure 3.17: Pooled dominant wind directions for the 270 cushions, shown as percent of combined total.

3.3 Temporal mapping of cushion health

3.3.1 Summer greening – winter browning

The repeat photography showed that there was a tendency for cushions at the revisit sites to change in colour from brown to green during the period of late November to mid December. Cushion sectors that were sheltered from south-westerly winds appeared to become green earlier than sectors that were exposed. Cushions also showed a tendency to change to brown again during the period of late February to late March (Figure 3.18). There were variations in time of browning and greening. At some sites cushion greening occurred earlier, and at others it occurred later. This was the same for cushion browning. Certain cushions were not observed to green as much as others and others were not observed to brown as much as others. As the observation period only extended from late October to late March, the full extent of the winter browning may not have been captured.

1: 31 October 2009
2: 22 November 2009
3: 13 December 2009
4: 6 January 2010
5: 28 January 2010
6: 23 February 2010
7: 22 March 2010

Scale
0   25   50 cm
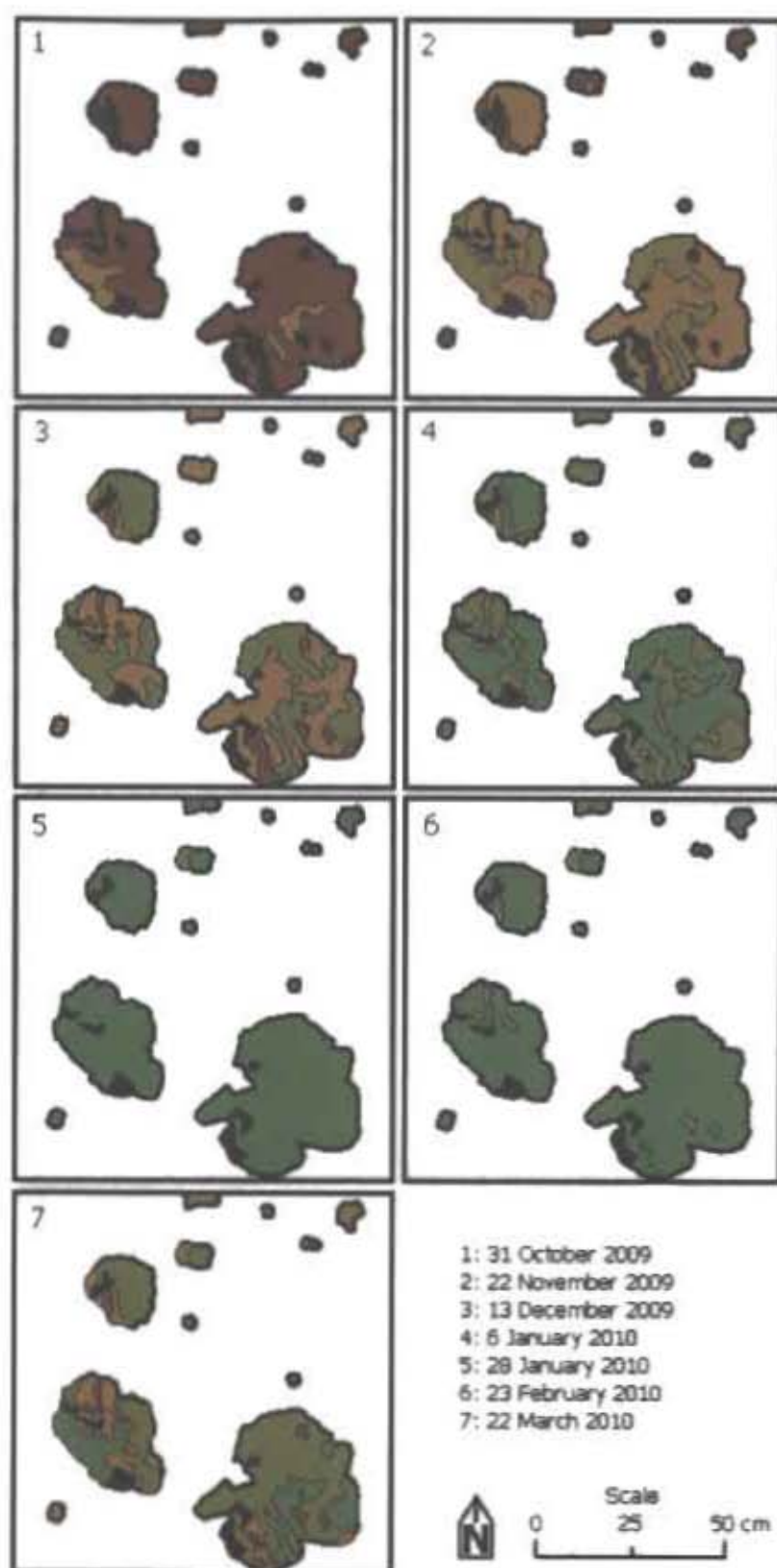
Figure 3.18: Summer greening and winter browning at site 1 as observed over 7 visits during the austral spring period of late October to the austral autumn period of late March. Colours approximate those observed in the field.

3.3.2 Type 1 damage

Type 1 damage was observed to have occurred on cushions in 28 of the 31 sites. It was observed to have occurred more frequently on areas exposed to south-westerly winds. However, this type of damage exhibited minimal variation during the repeat observation period, in some cases being replaced by green foliage between visits (Figure 3.19).

3.3.3 Type 2 damage

Type 2 damage was observed to have occurred on cushions in 26 of the 31 sites. Occurring in a series of small patches, it was observed to have occurred more frequently on areas sheltered from south-westerly winds. Mild damage often disappeared between visits while severe damage persisted (Figure 3.19). Overall damage remained more or less constant.

1: 30 October 2009
2: 23 November 2009
3: 12 December 2009
4: 7 January 2010
5: 27 January 2010
6: 23 February 2010
7: 22 March 2010

Scale
0   25   50 cm
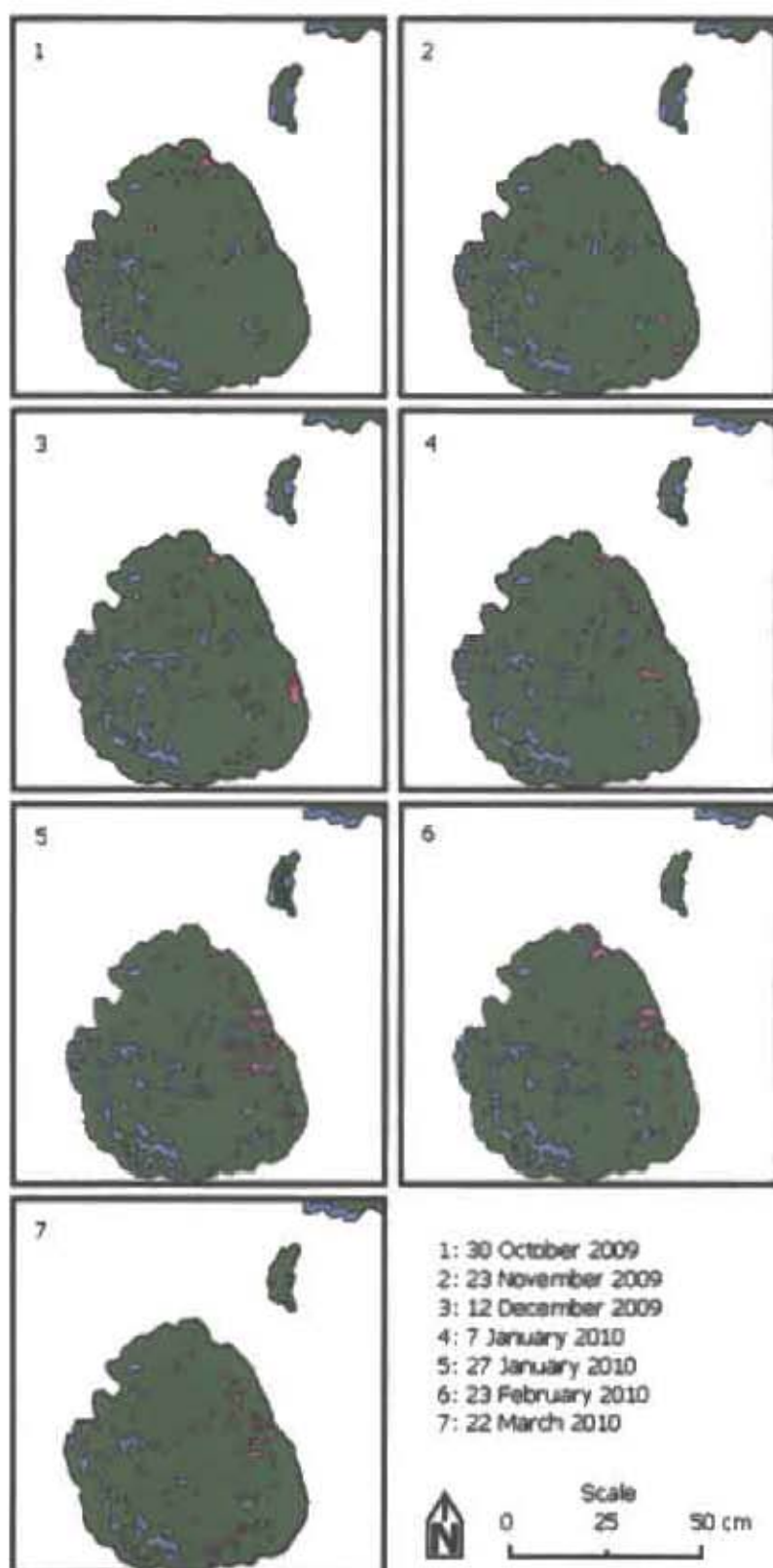
Figure 3.19: Types 1 and 2 damage at site 28 as observed over 7 visits during the spring period of late October to the autumn period of late March. Blue indicates Type 1 damage, and pink indicates Type 2 damage

3.3.4 Type 3 damage

Out of the 31 sites, Type 3 damage was observed to have only occurred in five. The pattern of rapid temporal change in the location of Type 3 damage is described and mapped for site 9 below. Temporal maps and descriptions of the spread of Type 3 damage at the other sites can be found in the Appendix.

Site 9 had four cushions all of which were affected by Type 3 damage by late March (Figure 3.20).
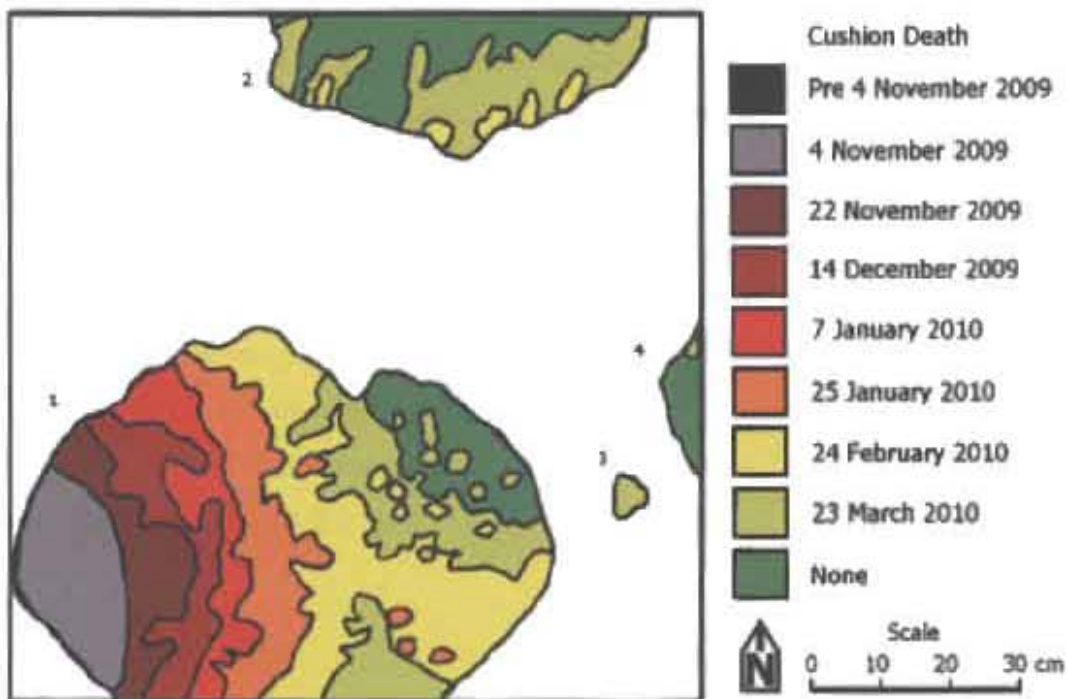
Figure 3.20: The spread of Type 3 damage at site 9. Numbers indicate individual cushions

The first sign of death was observed in the west sector of cushion 1 at the time of the first visit in early November. The damage spread eastward with a front that extended from the north edge to the south edge without much variation until late January, when four patches of damage occurred further west than the front. In late February, the damage had spread further east without affecting a region in the south sector. Five patches occurred to the north-east, ahead of the front. Cushion 2 to the north began to show signs of the damage in five patches along its south edge. By late March, only the

north-east sector of cushion 1 had remained unaffected. The damage on cushion 2 had spread along the edges and northward, linking four of the patches. Cushion 3 had become completely affected, and damage also had occurred on the north-west edge of cushion 4 in the east of the site.

The area of onset varied between cushions. Cushion 1 was first affected on its west sector, cushion 2 was first affected to the south, and cushion 4 was first affected to the north-west. It was difficult to determine the area of onset for cushion 3 as the whole cushion had become affected between visits. Type 3 damage appeared to have a contagion effect at this site, spreading radially from the west sector of cushion 1 between cushions as far as approximately 30 cm apart, in a westerly/south-westerly direction. Death had spread the most during the period of late February to late March, and least during the period of late November to mid December.

3.4 Cushion soils study

Total soil depth ranged from 10 to 100 cm. Site 11 had the shallowest soil, and site 14 had the deepest. Number of horizons ranged from 3 to 7. Sites 1, 7, 11 and 13 had the least number of horizons. Sites 12, 14 and 15 had the most horizons (Figure 3.21).
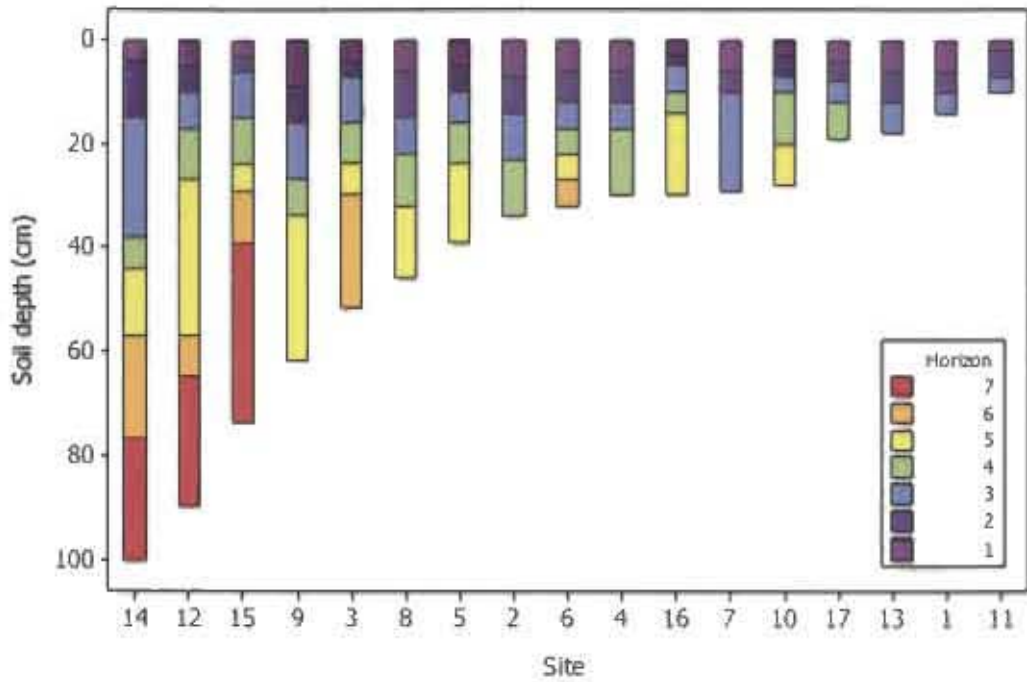
Figure 3.21: Soil horizon depths by site, sorted by decreasing total soil depth.

Although thickness was significantly different between horizons (ANOVA, F = 13.74, P < 0.001; Table 3.22), there was no significant difference in horizon thickness at each level between unhealthy and healthy cushions (ANOVA, P > 0.05), apart from horizon 5. A one-tailed t-test found horizon 5 to be significantly shallower where cushions were unhealthy (t = -2.36, P = 0.028; Figure 3.22).

Table 3.22: Means and standard deviations ( ) of horizon thickness by site (ANOVA). Means with the same letter are statistically identical at P > 0 05 using Tukey's test

Horizon	Thickness (cm)	
1	5d	(1.8)
2	5.4d	(2.3)
3	7.9cd	(5.5)
4	8.3bcd	(2.5)
5	14b	(8.9)
6	13bc	(7.6)
7	27.7a	(6.4)
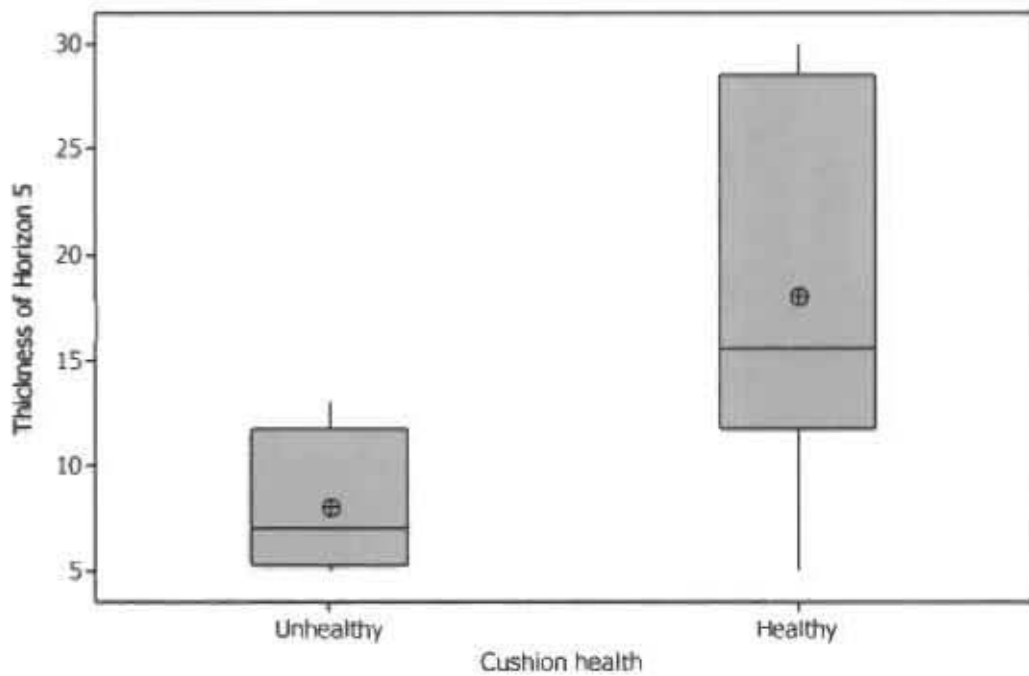
Figure 3.22: Cushion health related to thickness of Horizon 5, displaying means, medians, first and third quartiles, and lower and upper limits.

Total depth was not significantly related to cushion health (ANOVA, $F = 1.86$, $P = 0.193$), and neither was number of horizons (ANOVA, $F = 2.25$, $P = 0.154$), nor topographic position ($Chi^2 = 1.409$, $P = 0.235$).

There was a significant difference in thickness between horizon classes (ANOVA, F = 14.67, P < 0.001). The difference occurred between the top horizon and the other horizon classes, with the bottom horizon being significantly thicker. However, the thickness of each horizon class was not significantly related to cushion health (ANOVA, P > 0.05).

With a mean of 29.5 % (SD = 22.4), percentage organic matter in the top horizon ranged from 4.35 % (site 5) to 76.03 % (site 6). Percentage organic matter in the middle horizons had a pooled mean of 19.21 % (SD = 10.7), and ranged from 5.71 % (site 5) to 44.09 % (site 6). Percentage organic matter in the bottom horizon had a mean of 13.08 % (SD = 6.2), and ranged from 5.05 % (site 1) to 28 % (site 15; Figure 3.23).
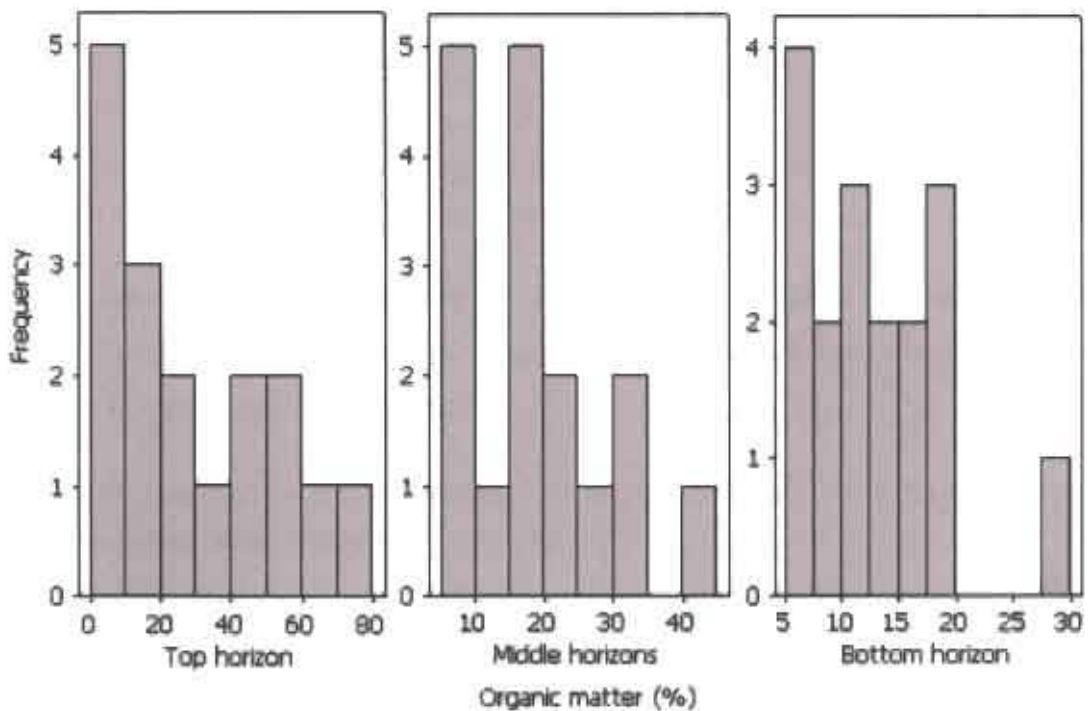
Figure 3.23: Pooled percentage organic matter frequencies by horizon class.

There was a significant difference in percentage organic matter between horizon classes (ANOVA, F = 5.35, P = 0.008; Figure 3.24). The difference occurred between the top horizon and the bottom horizon, with the bottom horizon having significantly less organic matter.
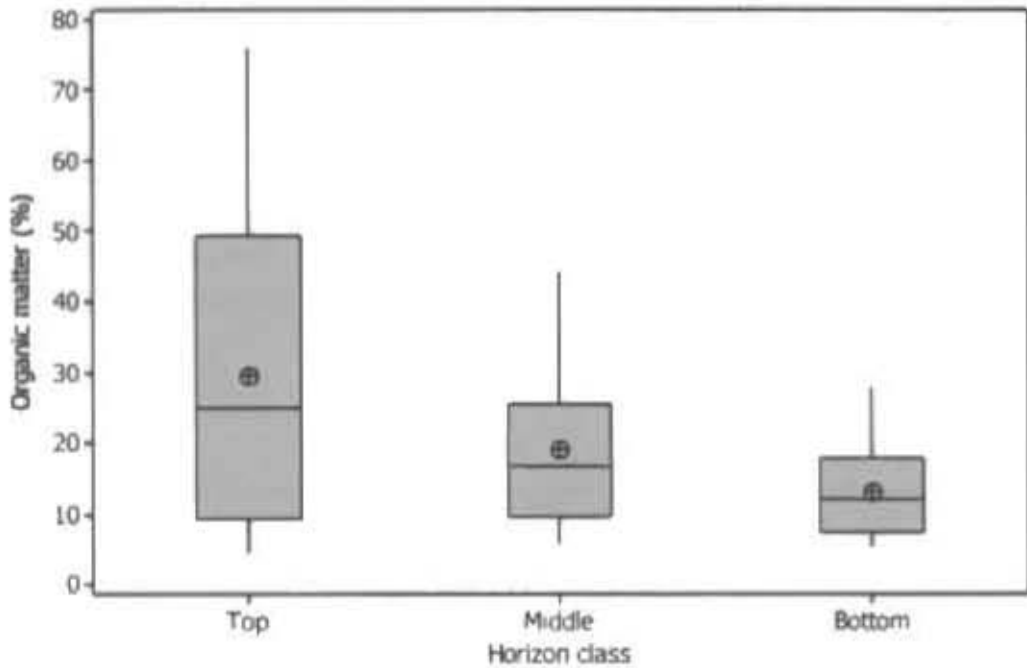
Figure 3.24: Percentage organic matter by horizon class: displaying means, medians, first and third quartiles, and lower and upper limits.

There was a significant difference in percentage organic matter between healthy and unhealthy cushions. However, the difference only occurred in the bottom horizon class (Table 3.23).

Table 3.23: Means and standard deviations ( ) of percentage organic matter for each horizon class by cushion health (ANOVA)

| Organic Matter (%) | Cushion Health | | F | P |
	Healthy	Unhealthy		
Top	24.21 (23.6)	39.18 (18)	1.82	0.198
Middle	17.49 (12.3)	22.37 (6.5)	0.8	0.385
Bottom	10.87 (5.3)	17.13 (6.1)	4.93	0.042

Soil pH values of the top horizons ranged from 5.3 to 7.5. Site 3 was the most acidic, and site 12 was the most alkaline. Soil pH was not found to be

significantly related to cushion health (ANOVA, F = 2.43, P = 0.14).

Total depth, number of horizons, horizon class thickness and percentage organic matter were each significantly related to vegetation community type (Table 3.24).

Table 3.24: Means and standard deviations ( ) of soil properties related to vegetation community type (ANOVA)

| | Vegetation community type | | | | F | P |
	Herbfield		Fjaeldmark			
Total depth (cm)	63.67	(28.8)	29.55	(15.1)	10.55	0.005
No. of horizons	6.17	(1.2)	4.09	(0.9)	15.94	0.001
Thickness (cm)						
Top	4.83	(1.5)	5.09	(2)	0.08	0.784
Middle	8.93	(3.6)	5.56	(1.7)	7	0.018
Bottom	20.17	(10.7)	12.09	(7.5)	3.37	0.086
Organic matter (%)						
Top	52.73	(16.5)	16.82	(13)	24.71	<0.001
Middle	28.66	(10.7)	14.06	(6.5)	12.44	0.003
Bottom	17.63	(6)	10.6	(4.9)	6.84	0.02

Herbfield had significantly more total depth and more horizons in comparison to fjaeldmark. Only the thickness for the middle horizon class was significantly different between vegetation community types, with the middle horizons being significantly thicker for herbfield. Percentage organic matter for each horizon class was significantly related to vegetation community type. Herbfield had significantly more percentage organic matter in all horizon

classes. Soil pH was not found to be significantly related to vegetation community type (ANOVA, F = 1.31, P = 0.271).

Chapter 4   Discussion

4.1 Causes of the different damage types

4.1.1 Type 1 damage

There was strong circumstantial evidence for strong winds being responsible for Type 1 damage. Type 1 damage was strongly associated with the sector of the cushion most exposed to the strongest and coldest winds (Table 3.20; Figures 3.10 – 3.11), and with cushions in general that were more exposed (Table 3.17) and growing in fjaeldmark (Table 3.18). The association between wind exposure and damage has been widely observed in cushion plants (Taylor 1955a; Molau 1996; le Roux and McGeoch 2008; Nyakatya and McGeoch 2008) and in other alpine plants (Watt and Jones 1948; Burges 1951; Whitehead 1951; Ingram 1958; Holtmeier 1980, 2009; Hadley and Smith 1983, 1986; Daly 1984; Hansen-Bristow 1986; Rushton and Toner 1989). Desiccation of leaf bud and foliage tissue and other types of deformation have been suggested to have been caused by wind and/or ice-crystal abrasion on the windward sides of the plants.

Another piece of circumstantial evidence for wind being responsible for Type 1 damage was its association with the tops and bases of cushions (Figure 3.3). This association has been observed in plants that grow in windy environments, where mechanical damage occurs in the form of abrasion by aeolian sediments. Wind speed increases with vertical distance from the ground surface as friction decreases (Whitehead 1951; Warren Wilson 1959). The tops of the plants thus receive the maximum impact of the suspended, finer particles. The bases of plants are affected by particles that are too heavy to be suspended, which travel by saltation or by ground surface creep (Liu *et al.* 2006; Udo and Takewaka 2007; Wang *et al.* 2008; Flores-Aqueveque *et al.* 2010). Another possible cause for basal wind damage is surface roughness, which causes turbulent boundary layers to form. These may result in scouring from eddying on the windward and leeward side of the

plant (Warren Wilson 1959; Armbrust *et al.* 1964).

4.1.2 Type 2 damage

The correlates of Type 2 damage strongly suggested that rabbits were responsible for it. This type of damage was strongly associated with herbfield, rather than fjaeldmark (Table 3.18), possibly reflecting the known relative abundance of rabbits (Copson *et al.* 1981). It was also strongly associated with shelter, as indicated by cushion exposure (Table 3.17) and relative exposure to strong cold winds within the cushion (Table 3.20; Figures 3.12 – 3.13), with the maximum amount of the type of damage being found in the lee of cushions on the less exposed sites. Rabbits are known to minimise their exposure to strong winds (Southern 1940, 1948; Rowley 1957; Copson *et al.* 1981; King *et al.* 1984; Fraser 1992; Ballinger and Morgan 2002), although they have been observed to remain above ground despite strong winds (Wheeler *et al.* 1981). The association between Type 2 damage and the sheltered sectors of the cushions is most evident in the windier fjaeldmark where rabbits may graze to avoid predation by skuas, at the cost of greater exposure to wind. Skua populations on the island are highest in coastal areas and the herbfields on the plateau where rabbit populations are highest (Jones and Skira 1979; Skira 1984).

Another piece of evidence for rabbits being responsible for Type 2 damage was the strong association of Type 2 damage with healthy cushions and the parts of the cushions with greatest depth (Tables 3.8, 3.10 and 3.15; Figure 3.4). This would reflect known feeding discrimination by rabbits between plants based on nutritional value (Somers *et al.* 2008).

4.1.3 Type 3 damage

Wind and rabbits are unlikely to have caused Type 3 damage. This is indicated by the lack of association between the damage type and any particular sector of the cushions (Table 3.20, Figures 3.14 – 3.15), cushion

exposure (Table 3.17) or vegetation community type (Table 3.18). If wind were responsible for Type 3 damage, the damage would have been associated with the more windward sectors of cushions, exposed cushions in general, and fjaeldmark, as illustrated for Type 1 damage (Section 4.1.1). These associations would have been inverted if rabbits were responsible, as described for Type 2 damage (Section 4.1.2).

An increase in ultraviolet-B radiation (UV-B, 280 – 320 nm) intensity (Frederick *et al.* 1994; Rousseaux *et al.* 1998, 1999, 2001; McKenzie *et al.* 1999) has been implicated in plant damage in the subantarctic and Antarctic (Rousseaux *et al.* 1998, 1999, 2001). However, this is also unlikely to be the cause of Type 3 damage, as Type 3 damage was not significantly associated with the northern sectors of the cushions (Table 3.20; Figures 3.14 – 3.15), which are the sectors that receive the most direct solar radiation due to the domed cushion shape (Auslander *et al.* 2003). In addition, the effects of increased UV-B radiation were found to be less dramatic in cushion plants (Day *et al.* 1999; 2001) and in vascular plants in general than in non-vascular plants (Searles *et al.* 2002).

Frost is also unlikely to have caused Type 3 damage, which is shown in the lack of association of the damage type with fjaeldmark or exposed cushions (Tables 3.17 – 3.18). Frost damage is usually associated with environments that are exposed to greater extremes of temperature (Neuner *et al.* 1999; Bannister *et al.* 2005). However, cushion plants are usually frost resistant (Bannister *et al.* 2005). It could be suggested that frost damage in cushion plants would be more associated with cushions in the less exposed herbfield because the cushions growing there may have a lower frost resistance (Larcher *et al.* 2010), but this hypothesis remains unsupported because Type 3 damage was not found to be significantly different between vegetation community types or cushion exposure levels.

Although soil moisture content, total soil depth, elevation, and topographic position were not specifically measured for Type 3 damage, drought is also unlikely to be the cause of Type 3 damage. This is because the damage was

not observed to be associated with the elevated centres of the cushions (Tables 3.20 – 3.21; Figure 3.14), which would be the sector of the cushion most obviously affected if it were caused by drought (Lookingbill and Urban 2004). The association of Type 3 damage with soil as the cushion substrate rather than gravel (Table 3.16) also suggests that drought is unlikely to be the cause. The effects of drought are usually more pronounced in gravelly soils because of their lower moisture storage capacity in comparison to finer-textured soils (Paruelo et al. 1988). However, the cushion substrate type does not necessarily indicate homogeneity of the soil profile below it. Therefore it is possible for gravel surfaces to have underlying soil. Soils situated beneath a layer of gravel, at any depth, have been found to contain significantly more moisture than soils without a gravel layer (Pérez 1998, 2009; Zavala et al. 2010).

The observed temporal variation in occurrence of the damage type suggests that it is spreading between cushions that were not in direct contact with each other above the soil surface (Figure 3.20 and Figures A.1 – A.4 in Appendix). Such a mode of spread is consistent with the association of Type 3 damage with soil characteristics. The variation of the incidence of the damage from complete absence to distinct domination (Figure 3.9), combined with the lack of any association with variables apart from soil, suggests that the cause of Type 3 damage might be a pathogen.

Gilligan (1995) notes that soil-borne pathogen-affected plants are patchy in their incidence and associated with edaphic variation. It has also been observed that the patchiness of pathogen distribution is largely a result of the dispersal dynamics of the pathogen, which is a function of the variability in pathogen infectivity and host susceptibility in the primary and secondary infection phases (Burdon et al. 1989; Kleczkowski et al. 1997; Kleczkowski and Gilligan 2007).

The possibility of Type 3 damage being caused by a pathogen is further supported by its physical characteristics. The leaflets were discoloured but remained physically intact (Figure 2.7), indicating a possibility the cause was

not external mechanical damage, but rather a failure of internal functions. A yellow discolouration of leaf tissue has been previously observed in pathogen-affected plants (Tamada and Baba 1973; Trapero-Casas and Jiménez-Díaz 1985). Brown discolourations have been observed in other cases (Scortichini and Lazzari 1996; Unger *et al.* 2005; Bobev *et al.* 2009), and a variety of discolourations ranging from yellow to brown in still others (Johnson and Littrell 1969; Fradin and Thomma 2006).

However, the yellowing and browning of plant tissue is also associated with nitrogen deficiency (Mulder 1948; Drew and Sisworo 1977; Schulze *et al.* 1994; Diaz *et al.* 2006) and waterlogging (Kramer 1951; Drew and Sisworo 1977; Kozlowski 1984; Kramer and Boyer 1995), both of which raise interesting questions to be discussed in Section 4.4.1.

4.2 What could be responsible for the putative accelerated dieback?

Care needs to be taken in attributing putative increased dieback in cushions to supposed causes on the basis of their associations with dieback, as association cannot separate cause and consequence (Kirkpatrick 2009). The direction of causation between the dieback and the different damage types may be uni-directional, however, the possibility of it being multi-directional cannot be fully rejected. This is because ecosystems have a tendency to form dynamic, complex, cyclic relationships between their different components (Austin *et al.* 1984; Cavieres *et al.* 2006; le Roux and McGeoch 2008). The complexities of these relationships are perhaps amplified in sensitive ecosystems, such as those of the subantarctic (Whinam and Copson 2006; Yeloff *et al.* 2007).

The task of determining causality may never fully succeed. This is because when the cushion plant is examined *in situ*, it is extremely difficult to completely control for confounding variables when attempting to identify the level of influence of different factors on cushion health. Because of the

nature of the cushion plant, *ex situ* experiments to resolve this problem may be confounded by unrealistic growing conditions (Hauri and Schröter 1914; Whitehead 1954, 1959). Nevertheless, it is possible to determine the most likely cause or causes of putatively accelerating damage with any set of data, and to eliminate some possibilities.

One possible approach is to regard the damage type with the highest means of percentage damage for each of the cushion health classes as responsible for the putative accelerated dieback, because the damage type that is most associated with unhealthy cushions is the damage type most responsible for the overall health of the cushions (Holland 1986). Wind would therefore be adopted as the main cause of change (Tables 3.14 – 3.15), supported by the association between cushion health and cushion exposure (Table 3.12), and by a long-term and short-term increase in wind speed interpreted by Whinam and Copson (2006) from the station meteorological data. However, wind (Type 1) damage was not observed to have increased dramatically in cushion plants over the period of austral spring 2009 to austral autumn 2010 (Figure 3.19). Thus, changes in wind regimes are unlikely to be responsible for the observed rapid rate of decline in cushion health, unless mortality from changes in wind climate has occurred in the recent past, and a new equilibrium has been established.

Another possible approach is to regard the damage type with the lowest mean percentage damage in healthy cushions as responsible for the putative accelerated dieback. Where there is an increase in percentage damage from healthy to unhealthy cushions, the damage type that is the least associated with healthy cushions may be the damage type most responsible for the overall health of the cushions (Holland 1986). According to this approach it would seem that Type 3 damage would be most responsible for the dieback crisis (Table 3.15). However, if this were correct it could reasonably be expected that Type 3 damage would also be the most prevalent damage type in unhealthy cushions, which is not the case (Table 3.15). A possible explanation for this is that unhealthy plants have decreased structural integrity, increasing their susceptibility to Type 1 damage. Because of the

physical characteristics of Type 1 damage, where the leaves are completely removed (Figure 2.7), it is possible that evidence of original Type 3 damage was lost.

The hypothesis that Type 3 damage is responsible for the putative accelerated dieback is supported by the rapid increase in area affected by Type 3 damage in particular cushions observed over the period of austral spring 2009 to austral autumn 2010 (Figure 3.20 and Figures A.1 – A.4 in Appendix). However, it must be noted that older photographic evidence (P. Selkirk pers. comm. 2010; Figure 1.6) indicates that similar patterns, with potentially similar rates of increase, have been observed in the past without the declaration of a biodiversity emergency.

Another possible approach to determining the damage type most responsible for the putative accelerated dieback is to consider the combination of damage types. This is because it may be suggested that damage as a whole affects cushion health more than each of the damage types on their own (Lichtenthaler 1996, 1998).

Alternatively, there may be a fourth damage type which has been inadvertently misclassified or excluded from the present study. This is unlikely, but it is possible that the putative accelerated dieback is unrelated to damage types 1, 2 and 3.

It may be suggested that damage evident on the cushions is a symptom of, not a contributor to, cushion health (Pertot and Vindimian 1998), with wind, rabbit and pathogen damage more evident upon the already weakened. If this were the case, damage could be used as an indicator of cushion health, but none of the causes of the measured damage types could be held responsible for the putative accelerated dieback. In this instance, other possible explanations for the direct cause of the perceived dieback crisis could include factors such as drought, frost, increased temperatures, and increased competition. However, these possibilities are inconsistent with the existing evidence.

Despite an observed increase in rainfall, an observed change in annual rainfall patterns from relatively constant mist and drizzle to heavier rainfall events (Brothers and Bone 2008) has caused drought to be of potential concern to the well-being of the island's vegetation (Bergstrom et al. 2006; Whinam and Copson 2006). However, drought is unlikely to be the cause of the dieback crisis because of the lack of association between cushion health and elevation and/or topography (Figures 3.5a, 3.5b and 3.7), which would be present if drought were the cause. In drought-affected areas plants are usually healthier in depressions, where there is increased soil moisture in comparison to rises (Lookingbill and Urban 2004).

Soil surface frost action, as observed in Bunt (1954), Taylor (1955a, 1955b), Löffler et al. (1983), and Selkirk (1998), could also be the cause of the dieback crisis. However, according to climatic data, the annual mean minimum ground surface temperatures have increased by 0.02 °C between the 30 year periods of 1951-1980 and 1981-2010 (Bureau of Meteorology 2010). Also, when adjusted to represent temperatures for the island's plateau by applying the approximate lapse rate calculated for the island (Taylor 1955b; Jenkin 1975), the coldest mean monthly ground temperature was -2 °C, which is not cold enough for deep frost penetration (Troll 1960; Hinzman et al. 1998), let alone cold enough to result in frost upheaval of cushions (Perfect et al. 1988), a phenomenon the obvious outcomes of which were not observed in the present study. In addition, it has been found that the domed shape of the cushion moderates temperatures (Goldstein and Meinzer 1983; Wilson et al. 1987; Smith et al. 1995; Körner 1999; Arroyo et al. 2003; Nyakatya and McGeoch 2008; Haussmann, Boelhouwers and McGeoch 2009) to the extent that other plant species epiphytically seek refuge (Alliende and Hoffmann 1985; Arroyo et al. 2003; Cavieres et al. 2005, 2007; Fajardo et al. 2008; Arredondo-Nunez et al. 2009).

It may also be suggested that an increase in long-term air temperatures (Adamson et al. 1988, Tweedie and Bergstrom 2000; Whinam and Copson 2006; Pendlebury and Barnes-Keoghan 2007) could be the cause of the dieback crisis. However, an increase in air temperature is unlikely to be the

cause of the dieback crisis because of the lack of association between cushion health and altitude, which would be present if warming were the cause (Smith and Mucina 2006; le Roux and McGeoch 2008).

Increases in rabbit grazing have led to decreases in vegetation cover and increases in mass movement (Taylor 1955b; Scott and Kirkpatrick 2008). Localised increases in ground surface temperature as a result of potential increases in radiation absorption and decreases in heat retention because of decreased vegetation cover (Hughes et al. 2006; Cannone and Guglielmin 2009) could be the cause of the dieback crisis. Although variations in temperature data across the plateau cannot be determined from climatic data for the island because of data collection being limited to the station isthmus, these localised changes may account for the spatial variation in cushion health. However, this is unlikely to be the cause of the dieback crisis because of the lack of association between cushion health and vegetation community type (Table 3.12).

Increased competition is another possible explanation for the putative accelerated dieback. Either as a result of the range expansion of other native species (Smith and Mucina 2006; le Roux and McGeoch 2008) or of the introduction of alien species (Scott and Kirkpatrick 2005, 2008; Whinam et al. 2005), increased competition has been considered a potential threat to certain subantarctic plant species (Bergstrom and Chown 1999; Whinam et al. 2005). Hauri and Schröter (1914) observed that full light exposure was essential to cushion plants as shaded portions would die out. However, cushion plants have also been observed to be positively associated with other plants, especially in more stressful environments such as the typical fjaeldmark environment (Selkirk et al. 1990; Carlsson and Callaghan 1991; Choler et al. 2001; Arroyo et al. 2003; Klanderud and Totland 2005; Fajardo et al. 2008; le Roux and McGeoch 2008). In addition, if increased competition were the cause of the putative accelerated dieback, cushion health would have been found to be poorer in herbfield where a greater number of other plant species occur (Table 3.12). Therefore, unless the fjaeldmark environment of Macquarie Island has become less stressful, causing the

benefits of negative interactions to outweigh the benefits of positive interactions, which is indeed possible (le Roux and McGeoch 2008), it is unlikely that increased competition is the cause of the putative accelerated dieback.

4.3 Is there convincing evidence for accelerated dieback?

Ubiquitous accelerated cushion dieback on Macquarie Island has not been established with any certainty by the present study or by previous observations. Certainty needs to be established through continued fine-scale monitoring.

Dieback is a natural process that has been observed to be common in cushion plants (Taylor 1955b; Armesto *et al.* 1980; Kleier and Rundel 2004). Occurring partially or fully, it has been considered to be an aspect of phenology (Taylor 1955b; Kleier and Rundel 2004) and possibly a result of a mortality trade-off (Forbis and Doak 2004). If there is an abnormal increase in dieback occurrence, it could be a peak in natural fluctuations.

Mortality has been found to have a significant positive correlation with age (Hegazy 1992; Kleier and Rundel 2004). Therefore, if the population structure of the cushion plant consists of an inflated oldest-age class, perhaps the phenomenon is caused by an increase in age-related mortality. However, such variability in the population dynamics is unlikely because longer life-spans in perennial plant species have been found to be correlated with population stability (Garcia *et al.* 2008). In addition, it is possible for older dead cushions that have remained intact to be labelled as victims of the dieback cause, even if the actual cause is completely unrelated.

A combination of only one of the above causes of apparently accelerated mortality with a limited spread of a pathogen could have caused a perception of accelerated dieback.

If there is accelerated dieback, it may not be a terminal decline. It should be noted that cushions have shown signs of recovery (J. Whinam and T. Rudman, pers. comm. 2010). In the course of the present study, regrowth has been observed to occur in some affected individuals (Figure 4.1), whilst others have been observed to be colonised by new cushions (Figure 4.2).
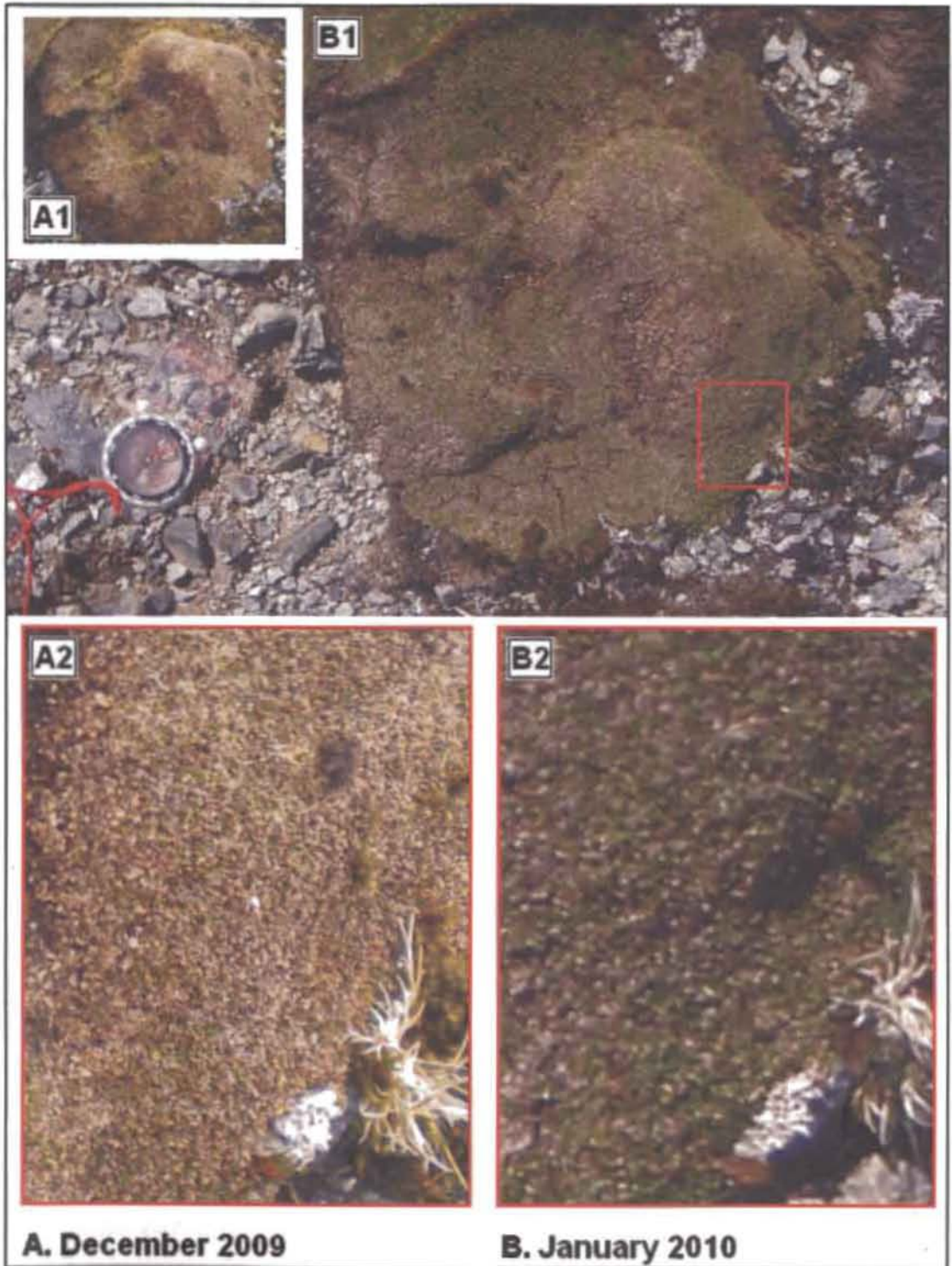
Figure 4.1: Signs of regrowth of a dieback-affected cushion plant from December 2009 to January 2010. The inset at the top left shows the cushion as it appeared in December 2009 and the larger image shows the cushion as it appeared in January 2010. Detail of the regrowth is magnified in the images at the bottom. Scale is indicated by the compass, which is approximately 12.5 cm in length. Photographs by Jared Abdul-Rahman.

Figure 4.2: Possible signs of colonisation of a dieback-affected cushion plant by new individuals. Detail of the colonisation is magnified in the inset at the bottom right of the image. Scale is indicated by the compass, which is approximately 12.5 cm in length. Photograph by Jared Abdul-Rahman.

4.4 Recommendations

4.4.1 Research

Research devoted to filling the gaps in knowledge outlined above is needed before we can be certain of a cushion dieback crisis or fully understand its causes. For example, as mentioned in Section 4.1.3, the known association of plant tissue discolouration with water-logging and nitrogen deficiency raises interesting questions. Yellowing caused by waterlogging is pertinent because of the increased annual rainfall and change in trend from constant mist and drizzle to heavy rainfall events (Brothers and Bone 2008).

Yellowing potentially caused by a nitrogen deficiency is also relevant

because in comparison to other areas on the island, the plateau has been associated with significant nitrogen fixation because of the nitrogen-fixing mosses, lichens and liverworts that occur there (Line 1992). In addition, although attention to the dieback crisis has mainly focused on its effect on *A. macquariensis*, it has also been attributed to mosses (Parks and Wildlife Service 2009). If nitrogen-deficiency is somehow involved in this mystery, the dieback's effect on the mosses is also worth investigating.

All possible explanations for the perceived dieback crisis are worth investigating. Because considerable expense would be associated with any attempt to rescue the cushion plant species, it would be prudent to establish the main contributing factors to the accelerated dieback, if indeed it exists.

4.4.2 Management

Until further investigations reveal more definite answers, the current worst-case scenario quarantine approach is wise. Thorough quarantine practices are essential to prevent the spread of a potential pathogen across the island and between islands. However, perhaps the use of the disinfectant Antec Virkon S® in quarantine practices on Macquarie Island should be considered. Virkon® has been measured to have a significant level of phytotoxicity (Avikainen, Kopenen, Meinander and Tahvonen 1993; Stijger 1999; Celar *et al.* 2007; Howard *et al.* 2007). As a result it has been recommended for use only when plants are not present (Hayes 2008). It may be argued that the concentration at which Virkon® is being used (1 %) is too low to be significantly phytotoxic. However, the same argument can be used in relation to its level of efficacy (Avikainen, Kopenen and Tahvonen 1993; Stijger 1999; Celar *et al.* 2007; Howard *et al.* 2007).

4.4.3 Rehabilitation

If the dieback is as critical as originally assumed, *in situ* rehabilitation should be concentrated on plants with characteristics that are associated with resistance to the dieback. For example, if Type 3 damage is the cause of the dieback, rehabilitation is likely to be more successful where cushions have a gravel substrate. It is likely that ex situ rehabilitation could also benefit from mimicking these conditions.

4.4.4 Monitoring

The characteristics of the dieback, as described in this study, are only representative of the changes over one summer growing season. They do not provide any insight into the variations that may occur in the winter senescent season or in any other summer growing season. More extensive, longer-term monitoring of these changes, especially the changes attributed to Type 3 damage, is needed.

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Appendix

Additional maps and descriptions of Type 3 damage

Site 4 had sixteen cushions, all of which were affected by Type 3 damage by late March (Figure A.1).
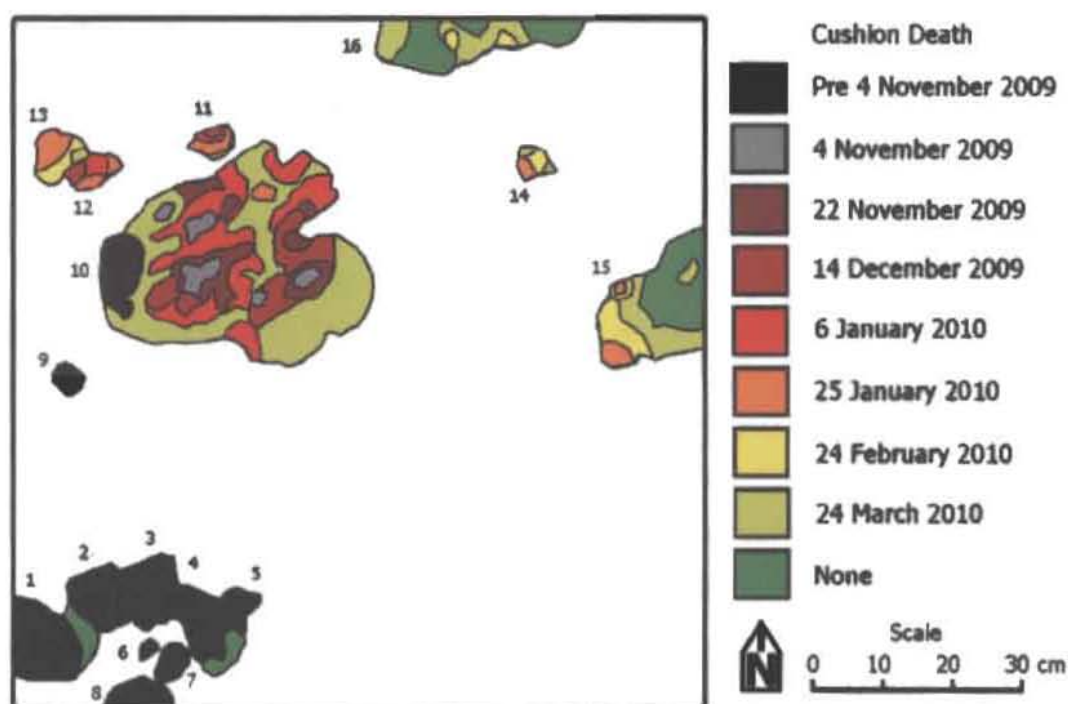

Figure A.1: The spread of Type 3 damage at site 4. Numbers indicate individual cushions.

The first sign of death was observed in cushions 1 to 10 in the south-west sector of the site, at the time of the first visit in early November. Cushions 1 and 5 were partially undamaged, cushion 10 was only partially damaged, and the rest were completely damaged. Apart from patchy damage in the centre of cushion 10, the other damage appeared to be old. In late November, the patchy damage in the centre of cushion 10 had spread to form larger patches and new patches occurred. In mid December, several patches of the damage on cushion 10 had spread further and linked, and damage occurred on cushions 11 and 12, to the north and north-west of cushion 10. In early January, the patches of damage on cushion 10 extended further and two new patches occurred in the north and south, affecting approximately half of the

cushion. The damage on cushion 11 had spread southward, and on cushion 12 it had spread eastward. In late January, most of cushion 11 and the rest of cushion 12 had become damaged. Only one new patch of damage formed on cushion 10, and damage occurred on three new cushions, cushions 13, 14 and 15. The damage on cushion 15 occurred in two patches. In late February, most of cushions 13 and 14 had become affected by the damage, and the two patches on cushion 15 had spread further and linked together. Damage occurred in two patches on the south sector of cushion 16 to the north. No further damage occurred on cushions 10 and 11. By late March, the damage had spread further and completely affected cushion 10, 11, 13 and 14. The damage on cushions 15 and 16 had also spread further, with a new patch occurring on each cushion, but there were areas that had remained unaffected. The unaffected areas on cushion 1 and 5 had remained unaffected throughout all the observation periods.

The area of onset varied between cushions. Cushion 10 was first affected on its centre, cushion 11 was first affected on its north sector, cushions 12 and 13 were first affected on their west/north-west sectors, cushions 14 and 15 were first affected on their south-west/west sector, and cushion 16 was first affected on its south sector. Type 3 damage appeared to have a contagion effect at this site, spreading radially between cushions as far as approximately 30 cm apart. However, according to the pattern of points of first occurrence, the damage appeared to have multiple sources. Not including the distance between cushions, Type 3 damage had spread the furthest during the period of late February to late March, and least during the period of early to late November.

Site 10 had four cushions, three of which were affected by Type 3 damage by late March (Figure A.2).
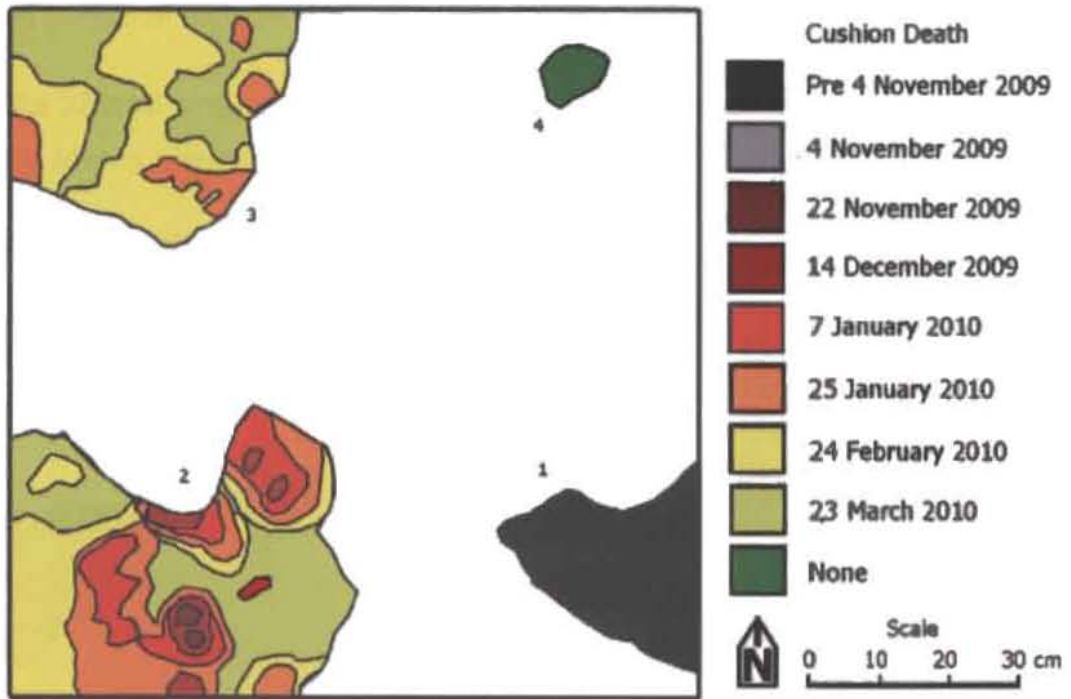
Figure A.2: The spread of Type 3 damage at site 10. Numbers indicate individual cushions.

The first sign of death was observed in cushion 1 in the south-east sector of the site, having already died by the time of the first visit in early November. In late November, cushion 2 showed death in two patches on its centre. In mid December, the death on cushion 2 had spread radially from the centre and had appeared in new patches in the north, north-west and south sectors of the cushion. In early January, the death all patches except for the one in the south sector had spread further and formed larger patches. In late January, the death had spread radially further on cushion 2 and it had appeared on cushion 3 in the north-east sector of the site. In late February, the death had radiated further and spread to approximately half of cushions 2 and 3. By late March, cushions 2 and 3 had become completely affected and only cushion 4 in the north-east sector of the site had remained unaffected.

The area of onset varied between cushions. Cushion 2 was first affected on its centre, and cushion 3 was first affected in patches along its edges. Type 3 damage appeared to have a contagion effect at this site, spreading radially between cushions as far as approximately 25 cm apart. Death had spread the most during the period of late February to late March, and least during

the period of early November to late November.

Site 33 had nine cushions, all of which were affected by Type 3 damage by late March (Figure A.3).
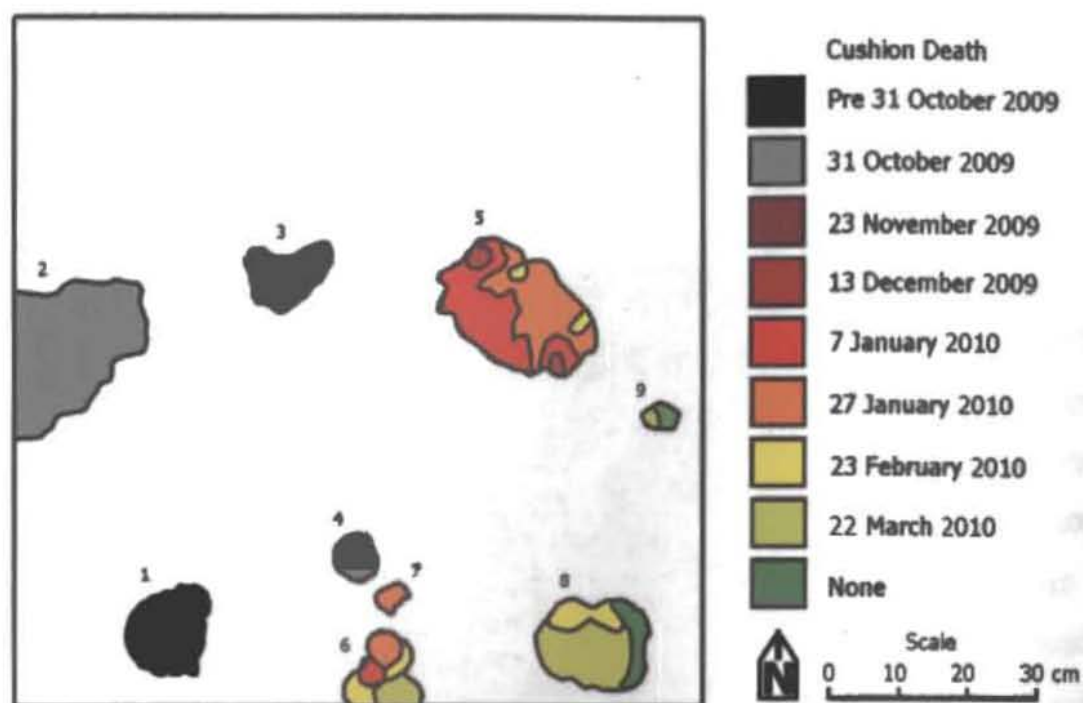

Figure A.3: The spread of Type 3 damage at site 33. Numbers indicate individual cushions.

The first sign of death was observed in four cushions at the time of the first visit in late October. Cushion 1 in the south-west sector of the site appeared to have died earlier than cushions 2, 3 and 4. In mid December, Type 3 damage had appeared on the north-west and south-east sectors of cushion 5. In early January, the death had occurred to the south-western half of cushion 5 and had appeared on cushion 6. In late January, the damage had spread to most of cushion 5, spread northwards on cushion 6, and it had appeared on cushion 7. In late February, it had spread to the rest of cushion 5, the whole north-western half of cushion 6, and the north sector of cushion 8. By late March, it had spread to the rest of cushion 6, the south sector of cushion 8, and the west sector of cushion 9. Only the east sectors of cushions 8 and 9 had remained unaffected by Type 3 damage.

The area of onset varied between cushions. The cushion sectors that first showed signs of the damage appeared to have been the sector closest to the affected neighbouring cushion. Type 3 damage appeared to have a contagion effect at this site, spreading between cushions as far as approximately 30 cm apart, in a south-westerly/westerly direction. Death had spread the most during the period of early to late January, and least during the period of early to late November.
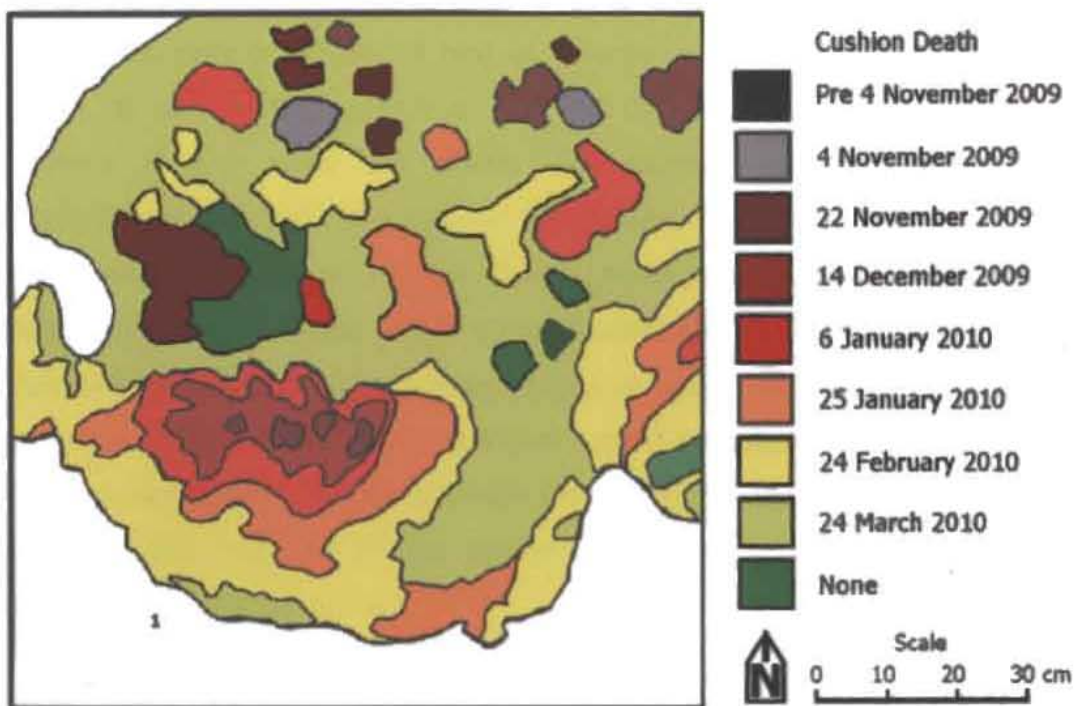
Site 38 only had one cushion (Figure A.4).

Figure A.4: The spread of Type 3 damage at site 38. Numbers indicate individual cushions.

The first sign of death was observed to have occurred in two patches in the centre of the cushion at the time of the first visit in early November. One patch was towards the north and the other towards the north-east. In late November, thirteen more patches had formed across the centre of the cushion. Of these patches, eight were in the north sector, four towards the south, and one larger patch was in the west sector. In mid December the four patches in the centre towards the south had spread and linked to form one large patch. In early January, this larger patch had spread further, and four

new patches had occurred. Of these new patches, three were across the centre and one was in the east sector. In late January, the large patch in the centre and the patch in the east sector had spread further, and three new patches had occurred. Of these new patches, two were in the centre and one was in the south sector. In late February, most of the southern half of the cushion had been affected, and five new patches had occurred across the northern half of the cushion centre. By late March, almost the entire cushion had been affected, with only four patches in the centre and one in the east sector having remained unaffected.

As the site only consisted of part of a large cushion, observations on the health of surrounding cushions and the direction of spread outside the cushion, if any, were not made. The damage did not seem to be concentrated to a particular area on the cushion. It showed signs of having a contagion effect in the southern half of the cushion, appearing to have spread from two main sources, in a south/south-westerly direction from each. However, the damage also showed signs of occurring randomly across the northern half of the cushion where it occurred as isolated patches, with new patches having formed by each visit. Death had spread the most during the period of late February to late March, and least during the period of late November to mid December.