Explaining the coexistence of species in mosaic cushion heath

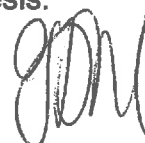by

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Submitted in fulfilment of the requirements for the degree of Master of Environmental Studies, School of Geography and Environmental Studies, University of Tasmania (November 2012).

Declaration

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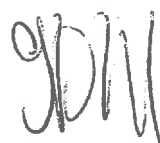
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Annotation

This thesis is an uncorrected text as submitted for examination.

Abstract

Cushion plants can occur in two-dimensional mosaics of species, which have been shown to be stable in their proportions of species, but unstable in their patterns (Gibson and Kirkpatrick 1992). Possible causes of this state of quasi-stability were explored for a cushion mosaic composed of four principal species, *Pterygopappus lawrencii*, *Abrotanella forsteroides*, *Dracophyllum minimum* and *Oreobolus pumilio* at Mount Field National Park, Tasmania. An area of a cushion mosaic was selected, the topography measured, temperature readings taken under different synoptic conditions and the ability of the two most common species, *Pterygopappus lawrencii* and *Abrotanella forsteroides* to repel moisture measured. Slope, aspect and radiation input in clear sky conditions were calculated for the 418 grid points at which topography and temperature were measured and the species noted. The differences between species in their distributions at the study site were related to slope, aspect, elevation, clear sky radiation input and temperature adjusted for radiation and slope. Chi-squared was used to determine the significance of differences between species for misting and droplet treatments. *O. pumilio* was associated with steep slopes and lower radiation inputs. *P. lawrencii* was at lower elevations than *A. forsteroides*. Water beaded on the surface of *P. lawrencii* at a higher rate than on *A. forsteroides*, regardless of drop size. Temperature alone was found to be a poor indicator of species occurrence. Species switched their temperature rankings in different weather conditions. To conclude, the data most closely fit a model of temporal environmental fluctuations with continuous competition. Differential

cushion growth appears to lead to variation in topography and therefore differences in interception of radiation. This negative feedback mechanism may be contributing to the perpetuation of coexistence.

Acknowledgment

Thank you Damien, for the help with the statistical explanations.

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Chapter 1   Introduction

Cushion plants

Cushion plants are an unusual and important life-form. They are a world-wide phenomenon, found in both northern and southern hemispheres. The cushion form is found in a wide variety of environments, from sea level to high alpine zones in New Zealand (Mark and Bliss 1970; Gibson 1988; Wardle 1991), sub-alpine and alpine areas of Australia (Kirkpatrick 1983; Gibson and Hope 1986; Gibson 1988), cushion mire or bogs to dry tundra in South America (Hodge 1946; Pisano 1983; Bosman, Molen et al. 1993), Europe (Billings 1974; Körner 1999) and North America (Bliss 1971; Huntly 1987).

The general name cushion plant encompasses those plants, which exhibit a compact flat to hemispherical growth habit. The cushion form was classified by Rauh (Rauh 1939) into 12 basic types, which included mosses, graminoids, herbs, shrubs and trees. They are hemicryptophytes or chamaephytes, with short internodes and closely packed shoots (Gibson and Kirkpatrick 1985), which form compact cushions. The growth form may be obligate (Spomer 1964; Körner 1999) or facultative (Parsons and Gibson 2009).

The cushion form is found in a large number of species in taxonomically disparate groups. There are 60 species in Australia that are described as cushion plants (Parsons and Gibson 2009).

The cushion form has the ability to ameliorate the microclimate (Gibson and Hope 1986) and is notable for increasing temperatures above that of ambient air temperature (Körner 1999). Cushions can act as a 'nursery' to other species by providing a suitable microclimate for seedlings to establish or shelter for insects (Alliende and Hoffmann 1985; Kirkpatrick, Minchin et al. 1985; Cavieres, Arroyo et al. 2002; Molina-Montenegro, Badano et al. 2006; Cavieres, Badano et al. 2007). Cushion species play an important role in the environments in which they are found, as a food source (Huntly 1987), as stabilisers of slopes, and as early colonisers. Cushion plants can vary in size, with some individuals growing to 3 m in diameter (Gibson and Kirkpatrick 1985).

Cushion mosaics

In some instances, individuals may coalesce to form a mosaic of different species (Gibson 1988). It is these two-dimensional mosaics of species and the nature of their persistence within the environment that is of particular interest in this thesis.

The particular state of co-occurrence in complex mosaics seems peculiar to the alpine areas of Tasmania, Australia. Cushion mosaics in Tasmania were found to be persistent through time; Gibson (Gibson 1988) calculating from fossil evidence that a particular cushion mosaic has existed on the study site for 850 years.

Vegetation mosaics are described in the literature, principally as large scale mixtures of vegetation, bare earth and rock. The cushion mosaics described in Turkey are hard cushions within a larger vegetation mosaic (Arslan, Guleryuz et al. 1999), which is unlike the mosaic assemblage of different cushion plant species in Tasmania. Gimingham et al. (Gimingham, Pritchard et al. 1966) describes a vegetation mosaic on the island of Gotland, in the Baltic Sea. This is an intricate mosaic of patches occupied by small groups of cushion mosses and bare ground that has similarities to the cushion mosaic. However, this is considered to be a seral continuum, which is a colonisation of bare ground and re-colonisation of formerly grazed areas, rather than a stable, persistent cushion mosaic. Muc and Bliss (1987) describe cushion moss, cushion lichen and dwarf shrub heath on Truelove Lowland, in Canada as species forming a mosaic pattern in the landscape.

Explanations for persistent mosaics

Individual species interact with each other within communities. The mechanisms of these interactions can be classified in a number of ways, for example, through predation, herbivory, parasitism, mutualism, disease interactions and competition (Krebs 2009). Competition can be further characterised as resource competition, where competing individuals are equally affected, and interference competition, where competing individuals harm each other seeking a resource, even if that resource is not in short supply (Birch 1957; Booth, Murray et al. 2008). Plants may compete for light, space, pollinators, nutrients and water.

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Competition for resources has been modelled mathematically with the Lotka-Volterra equations (Lotka 1925; Volterra 1926). Using this equation, and comparing two competing populations, there are three possible outcomes, either species one or species two becomes extinct if one species has a strong suppressing effect upon the other, if neither species has a strong effect upon the other, both will coexist. Interactions within plant communities may be further classified as equilibrium (Tilman 1977; Tilman 1982; Tilman 1988) or non-equilibrium (Chesson 1986). In competing animal species, by introducing very slight variations in the environment, or very slight differences in species habitats, coexistence can occur between animal species under laboratory conditions (Krebs 2009). This has been posited to have happened in nature with *Eucalyptus regnans* and *E. obliqua* (Ashton and Gill 1965; Wilson 1988).

An alternative hypothesis for co-existence in the one area is that the different species are occupying subtly different microhabitats or niches. In another example using *Eucalyptus*, *E. tenuiramis* and *E. obliqua* were shown to occupy distinct microhabitats (Battaglia and Williams 1996).

Comparative autecology of co-existing cushion species

The physical constraints of the environment are a principal factor in determining how alpine species sort themselves out in the landscape (Körner 1999). Thus, for those species, which are able to survive the conditions experienced in alpine environments, seemingly harsh is not harsh at all. This is certainly the case with the four species that co-exist in the mosaic cushion

that is the subject of this thesis. These are *Abrotanella forsteroides*, *Dracophyllum minimum*, *Oreobolus pumilio* and *Pterygopappus lawrencii* (Figures 1.1 to 1.4).

Pterygopappus lawrencii and *A. forsteroides* are both from the family Asteraceae, while *D. minimum* is from the family Ericaceae and *O. pumilio* is from the family Cyperaceae. *Pterygopappus lawrencii*, *A. forsteroides* and *D. minimum* are endemic to Tasmania (Curtis 1963), while *O. pumilio* is also found in New Guinea and on the Australian mainland (Kirkpatrick 1997). The Genus *Abrotanella* includes 20 species from Australia, New Guinea, New Zealand and South America (Swenson 1995; Swenson and Bremer 1997). *Abrotanella forsteroides* is a tetraploid species (Swenson 1995).

Figure 1-1 *Pterygopappus lawrencii*. Leaf size is 3 mm long (Photograph courtesy of Field Botany, University of Tasmania).

Figure 1-2 *Abrotanella forsteroides*. Leaf size is 2-4 mm long (Photograph courtesy of Australian National Botanical Gardens).

Figure 1-3 *Dracophyllum minimum*. Leaf size is 2-6 mm long (Photograph courtesy of Field Botany, University of Tasmania).

Variation in communities containing cushion plants in Tasmania is strongly related to a southwest to northeast edaphic and precipitation gradient, and to altitude (Minchin 1983; Kirkpatrick, Minchin et al. 1985). High altitude alpine communities and those on oligotrophic poorly-drained soils are most likely to be dominated by cushion species (Minchin 1983; Kirkpatrick, Minchin et al. 1985).
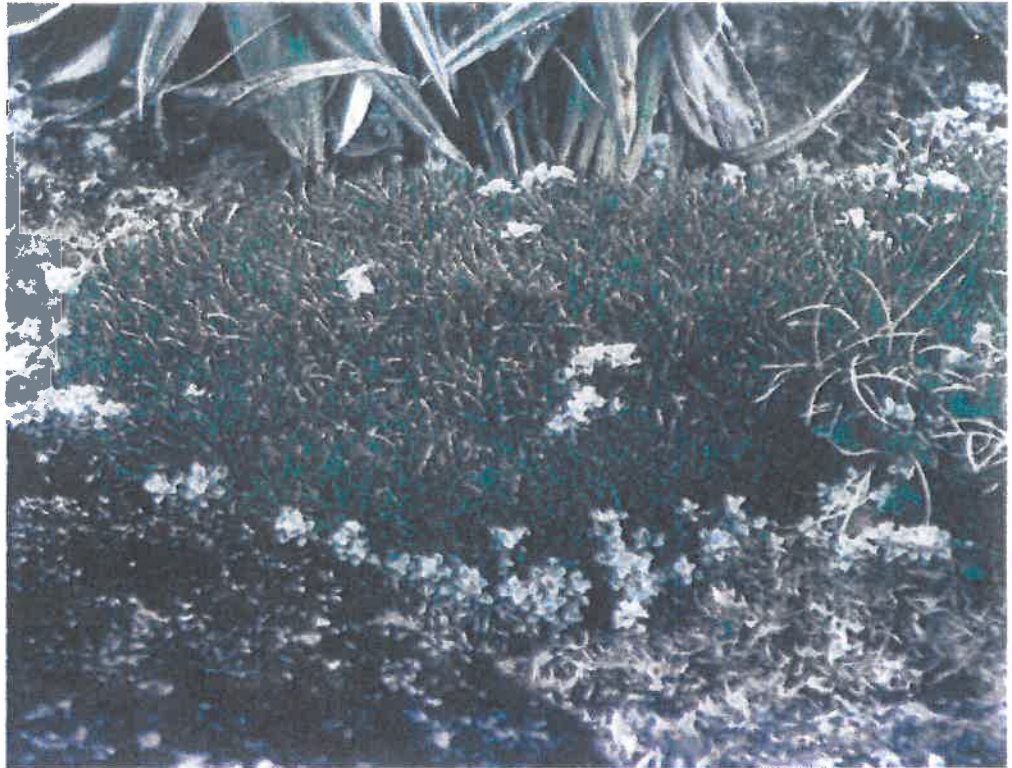
Figure 1-4 *Oreobolus pumilio.* Leaf size is 5-10 mm long (Photograph courtesy of Field Botany, University of Tasmania).

Cushion species are good indicators of poorly-drained soil (Kirkpatrick and Dickinson 1984; Kirkpatrick and Bridle 1999). The distribution of cushion plant mosaic heath is primarily alpine above the climatic treeline, whereas cushion heaths dominated by individual species extend into subalpine treeless areas (Gibson, Kiernan et al. 1987).

Abrotanella forsteroides and *D. minimum* are highly frequent dominants of cushion heath, and have overlapping geographic ranges (Kirkpatrick, Minchin et al. 1985). Mt. Field National Park is one of the few places where both *A. forsteroides* and *D. minimum* are found together (Kirkpatrick, Minchin et al. 1985). *Abrotanella forsteroides* and *D. minimum* are superficially

morphologically very similar, although the former species is dark green and has a hair on its leaf tips and the latter species has blunt leaf tips and reddish-green foliage (Kirkpatrick 1997). *D. minimum* is a shrub with a well-developed taproot, while *A. forsteroides* is an herb. They have slightly overlapping budding, flowering and seed set patterns, however the peak times for seed dispersal occurs separately (Gibson 1988).

Pterygopappus lawrencii has some morphological similarities to both *A. forsteroides* and *D. minimum*. For example, all of these species have leaves which are densely packed, imbricate, and are retained on the stem after death (Curtis 1963). However, there are some strong differences. *Pterygopappus lawrencii* leaves have transverse bands of densely packed hairs, and are a grey-green colour. This contrasts with *A. forsteroides* and *D. minimum,* the leaves of which are glabrous. *Pterygopappus lawrencii* does not have a taproot (Gibson and Hope 1986).

Oreobolus pumilio has flattened, glabrous leaves that protrude slightly above the cushion mosaic surface. It is associated with poorly-drained sites, including seasonal wetlands (McVean 1969; Kirkpatrick and Gibson 1984) and extends to higher altitudes than *A. forsteroides* (Gibson and Kirkpatrick 1985).

The literature suggests that *A. forsteroides* occurs on slightly better drained situations on average, than *O. pumilio*, that *D. minimum* occurs in slightly better-drained situations on average, than *A. forsteroides* and that *P. lawrencii* is found, on average in better-drained situations than any of the

other three species (Kirkpatrick and Gibson 1984; Gibson and Kirkpatrick 1985; Gibson and Hope 1986). As ponds drain, *P. lawrencii* is the last species to survive on the oxidising organic dams (Kirkpatrick and Gibson 1984).

Pterygopappus lawrencii is usually found above the treeline, in drier areas than the other species, and is often associated with *D. minimum* (Kirkpatrick and Gibson 1984; Gibson and Kirkpatrick 1985; Gibson and Hope 1986).

Dracophyllum minimum is also usually found above the treeline (Gibson and Hope 1986), and in areas of high wind speed (Lynch and Kirkpatrick 1995). It is more resistant to trampling than other alpine species (Gibson 1984), but least resistant to fire (Kirkpatrick and Dickinson 1984). *Dracophyllum minimum* is also more able to withstand a longer duration of snow cover than other cushion mosaic species (Gibson and Kirkpatrick 1985).

Abrotanella forsteroides occurs without the other three species over much of eastern Tasmania, such as at Mt Wellington (Kirkpatrick, Bridle et al. 2002), and often in treeless vegetation in the subalpine zone, such as Wombat Moor at Mt Field (Minchin 1989). *Dracophyllum minimum* occurs without the other three species in snow patches. *Pterygopappus lawrencii* rarely occurs by itself, but when it does, it is in drier situations than those ever occupied by the other species. *Oreobolus pumilio* occurs without the other three species in wetlands. While *O. pumilio* occurs from subalpine treeless areas to the highest of tarns, *P. lawrencii* and *D. minimum* are largely confined to above the climatic treeline and *A. forsteroides* extends from treeless subalpine

areas to the lower reaches of the alpine zone (Kirkpatrick, Minchin et al. 1985).

Aims and their justification

Gibson and Kirkpatrick (Gibson and Kirkpatrick 1992) showed that a mosaic cushion heath at Mt Field remained constant in its proportions of cushion species, while species shifted considerably in their locations, over a five year period. A further ten years of monitoring reinforced this observation (Kirkpatrick and Gibson, personal communication). This proportional constancy among changing distributions in a system in which variation in the vertical dimension is subdued was unexplained. It was a particular, and simplified, case of the general question: why do species of the same lifeform coexist in space? Two specific questions were asked:

1) Can the coexistence of the cushion species be explained in terms of their responses to micro-environmental variation?

2) Is the coexistence of the species related to their differential ability to grow in different synoptic situations?

Thesis structure

In chapter two, the study area is described and the distribution of the individual species in relation to the cushion topography is analysed and discussed. Chapter three considers the variation in radiation receipt of

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individual species as related to cushion topography. Chapter four examines relative variation in the temperature of species under varying synoptic conditions. Variation in water repellence between *Pterygopappus lawrencii* and *Abrotanella forsteroides* in mist and rain is the subject of chapter five. Chapter six uses the data in chapters' two to five to assess the causes of coexistence in the cushion mosaic.

Chapter 2 Topographic relationships

Introduction

The primary aim of this chapter is to determine whether the cushion species that form mosaic cushion heath have distributions that relate to the topography of its surface. The study area is described, the methods used to map the species and topography detailed and species distributions are related to slope, altitude and aspect, as indicators of variation in moisture and exposure to potentially damaging winds. The nearest neighbour relationships of the cushion species were documented to determine whether there were any repeating species associations.

Methods

Study Area

Location

Tasmania – the island state of Australia – lies between 40 degrees south and 43.5 degrees south (Figure 2.1). The study site is situated on Mount Mawson, part of the plateau of Mount Field (Figure 2.2). The Mount Field massif is in south central Tasmania, (40 degrees 40 minutes south, 146 degrees 35 minutes east). Mount Field National Park was first created to preserve the scenic beauty of Russell Falls, with the total area of Mount Field National Park now encompassing 16 977 hectares.

Figure 2-1 Map of Tasmania showing the location of the study site, and meteorological stations.
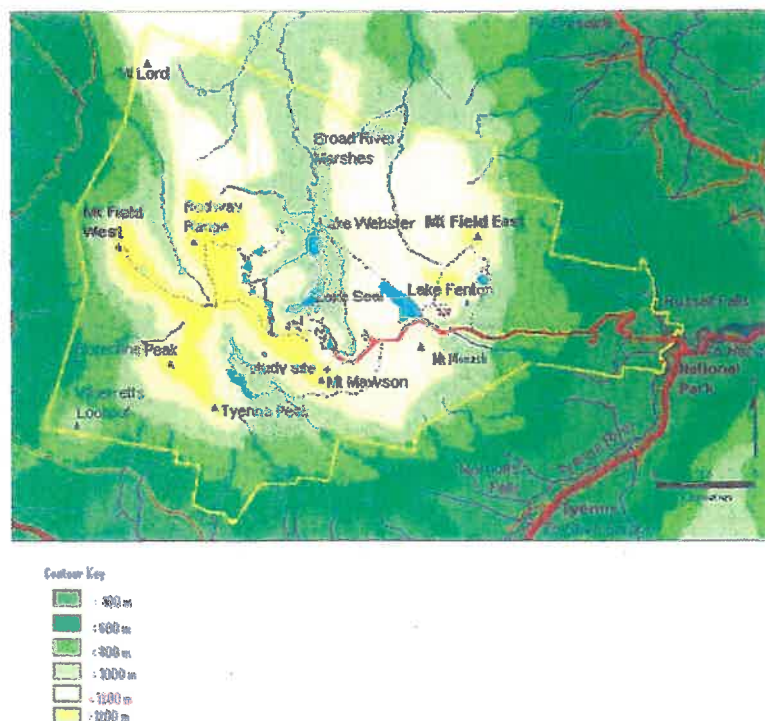
Figure 2-2 The location of the Mount Mawson Plateau within Mt Field National Park, Tasmania, the location of the study area within Mount Mawson.

Geology and Geomorphology

The Mount Field massif is a fault block, roughly triangular in shape, which is surrounded by the Derwent, Tyenna and Florentine Rivers. The plateau is formed of Jurassic dolerite, which commonly forms mountains in the eastern part of the state (Gibson 1988). The Mount Field area is part of what is known as the Tasmania Basin (Seymour and Calver 1995). The Tasmanian Basin is made up of unfolded, faulted rocks from the Carboniferous age, and younger. It includes sheets of Jurassic dolerite, and Carboniferous-Permo-Triassic age tillites, siltstones and sandstones. The tillites, siltstones and sandstones form the Parmeener Supergroup. Jurassic dolerite is almost ubiquitous above 760 metres in altitude and underlies the study site.

Tasmania was glaciated at least three times in the Quaternary (Colhoun 1985; Scanlon, Fish et al. 1990), and was the only part of Australia with significant glaciation at that time (Seppelt 1988). During the last glaciation approximately 18 to 20,000 years ago, Mount Field had a small cirque and valley glacier system, the locations of much of which are presently filled by lakes and tarns (Spanswick and Kidd 2000). During the Pleistocene, there was permanent snow cover over the entire top of Mount Field, and a series of valley glaciers were fed by this snowfield. In addition to this, there was a snowfield between Mount Mawson and Mount Monash which gave rise to the Broad River Valley Glacier, a second glacier of equal size from the Lake Seal Valley, and also a number of ice streams (Seppelt 1988). Some 6000 km^2 of Tasmania was glaciated, with about 4000 km^2 of the central plateau under an ice cap (Brown, Campbell et al. 1968). The study site on Mount Mawson is

situated where the Broad River Valley glacier originated (Seppelt 1988), so has been scraped by ice.

Soils

The soils on Mount Field are generally shallow, highly leached, and acidic, ranging in pH from 5.2 to 6.4 (at 5 and 45 cm deep respectively) (Collins 1990; Scanlon, Fish et al. 1990). The soils on the slopes of Mount Mawson belong to the Liawenee Association and have been described as yellow-brown soils. They have a shallow surface layer with an organic component, over an olive coloured, fairly compact loam or sandy loam. These horizons are underlain by strong brown friable clay loam or sandy loam. Dolerite fragments and stones are common throughout the profile, with the largest clasts being concentrated in the upper 60 centimetres (Spanswick and Kidd 2000). There is little mineral soil at the study site on the Mt Mawson Plateau, where organosols have formed on a rocky dolerite surface. Organosols are described as soils that are not regularly inundated by saline tidal waters and have organic materials extending from the surface to a minimum depth of 0.1 m, which directly overlie rock, gravel, cobbles or stones in which the interstices are filled with organic material (CSIRO The Australian Soils Classification).

Climate

Tasmania has a maritime climate, which is more temperate and equable than the mainland states of Australia, (Bond, Ryan et al. 1979; Seppelt 1988;

Meteorology 1993). This maritime climate is a product of the proximity of the surrounding ocean as there is no place in Tasmania that is more than 115 kilometres from the sea. The surrounding ocean temperatures only change by approximately 6^0C to 7^0C between seasons (Bond, Ryan et al. 1979; Meteorology 1993). This has the effect of ameliorating the temperatures experienced on land. The hilly and mountainous topography of Tasmania is climatologically influential, helping to reduce winds (Bond, Ryan et al. 1979), altering temperatures (lapse rates of 0.65^0C per 100 m elevation) and producing a rain shadow effect in eastern Tasmania.

The summer months of December to February, on average, are mild to warm, with approximately 15 sunlight hours, with a midsummer sun elevation of approximately 70 to 73 degrees. Westerly winds are weaker in the summer months, and afternoon sea breezes predominate in the coastal areas. More humid north-easterly winds occur mostly during the summer. On average, mean maximum temperatures range from 18 to 23^0C, and mean minimum temperatures range from 10 to 15^0C. Severe storms are more common during the summer, but may occur at any time.

The autumn months of March to May see temperatures cooling, and an increase in foggy conditions. The humid north-easterly winds begin to taper off and reduce during the middle of autumn.

During the winter months of June to August, fog is frequent. The mean maximum daily temperatures are reduced to 9 to 14^0C (from the summer mean maximum temperatures range of 18 to 23^0C). The mean minimum

temperatures are 4 to 6^0C. The elevated and inland areas of the state do show a slight continental effect, illustrated by the even lower mean minimum temperatures of 1.4^0C, and mean maximum temperatures of 13.3^0C (Meteorology 2006). The elevation of the sun during midwinter is 20 to 23 degrees, with the shortest day length of 9 hours.

The mean daily maximum and minimum temperatures by month for the study area have been estimated by applying the environmental lapse rate of 0.65^0 C (Nunez and Colhoun 1986) to the data from Strathgordon.

February is the warmest month and July is the coldest month. The difference between the maximum and minimum temperatures is larger during February (9.9^o C) than during July (6° C) (Figure 2.3). Mean daily minimum temperatures are subzero between April and November. Approximately two thirds of days are overcast on Mt Mawson. Cloud cover is a strong modulator of incoming solar radiation, and can reflect or transmit solar radiation at varying rates, depending upon the height and type of the cloud (Oke 1992).
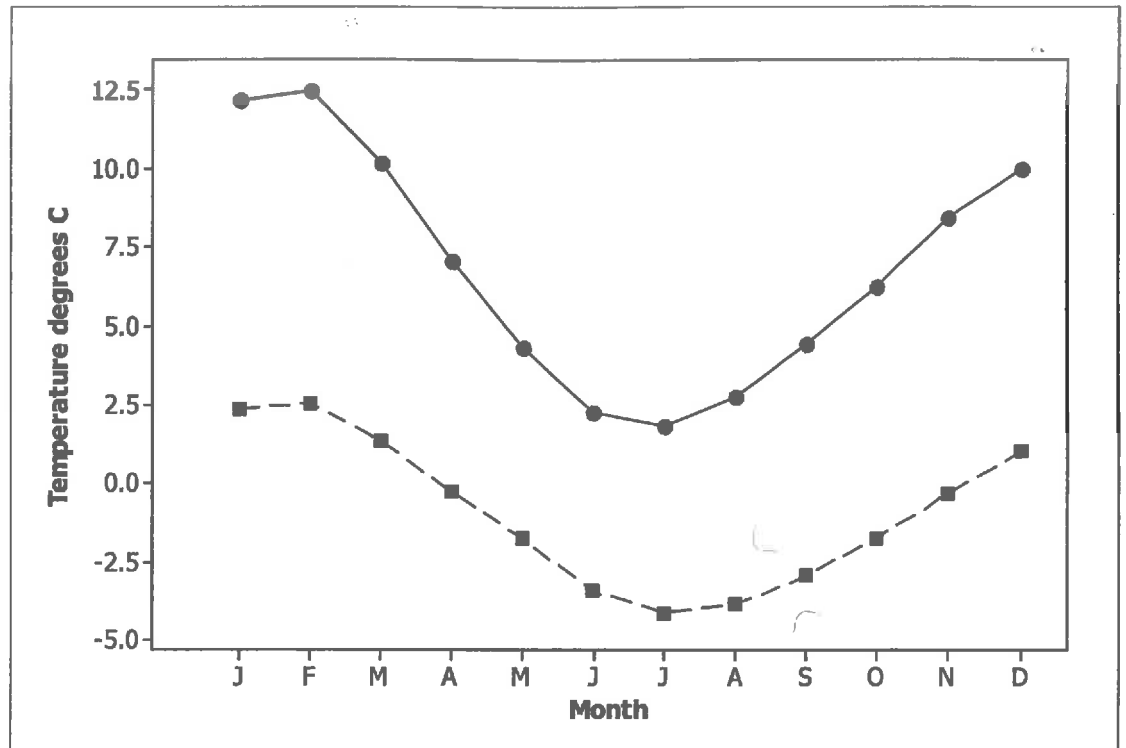
Figure 2-3 Variation in mean daily minimum and maximum temperatures by month at the study site, as approximated by application of the environmental lapse rate of Nunez and Colhoun (1986) to the data from Strathgordon.
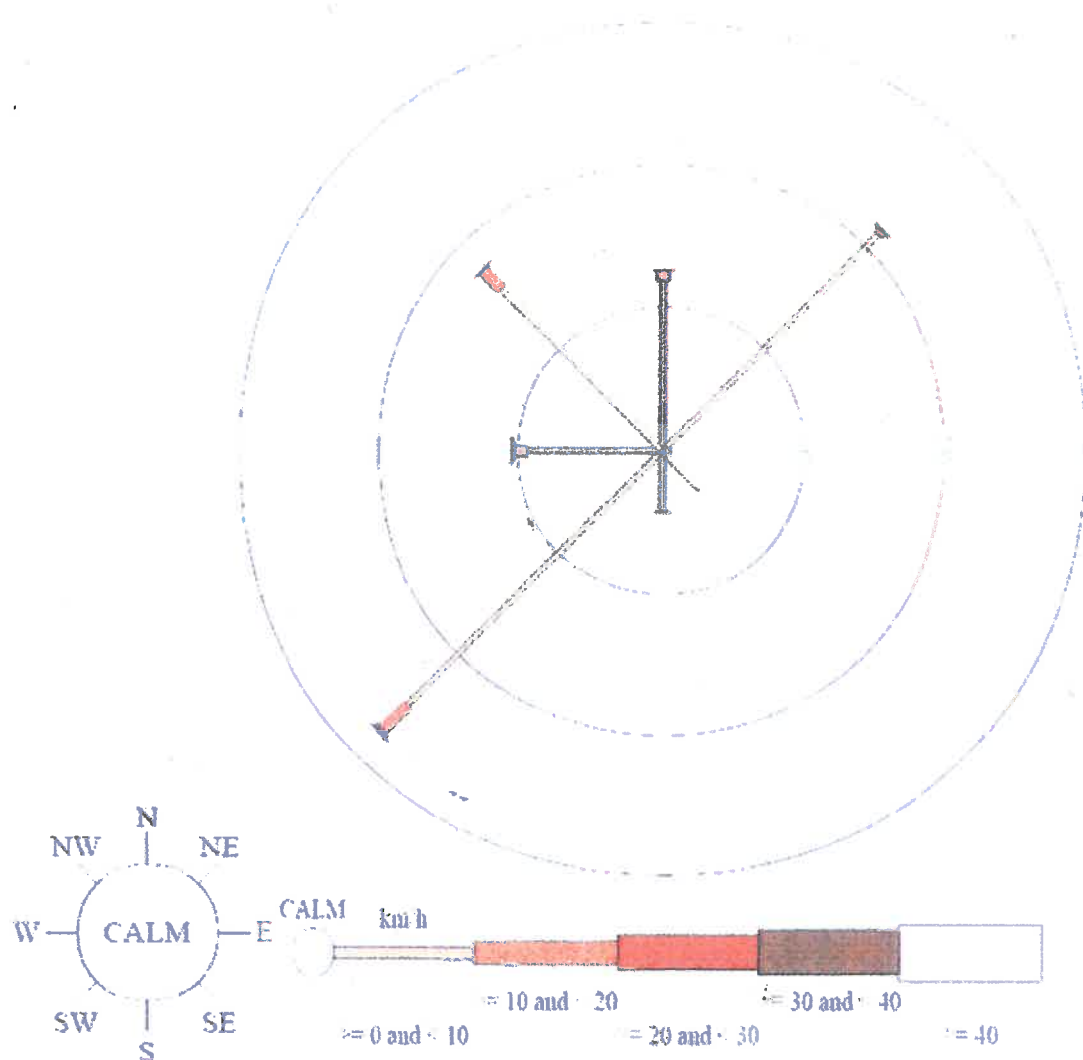
Figure 2-4 Wind rose of annual direction versus speed (km/h) recorded at 9 am from Bronte Park, elevation 712 m a.s.l. A total of 4305 observations were recorded from 01/01/1957 to 31/12/1976 (Bureau of Meteorology 2008).
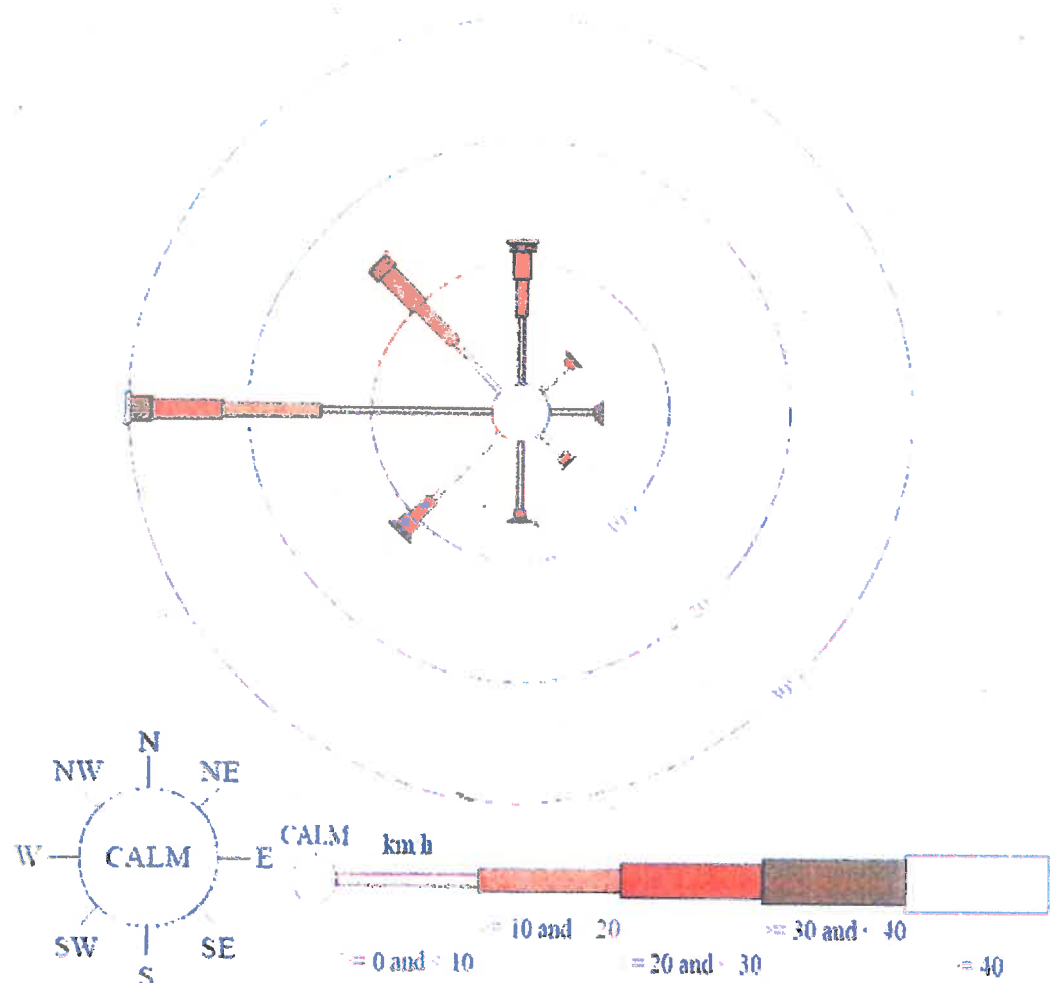
Figure 2-5 Wind rose of annual direction versus speed (km/h) at 9 am
recorded from Liawenee, elevation 1065 m a.s.l. A total of 5182 observations
were recorded from 21/10/1985 to 20/06/2003 (Bureau of Meteorology 2008).

The heaviest snowfalls occur during the winter months; however snow patches can remain until summer. Snow rarely lies for more than a few days at the study site, which is not within a snow patch.

During the spring months of September to November the westerly winds remain strong, giving a distinct maximum to wind speed and rainfall to the north-west and west of the state. The airstream over Tasmania is westerly (known as the Roaring 40's) however the actual winds can vary in direction from north-west to south-west and tend to strengthen with elevation (Figures 2.4 and 2.5).

The amounts and distribution of rainfall vary enormously. The western portion of the state receives the greatest falls, and the amounts taper off over the eastern portion of the state. In the west there is a winter maximum, whereas, in the east, rainfall is distributed, on average, evenly throughout the year. Rainfall is largely governed by the interaction of air stream and topography; therefore it varies from approximately 500 mm per annum in the sheltered areas of the east, south-east and the Midlands, to in excess of 3200 mm per annum in the mountainous west of the state (Meteorology 1993). As the prevailing winds are westerly, there is a higher annual rainfall over the mountainous areas in the west of the state. The rain shadow area is over the eastern part of the state. Thunderstorms are more common in the north and west of the state, and are local in nature. The north and west average 10 to 15 storms per year, while the Midlands of Tasmania will experience 3 storms on average, or less. Over the Mount Field area, rainfall increases progressively from the east to the west, with annual averages ranging from

450 mm in the Gretna district to 1700 mm at Lake Fenton (elevation 1000 m on the Mount Field plateau). It is suggested that the highest parts, including the study area, would probably receive more that 1780 mm (Spanswick and Kidd 2000). The mean data from Strathgordon (322 m, 42.77 $^\circ$ S, 146.05 $^\circ$ E) give a good indication of the seasonal distribution likely to occur on Mount Mawson, with the least precipitation in summer and the most in winter (Figure 2.6).
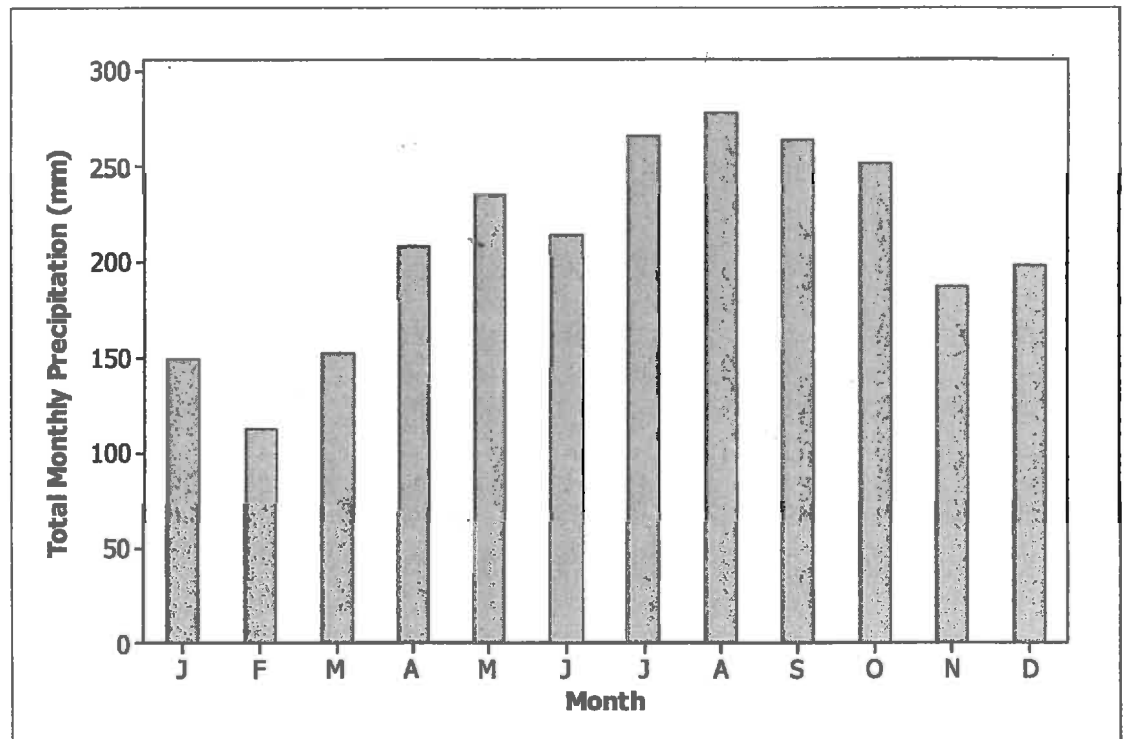
Figure 2-6 Mean monthly rainfall (mm) at Strathgordon (Bureau of Meteorology 2008).

Vegetation

The vegetation of the Mawson Plateau is a complex mosaic of coniferous heath, alpine heath, alpine sedgeland and mosaic bolster heath interspersed with small ponds and lichen-dominated vegetation on rocky areas (Minchin 1989)

Site selection

An area of mosaic bolster heath of approximately 1.5 m x 1 m was chosen for intensive study on the basis of the following criteria: contained the principal cushion species present in the area; was relatively accessible, at approximately 72 km from Hobart (1.5 hour drive from Hobart, 1.5 hour walk to the cushion); and, minimised potential influence from other vegetation types or environments. The chosen study site was on the Mount Mawson Plateau at 1273 metres above sea level and at. 42 degrees 41.277 minutes south, 146 degrees 35.076 minutes east (Figure 2.2).

Field data collection

The cushion mosaic section surface contours were measured during the summer of 2002. A framework was built and installed above the chosen 1.5 m x 1 m mosaic bolster heath section. The frame was fabricated from aluminium angle and was marked with graduations to assist with surface measurements. The framework was squared by measuring and adjusting the diagonal frame length, and then measuring and adjusting the corner angles. Once in position over the plant, the framework was checked by using a spirit

level, to ensure it sat correctly and was level above the cushion surface (Figure 2.7). This frame was integral to the methods of surface contour measurement as it provided a datum for surface measurement.

The cushion surface contours were measured and recorded using a contour jig. The contour jig was fabricated from a metre length of 20x20 mm rolled hollow section square-shaped pipe, with small diameter holes drilled every 0.5 cm to allow fitting of specially made wires. Wires were fabricated from welding filler wire, and were approximately 20 cm long and 1.2 mm diameter.

The method used to measure and record the surface contours was to place the jig onto the frame above the cushion plant and allow the wires to fall onto the cushion surface. The wires were then locked into position using a clamping device. The jig could then be taken off the plant, then be placed on graph paper and measurements marked from the end of the wires. The species that was present at each of the points for which topographic data were collected was also recorded (Appendix 1).

This method allowed measurements to be taken quickly and accurately. This was repeated every 0.5 cm within the frame to collect an overall surface contour measurement of the cushion mosaic.

Once the data were transferred from the jig to the graph paper, the lengths were then measured in mm and recorded into the statistical package Microsoft Excel (Microsoft 2003). Using the graphical information system package ENVI 4.7 (Solutions 2009), a topographic surface map of the cushion was created.

For each point, the slope (degrees from zero) and aspect (degrees from true north as zero) were calculated using the environmental modelling program ArcView 3.3 (ArcView 3.3 Environmental Systems Research Institute Inc.).
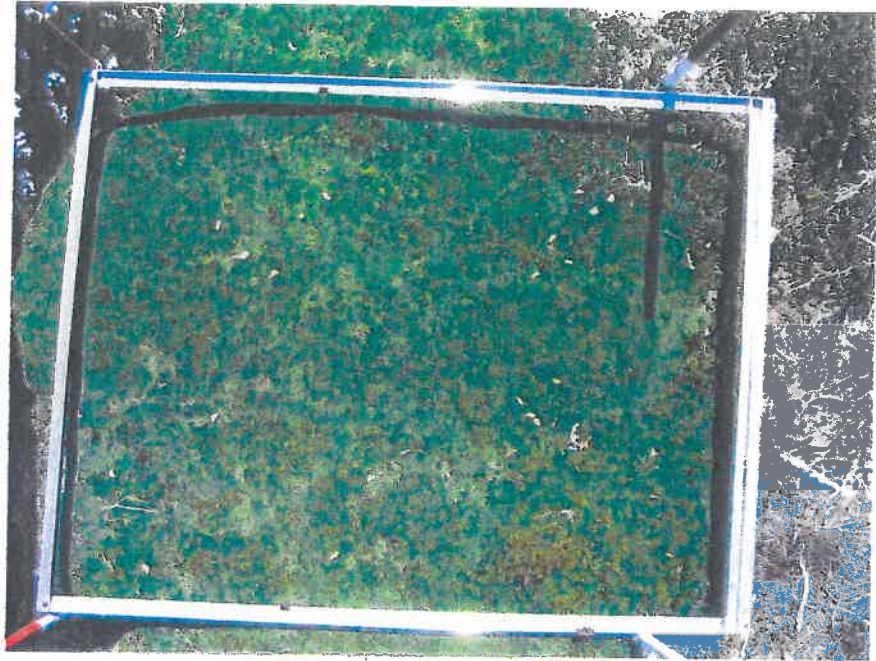
Figure 2-7 The frame used for the topographic survey. North is to the top of the picture. *Pterygopappus lawrencii* is the light coloured cushion species.

Analytical methods

Species distribution and association

A five cm by five cm grid was used. For each individual recording point on the species map over a one metre area within the framework, the frequencies of the species on the 8 neighbouring points on the grid surrounding it were noted. The edge points were counted as neighbours only, as the edges did not have the required 8 neighbours. The table is not symmetrical, due to the edge points as counting as neighbours for the core points, but the core points did not count as neighbours for the edge points.

If species were randomly distributed at points it would be expected that the frequencies of their neighbours would be in the same proportions as the frequencies of the species in the total population. A Chi-squared test was used to test the null hypothesis that the neighbours were randomly distributed.

Topographic relationships of species

The species occurrence data were organised within 8 aspect classes, centred on north, northeast, east, southeast, south, southwest, west and northwest. The degree of association of species with aspect classes was assessed using Pearson's Chi-squared. One way ANOVA followed by Tukeys post-hoc test was used to determine whether species differed in their slopes and elevations within the study site. ANOVA was used in order to compare the means of the four species. The data appeared to fit the

assumptions associated with ANOVA, namely normality and constant variances.

Results

Topographic patterns

The topography of the 1 X 1.15 m area within the framework that was able to be measured (Figure 2.8) is gently undulating, with the lowest point on the southern-most side of the study area. The maximum difference in elevation was 10.08 cm.
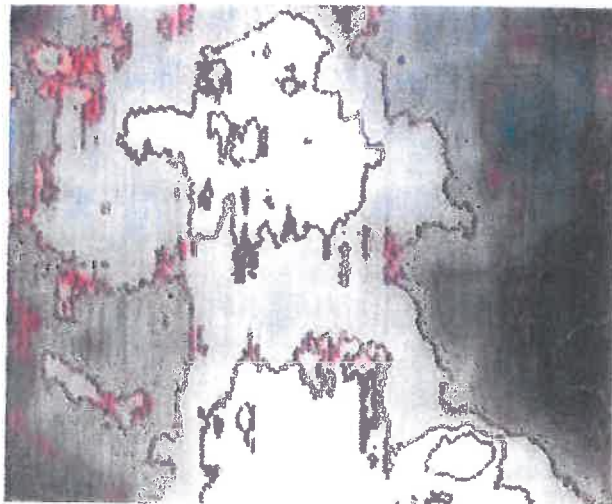
Figure 2-8 Contour map of the study site. Darker areas are at lower elevations. The contour interval is 2 cm. North is to the top of the figure.

Distribution and association of species

The matrix of the mosaic cushion heath was formed by *A. forsteroides*, which constituted 61% of the cover. The next most abundant species was *P. lawrencii* with 23 % of the cover. *Dracophyllum minimum* had 9% of the cover, while *O. pumilio* had 7%.

Species	Pterygopappus lawrencii	Abrotanella forsteroides	Dracophyllum minimum	Oreobolus pumilio
Pterygopappus lawrencii	208 (156.58) 132% +++	365 (389.9) 94% ---	36 (57.67) 62% ---	39 (43.85) 89% neutral
Abrotanella forsteroides	374 (397.97) 94.2% ---	1001(990.99) 99% neutral	172 (146.59) 117% +++	100 (111.46) 90%neutral
Dracophyllum minimum	37 (56.06) 65.4% --	162 (139.50) 116.1% ++	19 (20.65) 90% neutral	14 (15.7)87% neutral
Oreobolus pumilio	39 (46.39) 84.1% neutral	108 (115.52) 93.5% neutral	15 (17.09) 13.8% neutral	31 (12.99) 238% +++

Table 2-1 Comparison of observed and expected neighbouring species and the observed as a percentage of the expected value. Observed numbers, ( ) – expected numbers, +++: P value < 0.001 toward more than expected, ++: P value < 0.01 toward more than expected, --- : P value < 0.001 toward less than expected, --: P value < 0.01 toward less than expected, neutral: P value >0.1.

Pterygopappus lawrencii was its own neighbour more often than expected, as was *O. pumilio*. *Pterygopappus lawrencii* occurred with both of *A. forsteroides* and *D. minimum* much less than would be expected by chance. *Dracophyllum minimum* had a neutral relationship with itself, as did *A.*

forsteroides (Table 2.1). *Abrotanella forsteroides* and *D. minimum* occurred together more than expected by chance.

Distribution of species in relation to microtopography

There was significant variation between species for slope (Figure 2.9; ANOVA, F = 5.08, d.f. = 3, P = 0.002). Only *O. pumilio* had a significantly different slope from any other species. The average slope for *O. pumilio* was steeper than that for *A. forsteroides* and *P. lawrencii*. There was significant variation between species for elevation (Figure 2.10, ANOVA, F = 4.17, d.f. = 3, P < 0.006). *Abrotanella forsteroides* was higher in elevation than *P. lawrencii*. A sine and cosine transformation of the aspect data for each individual species was plotted to enable a visual investigation for any pattern in the distribution. Aspect angles were divided into 8 aspect classes. There was no statistical relationship between aspect class and species occurrence (Figures 2.11-14, Pearson's Chi-square = 14.520, DF = 7, P-value = 0.105).
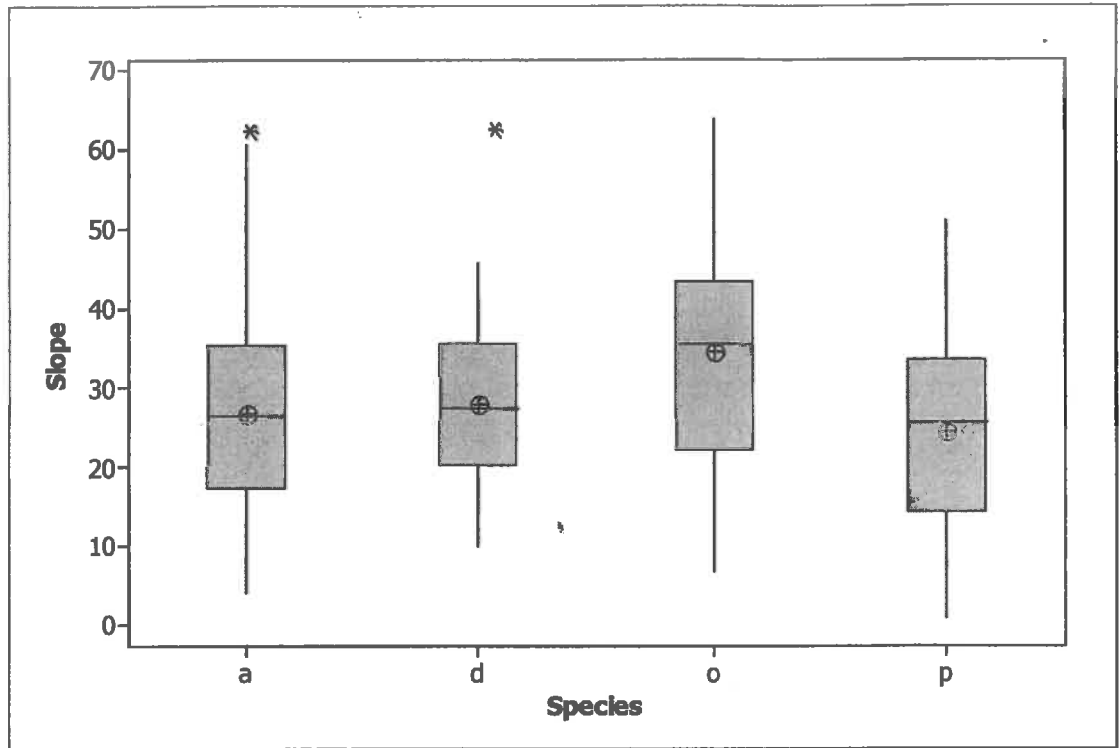
Figure 2-9 Box plots for slope (°) by species. The box represents 50 % of the observations; the horizontal line within the box represents the median; the whiskers and the asterisks for outliers represent the range, the cross represents the mean. a-*Abrotanella forsteroides*, d-*Dracophyllum minimum*, o-*Oreobolus pumilio*, p-*Pterygopappus lawrencii*.
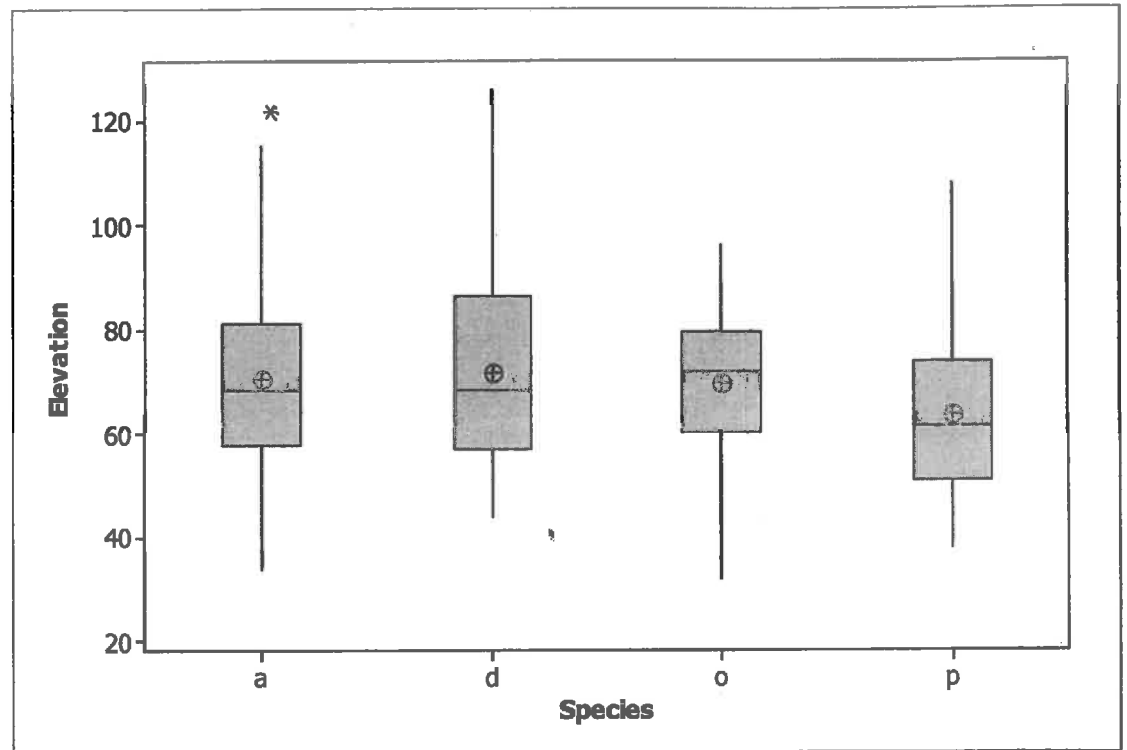
Figure 2-10 Box plot for elevation (cm) in relation to an arbitrary datum by species. The box represents 50 % of the observations; the horizontal line within the box represents the median; the whiskers and the asterisks for outliers represent the range, the cross represents the mean. a-*Abrotanella forsteroides*, d-*Dracophyllum minimum*, o-*Oreobolus pumilio*, p-*Pterygopappus lawrencii*.
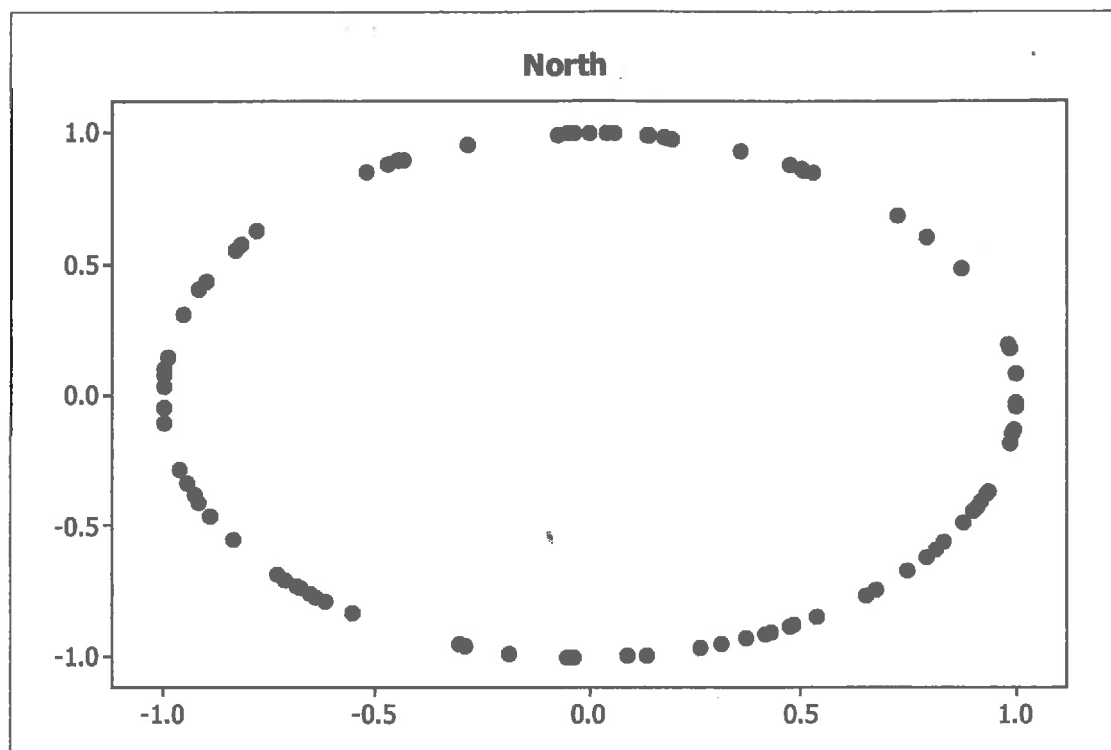
Figure 2-11 The distribution of *Pterygopappus lawrencii* in relation to aspect (true north).
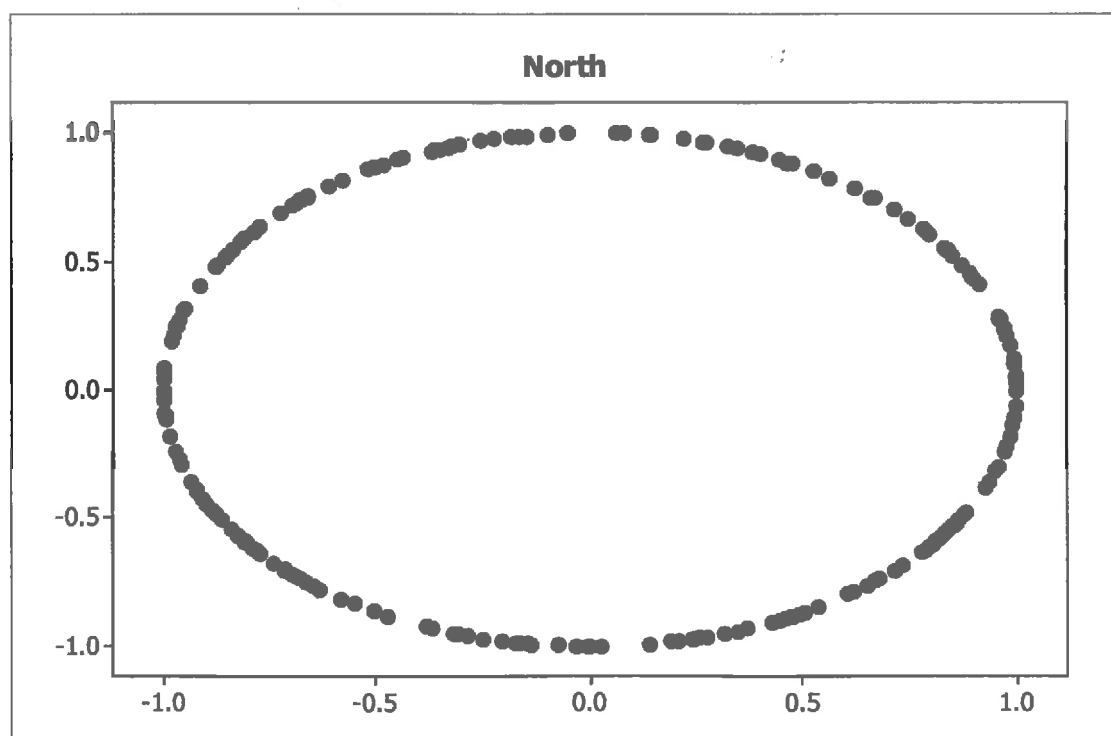
Figure 2-12 The distribution of *Abrotanella forsteroides* in relation to aspect (true north).
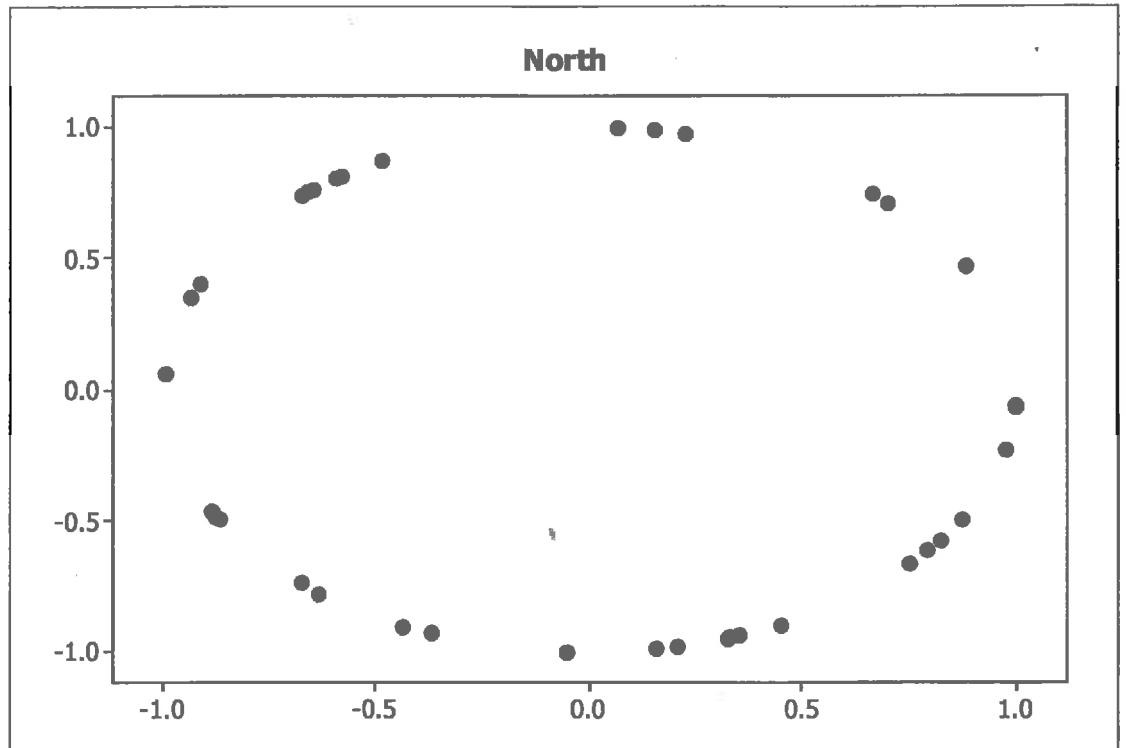
Figure 2-13 The distribution of *Dracophyllum minimum* in relation to aspect (true north).
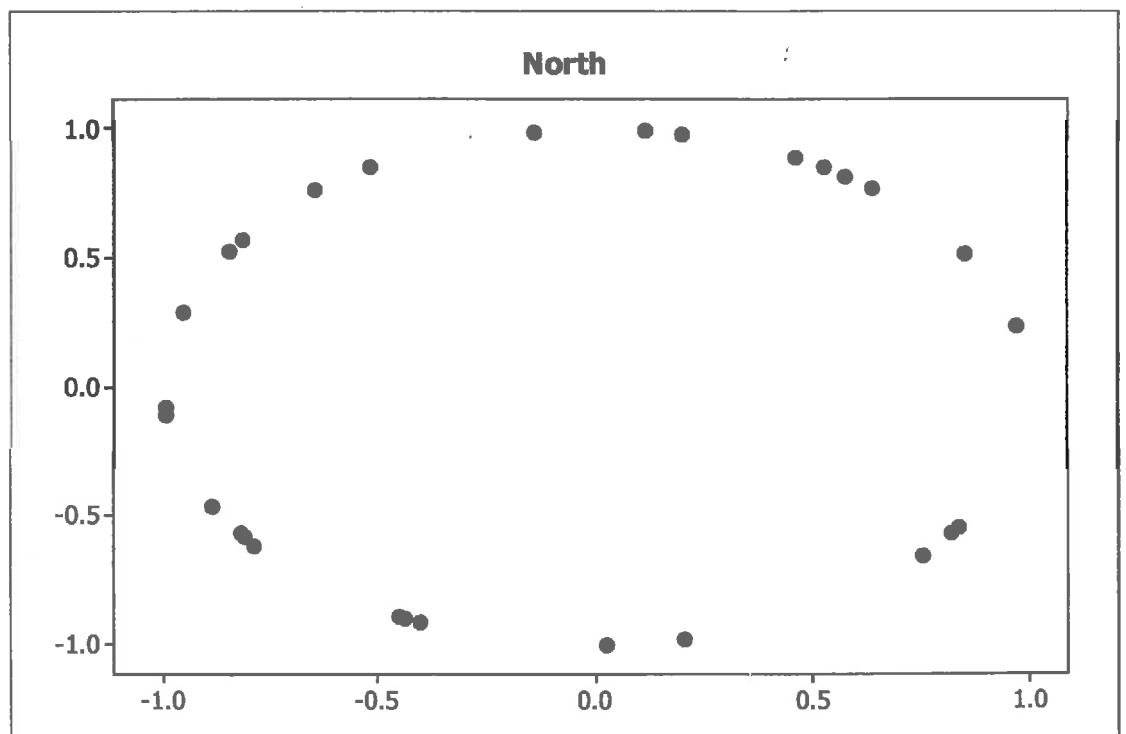
Figure 2-14 The distribution of *Oreobolus pumilio* in relation to aspect (true north).

Discussion

The positive spatial association of *A. forsteroides* and *D. minimum* indicates that the latter species was, more often than not, situated within a matrix of the former species. *Oreobolus pumilio* and *P. lawrencii* tended to occupy distinct sections of the surface. However, there was no distinct sequence of species perceptible from Table 2.1, suggesting that if species were responding to environment within the cushion surface, there was more than one gradient.

Aspect affects the distribution of plant species through its effects on irradiation (see next chapter) and wind exposure. Given that there is a strong effect of the principal wind direction on vegetation (Anderson 1981; Okitsu and Ito 1984; Chen, Hsieh et al. 1997; Morgan, Kirkpatrick et al. 2010), it could be expected that species that vary in their resistance to the effects of wind would occur on different aspects. The principal wind directions in western Tasmania are from the north-west and the south-west (Morgan, Kirkpatrick et al. 2010), yet none of the species in the cushion mosaic preferentially occurred on any aspect.

Lack of evidence for a relationship between aspect and individual plant species preference is not surprising. Other studies have shown a similar lack of relationship (Searcy, Wilson et al. 2003). In the present case, the lack of differentiation may be because the cushion plant mosaic is shaped and situated in a manner that shelters its surface from strong wind effects. Low stature in alpine species is a key to avoiding strong winds (Wilson 1959;

Körner 1999). Alternatively, the species may not differ in their susceptibility to wind damage.

Pterygopappus lawrencii is softer and therefore more compressible than *A. forsteroides* and *D. minimum* (Kirkpatrick and Gibson 1984) and also *O. pumilio*. *Abrotanella forsteroides* and *D. minimum* have very similar slopes and occupy similar areas within the cushion areas. *Oreobolus pumilio* has the highest average slope, enhanced by the longer leaves protruding from the cushion surface. The average slope for the species and the relative smoothness of the contour map does not appear to reconcile. However, while there are large seemingly flat areas, there are sections where the contour lines exhibit high curvature.

The lack of any very strong differentiation of species ranges within the cushion – that could be related to slope, aspect and elevation individually – does not necessarily mean that their combined influence on incident solar is not important. The next chapter addresses this issue.

Chapter 3   Radiation

Introduction

Species are known to differ in the radiation levels that maximise their productivity (Riebesell 1981; Knapp 1984). Searles et al. (Searles, Flint et al. 2002) show how reductions in UV-B radiation receipt for the moss *Sphagnum magellanicum* leads to increases in height growth. Under high light regimes, three different species of mangrove seedlings were found to grow differentially, however under low light conditions the variation between species was reduced (McKee 1995).

If cushion species have inherently different growth responses to variation in photosynthetic radiation input, vegetation with a mixture of species would soon develop an uneven surface. This would, in turn, create spatial variation in solar radiation receipt related to topography (Terjung, Kickert et al. 1969; LeDrew 1975; Nunez 1980; Young, Woo et al. 1997). This would allow species that have optimum growth at lower or higher levels of radiation to find conditions in which their growth would be superior to that of the species that have optimum growth on the flat surface. If this were to be the case, it could be expected that species would differ in their topographic situations in a cushion mosaic in a manner that is consistent with differences in radiation receipt. Temporal variation in radiation receipt created by the interaction of topography with azimuth and altitude of the sun might be expected to result in particular species receiving more radiation than other species at some times but not others.

This chapter tests whether the cushion species might persist in a mosaic because of differences in radiation receipt related to the topography created by their relative growth rates.

Methods

ArcView 3.3 Solar Analyst was used to calculate the direct solar radiation in clear sky conditions for each point using the slope and aspect data, the site latitude, the day and the time of day. The resulting radiation figures were converted from $WH/m^2 s^{-1}$ to $mEm^{-2} s^{-1}$, using a standard 550 nm (considered to be the peak photopic response).

Analysis of variance (ANOVA) and Tukey's post-hoc test were used to determine whether radiation varied between species at each measurement time. The mean radiation values and their standard deviations were calculated. The number of date/times the points occupied by each species received more average radiation than each other species was calculated as a percentage.

The mean radiation figures for each individual species at each date/time were subtracted from each other: *P. lawrencii* from *A. forsteroides*, *P. lawrencii* from *D. minimum*, *P. lawrencii* from *O. pumilio*, *A. forsteroides* from *D. minimum*, *A. forsteroides* from *O. pumilio* and *D. minimum* from *O. pumilio*. Three classes of radiation for the cushion surface as a whole were derived by dividing the data into three classes of n = 13 each: high = 14407.2-23184 $mE m^{-2} s^{-1}$, medium = 2415.84-13198.32 mE m-2 s-1, low = 0-2301.84 $mE m^{-2}s^{-1}$. ANOVA and Tukey's post-hoc test were used to

determine if differences in mean radiation receipt between species varied by classes of cushion mean radiation.

The F-statistic for the relationship between species and radiation at date/times was predicted by the altitude of the sun using linear regression, to test the hypothesis that the differentiation between species was greatest when the sun was at its highest.

Results

Radiation significantly ($P < 0.1$) varied between species in 21 of the 39 models (Table 3.1). A P value of < 0.1 is considered to provide weak evidence against the null hypothesis. This level of significance was selected in order to capture the possibility of variation. As the species exist in a mosaic, the expectation may be that all conditions will be the same. In order to capture any variation, one is prepared to accept a higher chance of falsely rejecting that assumption in order not to miss any evidence of difference.

The level of explanation was low, with R^2 values ranging between 7.11% and 1.51%. There were no significant differences between species that did not involve *O. pumilio*, which received significantly less radiation than the other three species on most day/times.

Pterygopappus lawrencii, A. forsteroides and *D. minimum* all had higher percentages of times when they received more radiation than *O. pumilio* than the reverse situation (Table 3.2). In the most uneven distribution of radiation, *A. forsteroides* received more radiation than *O. pumilio* 82% of the time. At

the times that *D. minimum* received more radiation than *A. forsteroides* and *P. lawrencii*, the average level of radiation was the lowest for any such comparison (2864.88 and 6325.92 mE m^{-2} s^{-1}).

In conditions with a low amount of average radiation on the mosaic, the order of mean radiation receipt by species was *D. minimum* > *A. forsteroides* > *P. lawrencii* > *O. pumilio* (Table 3.3). When average radiation receipt was medium, the order was *P. lawrencii* > *D. minimum* > *A. forsteroides* > *O. pumilio*. When average radiation receipt was high, the order was *P. lawrencii* > *A. forsteroides* > *D. minimum* > *O. pumilio* (Table 3.3). In almost all cases, the differences between pairs of species differed in magnitude between the three average radiation receipt classes (Table 3.3). *A. forsteroides* and *D. minimum* had a significant reversal in their radiation receipt between medium and high levels on the mosaic as a whole.

The F-statistic (Figure 3-1) from the relationship of radiation with species (F) was associated with the altitude of the sun (A). Significant models were found above approximately 25 degrees.

Year	Day, Month	Time	Average Radiation mE m⁻² s⁻¹	Anova Radiation Vs Species P-Value	Anova R² value Radiation Vs Species%	Pterygopappus lawrencii average radiation mE m⁻² s⁻¹	Abrotanella forsteroides average radiation mE m⁻² s⁻¹	Dracophyllum minimum average radiation mE m⁻² s⁻¹	Oreobolus pumilio average radiation mE m⁻² s⁻¹
2005	12-Oct	11.17	17309	<0.001	5.75	18337 a	17640 a	16604 a	11710 b
2006	22-Jan	7.32	4128	0.03	2.07	4623 a	4127 a	4489 a	1952 b
2006	22-Jan	8.34	9346	<0.001	3.73	105223 a	9302 a	9849 a	5027 b
2006	22-Jan	9.35	14892	<0.001	6.23	16388 a	14936 a	15340 a	8753 b
2006	22-Jan	10.28	18929	<0.001	7.11	20355 a	190956 a	18913 a	12538 b
2006	22-Jan	11.34	22063	<0.001	5.94	231328 a	22272 a	21702 a	16974 b
2006	22-Jan	12.36	22831	<0.001	3.77	23426 a	23093 a	22182 ab	19281 b
2006	3-Mar	8.11	4168	0.06	1.75	4606 a	4185 a	4489 a	2070 b
2006	3-Mar	9.13	9128	<0.001	4.06	10281 a	9205 a	8934 a	4731 b
2006	3-Mar	10.18	13826	<0.001	5.27	14973 a	14076 a	13335 a	8280 b
2006	3-Mar	11.14	16857	<0.001	5.84	17940 a	17168 a	16168 a	11237 b
2006	3-Mar	12.14	18014	<0.001	4.44	18665 a	18417 a	16996 a	13485 b
2006	3-Mar	13.11	17166	0.02	2.45	17405 a	17576 a	15993 a	14194 b
2006	3-Mar	14.05	17166	0.02	2.45	17405 a	17576 a	15993 a	14194 b
2006	3-Mar	15.1	3019	0.1	1.51	3105 a	3002 a	3094 a	2780 b
2006	3-Mar	16.03	5107	0.08	1.64	4399 ab	5266 b	4837 ab	6447 b
2006	29-Jul	11.42	4746	0.03	2.07	4882 a	4949 a	4489 ab	2780 b
2006	9-Dec	7.09	3898	0.05	1.91	4382 a	3914 a	4053 ab	1893 b
2006	9-Dec	12.09	23834	<0.001	4.58	24547 a	24083 a	23140 a	20049 b
2006	9-Dec	12.45	23814	<0.001	4.69	24374 a	24070 a	23228 a	20345 b
2007	30-Mar	10.33	9516	<0.001	4.19	10523 a	9671 a	9152 a	5145 b

Table 3-1 Average radiation, P-values for ANOVA tests, and individual species average radiation values. Radiation values for date/times that have the same adjacent letter are identical at P > 0.1 (Tukey's)

	Pterygopappus lawrencii		Abrotanella forsteroides		Dracophyllum minimum		Oreobolus pumilio	
	%ofTimes More Radiation	Mean,SD Radiation mE m-2 s-1	%ofTimes More Radiation	Mean,SD Radiation mE m-2 s-1	%ofTimes More Radiation	Mean,SD Radiation mE m-2 s-1	%Times More Radiation	Mean,SD Radiation mE m-2 s-1
Pterygopappus		X	30.77	7783.2 (8660.88)	23.08	2864.88 (2020.32)	7.69	8694 (9356.4)
Abrotanella	58.97	11542.32 (8495.25)		X	38.46	6325.92 (5925.48)	5.13	12155.04 (10167.84)
Dracophyllum	64.1	13297.68 (8246.88)	48.72	13562.64 (8809.92)		X	12.82	12022.56 (8031.6)
Oreobolus	79.49	10780.56 (8594.64)	82.05	10200.96 (8445.6)	71.79	10333.44 (8263.44)		X

Table 3-2 The percentage of times (n=39) that each species received more radiation than each of the other species (%Times More Radiation) and the mean and standard deviation ( ) of the radiation on these days (Mean, SD Radiation). Radiation Units are mE m-2 s-1

Difference	Radiation Classes			
	Low 0-2301.84 mE m^{-2}s^{-1} (n=13) median	Medium 2415.84-13198.32 mE m^{-2}s^{-1} (n=13) median	High 14407.2-23184 mE m^{-2}s^{-1} (n=13) median	ANOVA P-values
p-a	0.00 a	391.13 b	284.62 ab	0.01
p-d	0.00 a	94.24 a	911.31 b	<0.001
p-o	8.12 a	2543.04 b	4053.6 b	<0.001
a-d	0.00 a	-197.8 a	485.15 b	<0.001
a-o	128.37 a	2152.95 ab	3604.15 b	<0.001
d-o	0.00 a	2559.98 ab	3136.66 b	0.02

Table 3-3 Median radiation classes related to the mean and median radiation differences (mE m^{-2} s^{-1}) between species. Numbers with the same letters adjacent to them in rows for radiation classes are statistically identical at P>0.1 (Tukey's range test). p-*Pterygopappus lawrencii* a-*Abrotanella forsteroides* d-*Dracophyllum minimum*, o-*Oreobolus pumilio*
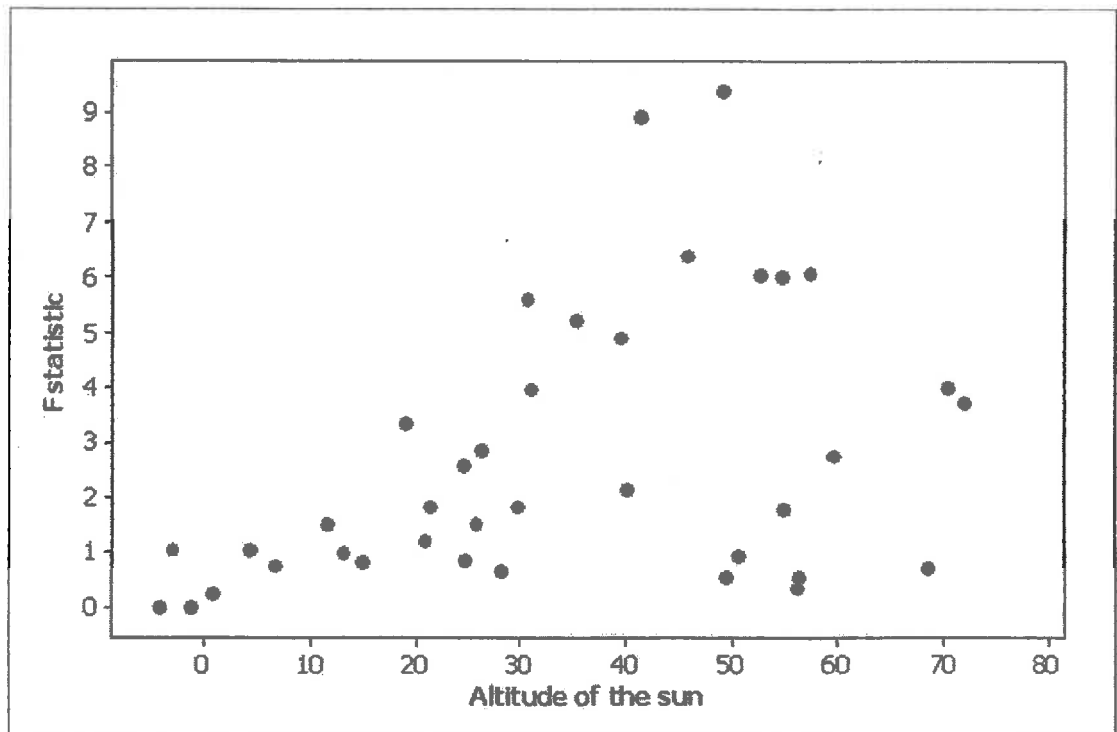
Figure 3-1 The relationship between the F statistic for species against radiation at date/times and the altitude of the sun (°).

Discussion

Radiation was calculated assuming clear sky conditions which do not frequently prevail in the alpine environment (Körner 1999). Of the 9 recording days, 7 days did not have a significant variation in radiation receipt by species. Two of these 7 days, the 27th May, and the 23rd June were those closest to the winter solstice, when the sun was very low in the sky. There was a general direct relationship between the height of the sun in the sky and the strength of species differentiation, but with considerable variability at high values of altitude (Figure 3.1). This variability was probably related to variability in azimuth.

There is good reason to believe that radiation receipt in the low class defined in the present chapter is sufficient to allow plant growth. Regher and Bazzaz (Regher and Bazzaz 1976) found the low light compensation point for plant species ranged between 75 mE m^{-2} s^{-1} at 25°C, to 18 mE m^{-2} s^{-1} at 5°C, compared to 2300 mEm^{-2} s^{-1} at the boundary between the low and medium classes (Table 3) The start-up lag time from a dark period to photosynthesis ranges between a few minutes, reaching a maximum at 12 minutes (Regehr and Bazzaz 1976). This would allow for species to begin photosynthesis, as soon as sunlight struck the plant. Bjorkman and Demmig (1987) calculated that at low photon fluxes (>100 mEm^{-2} s^{-1}) more than 80% of the absorbed light quanta would be utilised, thus in the low radiation class there would be adequate radiation available for the individual species to photosynthesise.

As the levels of radiation increase, the species that receive the greatest amounts also changes. The species variation in radiation reception allows for individual species to exploit radiation niches, and for those niches to be maintained.

Not only do individual species receive variable amounts of radiation, but also their placement within the cushion enhances this. Lantz et al. (Lantz 2010) outline how variation in vegetation can lead to changes in the surface energy balance and sensible and latent heat flux. Givnish et al. (Givnish, Montgomery et al. 2004) shows radiation adaptations that are strongly correlated with light regimes that species inhabit. The rates of radiation received by each cushion species changes between the low, medium and high categories, this indicates species are creating and occupying specific niches. The percentage of time individual species received more radiation in comparison to the other species demonstrates the variation in radiation receipt (Table 2). The combination of species placement within the cushion, and sun angle results in variation in amounts of radiation received.

The undulating surface of the cushion section is a noteworthy influence on the receipt of radiation by individual species. No section of the cushion is shaded when the sun is overhead; however, there are sections of the cushion that do receive higher rates of radiation, when the sun is low in the sky, early morning and late evening. The undulating surface of the cushion leads to greater surface area than a flat surface, allowing for increased radiation interception.

The results of the present chapter indicate that the four species of cushion plant are associated with declining radiation input in the sequence *P. lawrencii, A. forsteroides, D. minimum, O. pumilio*. While *O. pumilio* generally receives the least radiation the other species change their orders depending on the magnitude of flat surface radiation input. These results are consistent with the hypothesis for maintenance of mixed species cushions that was described in the introduction to the present chapter and are also consistent with the hypothesis of physically controlled distribution patterns.

Both radiation and temperature affect photosynthesis and respiration (Colinvaux 1993; Körner 1999; Larkindale, Mishkind et al. 2005). The following chapter takes out the effects of radiation to determine whether the cushion species coexist because of different surface temperatures in different synoptic conditions.

Chapter 4   Synoptic influences on relative temperatures of species

Introduction

One possible explanation for the persistence of intimate intermixing of species is that different climatic conditions at different times favour the growth of different species and that the variability in conditions is such that no one species can completely outcompete any or all others, because of alternating growth advantage (Ashton and Gill 1965; Wilson 1988).

The outstanding ability of cushion plants to absorb and retain radiation is well documented (Mosely 1877; Sailsbury and Spomer 1964; Wace 1965; Longton 1970; Bliss and Mark 1974; Seppelt and Ashton 1978; Turner and Hill 1981; Fisher and Kuhn 1984; Gibson 1988; Körner 1999). This ability results in higher temperatures on and within the cushion than in the surrounding environment. Cushion surface temperatures can reach $10°$ to $15°C$ above ambient temperatures of $0°$ to $5°C$ (Longton 1970; Seppelt and Ashton 1978). Gibson (Gibson 1988) found that cushion plant surface temperatures were $10°C$ higher than ambient temperatures in winter at Mount Field. There are no published data comparing cushion surface temperatures between cushion species, although differences in morphology and colour (Bell 2008) could be expected to result in differences in temperatures.

There has been a recent resurgence in interest regarding the effects of temperature upon alpine vegetation, driven by concern about large-scale changes in climate. Variation between co-existing species in their responses to global warming has been recently observed (Kullman 2007; Gerdol, Bragazza et al. 2008; Jonas, Rixen et al. 2008; Kudernatsch, Fisher et al. 2008; Nybakken, Klanderud et al. 2008; Pickering, Hill et al. 2008; Toshiki 2008).

The hypothesis tested in this chapter is that temperatures differ between the four species of cushion plant in the study area mosaic cushion heath in ways that are consistent with the alternating growth advantage hypothesis.

Methods

Field data collection

The collection of topographic and species distribution data is described in earlier chapters. During the summer of 2004/2005, surface temperature was recorded at each of the 5 x 5 cm grid points used in the topographic and radiation studies, using a series of 20 thermocouples, which were covered with aluminium piping (Figure 4.1). This added weight to the thermocouple wire, as well as protecting it from the elements. Each individual thermocouple wire was positioned at 5 centimetre intervals along a horizontal section of square hollow tubing. Holes were drilled through the square horizontal tubing, allowing the thermocouples to move freely vertically. When placed onto the

bolster surface, the thermocouples made contact with the surface, and temperature was recorded. This constituted one linear recording. One full surface temperature reading consisted of 20 linear recordings, and took approximately 3 minutes to complete. The temperature observations on the complete grid were taken hourly, sequentially from east to west to minimise shading from the temperature recording rig. The temperature readings were repeated under varying synoptic conditions, and at different times of the day from October 2005 to March 2007. Cloud cover data were observed in eighths of the sky at each temperature observation time.
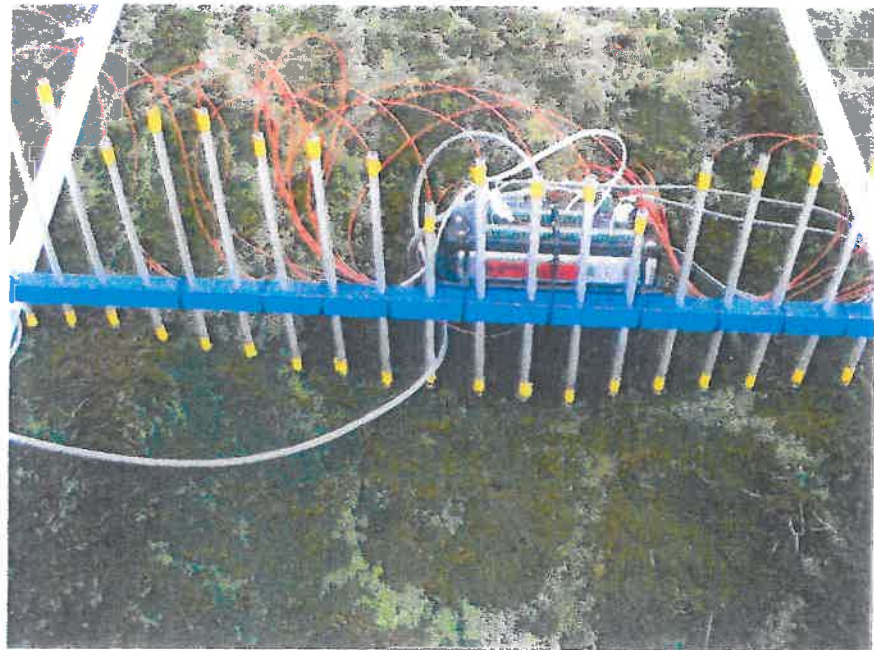
Figure 4-1 Thermocouple device supported by framework

Analytical methods

General linear models with temperature as the dependent variable, species as the independent fixed variable, and slope and radiation as random co-variates were also derived for each of the times. This analysis was undertaken to remove any effects of different microtopographic distributions from the relationships between species and temperature. The temperature values used in further analyses were those that removed the effects of radiation and slope. For the six times at which species affected temperatures at $P < 0.1$ differences from *O. pumilio* were calculated. The significance of the temperature differences between species at these times was determined by an F-test on between subject effects, as part of the general linear model. A P value of < 0.1 is considered to provide weak evidence against the null hypothesis. This level of significance was selected in order to capture the possibility of variation. In order to capture any variation, one is prepared to accept a higher chance of falsely rejecting that assumption in order not to miss any evidence of difference.

The mean temperatures of the four species were ranked 1 (coldest) to 4 (warmest) for all times. For each combination of species, a variable was created from these ranks. If species A was warmer than species B the score was one and if species B was warmer than species A the score was zero. Chi –squared was used to test whether each of these six qualitative variables was significantly related (at $P < 0.1$) to two classes of cloud cover (less than 51% and 51-100%). ANOVA was used to determine the relationship between each of the six variables and mean cushion temperature.

For each of the six combinations of species a variable was created by subtracting the temperature of species A from species B. The Kruskal-Wallis H test adjusted for ties was used to relate the medians of each of these variables to the cloud cover classes described above and to three classes of mean temperature (< 5°C, 5-20°C, > 20°C). These latter classes were determined after graphing the relationships between mean temperature of the cushion mosaic and each of the six variables. The significance of the differences between medians for temperature classes was determined using the Mann-Whitney U test. ANOVA and the Kruskal-Wallis H test yielded similar results, thus supporting the assumption of normality of the data.

Results

Species contributed significantly to temperature in six of the 39 models (Table 4.1). In no cases was the level of explanation high, varying between an r^2 of 26.87% and 4.24%. The maximum observed significant difference in temperature between two species at any time was 0.86°C (Table 4.1). On the three cloudy times out of the six with significant models, *P. lawrencii* was warmer than *A. forsteroides*, whereas on two of the three sunny times *A. forsteroides* was warmer than *P. lawrencii*, while being conjointly warmest with *P. lawrencii* on the third. On two out of three cloudy times and one of the three sunny times, *P. lawrencii* was warmer than *D. minimum*. *Pterygopappus lawrencii* was warmer than *O. pumilio* only once, at a cloudy and cold time. *Abrotanella forsteroides* was warmer than *D. minimum* at all

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three sunny times. *Abrotanella forsteroides* was warmer than *O. pumilio* at one sunny and cold time and cooler than *O. pumilio* at one cloudy and warm time. *Dracophyllum minimum* was cooler than *O. pumilio* at the same cloudy and warm time.

Generally, no evidence was found for differences in temperatures between species. However, all species were found to be non-significantly warmer and colder than all other species for a substantial percentage of the times (Table 4.2). There were no tendencies toward differences between species.

In the most uneven distribution between warmer and colder, *D. minimum* was warmer than *A. forsteroides* 26% of the times (Table 4.2).

When *O. pumilio* had a higher temperature than *D. minimum* it tended to be sunny (P = 0.034) and the mean cushion temperature was 20.4°C, compared to 11.8°C when the reverse pertained (ANOVA, F = 7.11, d.f. = 1, P = 0.011). When *A. forsteroides* had a higher temperature than *D. minimum* it tended to be sunny (P = 0.040) and the mean cushion temperature was 19.3°C, compared to 10.6°C when the reverse pertained (ANOVA, F = 5.69, d.f. = 1, P = 0.022). When *P. lawrencii* had a higher temperature than *D. minimum* it tended to be sunny (P = 0.012) and the mean cushion temperature was 19.6°C, compared to 13.5°C when the reverse pertained (ANOVA, F = 3.39, d.f. = 1, P = 0.074). Thus, in sunny warm conditions the other three species had higher temperatures than *D. minimum*.

The temperature differences between species were greatest when the temperature of the mosaic cushion heath was between 5 and 20°C than at

higher or lower temperatures (Table 4.3). This tendency was most striking in the comparison of *P. lawrencii* and *A. forsteroides* (Table 4.3). The temperature differences between *A. forsteroides* and *D. minimum* were greater above 5°C than below (Table 4.3).

The temperature differences between species were greater in sunny than cloudy conditions, a tendency that was strongest in the comparisons of *P. lawrencii* and *D. minimum*, *A. forsteroides* and *D. minimum* and *D. minimum* and *O. pumilio* (Table 4.3).

Date	Time	Ambient Temperature °C	Cloud Cover (oktas)	Pterygopappus lawrencii	Abrotanella forsteroides	Dracophyllum minimum	Oreobolus pumiliio	P value
3rd March	7.03	5.5	1	-0.17 (b)	0.11 (a)	-0.26 (b)	0 (ab)	0.1
3rd March	11.14	10	1	0.29 (b)	0.76 (a)	0.12 (b)	0 (b)	0.03
9th December	12.45	31.2	1	0.37 (a)	0.06 (a)	-0.49 (b)	0 (ab)	0.06
27th May	9.08	5.1	5	0.06 (a)	-0.00 (b)	0.01 (b)	0 (b)	<0.001
24th June	13.1	9	5	0.10 (a)	0.01 (b)	0.03 (ab)	0 (ab)	0.05
3rd March	15.1	30.5	5	-0.03 (a)	-0.29 (b)	-0.55 (c)	0 (a)	0.05

Table 4-1 Synoptic conditions, species temperatures in relation to Oreobolus pumilio and the significance of the models for the models in which P < 0.1. The same letter adjacent to temperature values in rows indicates that the values are statistically identical.

	Pterygopappus lawrencii		Abrotanella forsteroides		Dracophyllum minimum		Oreobolus pumilio	
	TW	MT	TW	MT	TW	MT	TW	MT
Pterygopappus lawrencii		X	64	16.7 (9.4)	41	13.5 (11.1)	51	16.7 (9.5)
Abrotanella forsteroides	36	17.8 (12.7)		X	26	10.6 (12.6)	36	17.5 (11.1)
Dracophyllum minimum	59	19.6 (9.6)	74	19.3 (9.0)		X	62	20.4 (8.3)
Oreobolus pumilio	49	17.5 (11.9)	64	16.9 (10.5)	38	11.8 (11.9)		X

Table 4-2 The percentage of times (n = 39) that each species was warmer than each of the other species (TW) and the mean and standard deviation () of their temperatures at these times (MT)

Difference	Temperature classes								P	Cloud cover classes				P
	<5°C (n=10)		5-20°C (N=8)		>20°C (N=21)					0-50% (n=26)		>50% (n=13)		
	mean	median	mean	median	mean	median				mean	median	mean	median	
p-a	0.04	-0.00 a	-0.17	-0.14 b	-0.01	-0.03 a		***		-0.05	-0.06	-0.02	-0.01	ns
p-d	0.01	0.00	0.02	0.03	0.15	0.15		ns		0.13	0.13	0.00	-0.01	**
p-o	0.03	0.02	-0.07	-0.04	0.03	0.01		ns		0.02	0.00	-0.01	-0.01	ns
a-d	0.01	-0.01 b	0.19	0.19 a	0.16	0.16 a		***		0.18	0.16	0.02	0.02	***
a-o	0.02	0.01	0.11	0.08	0.04	0.04		ns		0.07	0.05	0.02	0.00	ns
d-o	0.01	0.02	-0.08	-0.05	-0.11	-0.11		ns		-0.11	-0.09	0.00	0.01	*
mean difference	0.02		0.11		0.08					0.09		0.01		

Table 4-3 Mean temperature and cloud cover classes related to the mean and median temperature differences (°C) between species adjusted for radiation and slope. Kruskal-Wallis H test: ns, P > 0.1; * P < 0.1; ** P < 0.05; *** , P < 0.01. Numbers with the same or no letters adjacent to them in rows for temperature classes are statistically identical at P > 0.1 (Mann-Whitney U test).

Discussion

Despite the absence of any large differences in temperature between species in a wide variety of synoptic conditions (Tables 1, 2 and 3), our results do not allow us to reject the research hypothesis that the mosaic of species is maintained by variability in temperature responses to different synoptic conditions, as all pairs of species reversed their temperature order, and some did so strongly in response to variation in synoptic conditions.

The consistent reversal in relative warmth between *P. lawrencii* and *A. forsteroides* in response to variation in cloudiness is the most striking result from the six significant models (Table 4.1). This reversal may relate to a greater absorption of direct solar radiation by the dark green *A. forsteroides* cushion surfaces than the sage green *P. lawrencii* surfaces, and to a greater capacity to trap outgoing long wave radiation in the more hairy *P. lawrencii* cushion surface. The only other example of a reversal between times in a significant model involved *A. forsteroides* and *O. pumilio*, with only one instance of each (Table 4.1).

The fact that no species was always, or almost always, warmer than any other species (Table 4.2) is also strongly consistent with the research hypothesis, especially given that the means and standard deviations for surface temperatures of individual species indicate the possibility of photosynthetic activity when both colder or warmer than the temperatures of other species.

In this specific location, and for the data set as a whole, *D. minimum* reversed with each of the other three species for both average temperature and cloudiness, but no other reversals were significantly related to these conditions. The lower temperatures of the surface of *D. minimum* than other species in sunny, warm conditions is consistent with its tendency to avoid the lower altitudes occupied by the other three species and to be most abundant at the highest altitudes (Kirkpatrick, Minchin et al. 1985). There is no obvious morphological cause of the strong difference in temperature responses in different synoptic conditions between *D. minimum* and the other three species. The low incidence of *D. minimum* in the mosaic and its tendency to be colder than other species are consistent with the location of the study site close to its lower altitudinal limits on Mt Mawson.

Chapter 5   Interspecific differences in water repellence

Introduction

Water on the surface of leaves can have a variety of effects upon both the leaf and the plant as a whole. Wet leaf surfaces can result in reduced photosynthesis and gas exchange (Smith and McClean 1989; Hanba, Moriya et al. 2004). The wettability of leaves can be important to crop species in determining whether pesticides and herbicides cover leaf surfaces (Holloway 1970; Stevens and Baker 1987). Leaves with a film of surface water can experience increased attack from fungal pathogens (Bradley, Gilbert et al. 2003; Toome, Heinsoo et al. 2010). Pollutants may be deposited onto leaf surfaces with the water (Adams and Hutchinson 1987). Wetted leaves are more susceptible than dry leaves to cell and leaf damage from wind (Grace 1988), and water on leaf surfaces can freeze, internally damaging leaves (Pearce 2001).

Leaves that shed water have more time for photosynthesis and gas exchange. Other advantages can include the capture and channelling of water from the leaves down to the root zone of the plant (Westman 1978). In the process of shedding, dirt and dust can be washed from the leaves (Günther and Wortmann 1966), potentially allowing for more effective gas exchange, and photosynthesis. Part of the process of shedding is the formation of large drops of water on the leaf surface. These can act as

lenses, potentially increasing photosynthesis (Brewer, Smith et al. 1991), reducing transpiration from the leaf surface and increasing photosynthesis due to greater stomatal opening (Smith and McClean 1989).

The degree of adherence of surface water to leaves is influenced by the chemical composition of the cuticle (Holloway 1970) and surface roughness (Fogg 1947; Challen 1960; Challen 1962) . Trichomes can aid in the repellence of water from leaf surfaces (Brewer and Smith 1997), as can rod and plate waxes.

Brewer and Smith (Brewer and Smith 1997) investigated patterns of leaf surface wetness between habitats and species, concluding that the probability of dewfall is higher in open habitats, and that plants within these habitats have a set of morphological characteristics which reduce leaf surface wettability and droplet retention.

The purpose of this study was to evaluate the variation between the two major cushion mosaic species, *A. forsteroides* and *P. lawrencii*, in their ability to shed water, and to determine whether their relative and absolute abilities varied between misty conditions and rainfall events. The relevance of this work to the question of maintenance of the cushion mosaic lay in the possibility that one species may shed more effectively than the other in mist, with the relativity being reversed in rain and in the possibility that a higher degree of water repellence of one species might give it a growth or survival advantage within the mosaic.

Methods

Rain treatment

A ten by ten centimetre grid was placed across the cushion section surface. There were nine grid points south to north, and ten grid points west to east. The species underneath each grid intersection was recorded, making a total of 90 points. Water drops were allowed to fall from a pipette onto the surface of the cushion from a height of 20 cm. The behaviour of each drop was recorded. If the drop soaked into the cushion surface, it was recorded as 'soak', if the drop beaded on the cushion surface, without soaking into the surface, it was recorded as 'bead'. The water drop tests were completed under various synoptic conditions and at different times of the year. As there were insufficient representations of *D. minimum* and *O. pumilio*, these 2 species were removed from calculations. A Chi-squared test was used to determine if there was any variation between the two remaining species with regard to the behaviour of the water droplets at each data collection time.

Initially, the cushion section was chosen in such a way as to reduce the influence of edge effects. However, there was the possibility of variation in water drop behaviour due to the principal wind direction from the west on to the leading edge of the cushion section due to the surface contours of the cushion section. The working hypothesis was that any hairs or waxes on leaf surfaces might be worn away by abrasion.

To investigate if there was influence of the principal wind direction upon the cushion surface and water drop behaviour, the westerly first 3 and first 5 rows of the data were separated from the remainder of the water drop data. The leading edge zone was extended to 5 rows to determine where the influence of the leading edge might extend. The first 3 and first 5 row data was compared to the remainder of the surface data using chi-squared tests. Further to this, the data for both *P. lawrencii* and *A. forsteroides* were isolated from the main body of the data. The individual species information for the first 3 and first 5 rows was then compared to the remainder of the individual species data for the remainder of the cushion section.

Mist treatment

A variety of different locations were chosen in the study area for the water mist experiments. Each location had an area of *P. lawrencii* of at least 15 cm surrounded by *A. forsteroides*. Each location was within a 20 m radius from the original cushion section site. Distilled water was sprayed onto the dry surface of the cushion surface using a garden water atomiser at a distance of 20 cm. This method was chosen because marking a grid directly onto the cushion surface would alter the behaviour of the mist droplets. The dry cushion surface was initially photographed. After being sprayed 10 times in quick succession, the site was photographed again. This process was repeated, using up 500 ml of water. The photographs were then analysed, with 20 data points chosen across the surface of the 2 species. The behaviour of the water mist upon the cushion surface was recorded as either soaking into the cushion surface or beading on the cushion surface. The

water mist tests were completed under various synoptic conditions and at different times of the year.

Data analysis

Chi-squared tests were used to determine if there was any variation between the two species in the behaviour of mist or droplets on the cushion surface and whether, within *A. forsteroides*, mist and droplets behaved differently. Within *P. lawrencii*, the two sample t-test was used to compare mist and droplets. A chi-squared test was used to analyse the *A. forsteroides* data, due to the consistent 100% soaking for the mist method, a t-test could not be used, as the data is not normally distributed.

Results

On all days of observation, using the full data set, droplets soaked more into *A. forsteroides* than *P. lawrencii* (Table 5.1). *Abrotanella forsteroides* had percentage soak figures that varied between 49 and 96, while those for *P. lawrencii* varied between 19 and 60. With the exception of one day in the three row analysis, *A. forsteroides* had a higher percentage of soaking than *P. lawrencii* in all the analyses using three or five rows (Table 5.1).

		All rows		West 3 rows only		West 5 rows only	
Date	Species	%	Chi-squared p-value	%	Chi-squared p-value	%	Chi-squared p-value
27.5.07	a	49	< 0.001	35	0.05	45	< 0.001
	p	19		22		21	
29.6.07	a	71	< 0.001	75	0.01	71	<0.001
	p	26		33		29	
9.3.09	a	80	0.01	89	0.2	86	0.01
	p	60		75		62	
13.2.10	a	96	< 0.001	100	< 0.001	99	< 0.001
	p	21		25		7	
22.5.10	a	96	< 0.001	96	< 0.001	97	< 0.001
	p	30		38		28	
3.7.10	a	95	< 0.001	95	< 0.001	95	< 0.001
	p	43		67		36	

Table 5-1 Chi-squared test p-values for percentage water drop soak (%) against species for the full data set, the westward 3 rows and the westward 5 rows. a-*Abrotanella forsteroides*, p-*Pterygopappus lawrencii.*

For *A. forsteroides*, on one third of the days there was a significant difference between the westward three rows and the rest, and the westward five rows and the rest. These were not the same days, and the direction of the differences varied between the two significant days for both the three and five row analyses (Table 5.2 and Table 5.2.1 (raw data)).

| *Abrotanella forsteroides* | | First 3 Rows | | | First 5 Rows | |
| | | Chi-test | | | Chi-test | |
Date		p-value	%		p-value	%
27.5.07	edge	<0.001	35		0.11	45
	remainder		55			53
29.6.07	edge	0.51	75		0.96	71
	remainder		69			71
9.3.09	edge	0.12	89		0.18	86
	remainder		76			76
13.2.10	edge	<0.01	100		<0.001	99
	remainder		93			91
22.5.10	edge	0.83	96		<0.001	94
	remainder		96			99
3.7.10	edge	0.72	95		0.70	95
	remainder		94			94

Table 5-2 Variation in percentage soaking of droplets by *A. forsteroides* or the first 3 and 5 westward rows compared to the remainder of the cushion surface. Chi-squared test p-values and percentage (%) for water soak against species. Edge-leading edge of surface, remainder-remainder of surface.

13.2.10 1st 3 rows vs. remainder		Soak	Bead	27.5.09 1st 5 rows vs. remainder		Soak	Bead
	Edge	120 (114.7)	0 (5.3)		Edge	47 (66.7)	88 (68.3)
	Remainder	161 (166.3)	13 (7.7)		Remainder	193 (173.3)	158 (177.7)
13.2.10 1st 5 rows vs. remainder		Soak	Bead	22.5.10 1st 5 rows vs. remainder		Soak	Bead
	Edge	155 (149.1)	1 (6.9)		Edge	272 (278.4)	18 (11.6)
	Remainder	126 (131.9)	12 (6.1)		Remainder	208 (201.6)	2 (8.4)

Table 5-2-1 Original data for days with significant results. Observed counts, (expected counts).

For *P. lawrencii*, water tended to soak into the cushion more in the first three rows than the rest on all days, although the difference was only significant on one third of the days (Table 5-3 and Table 5-3-1). The results for the first five rows were very different with water soaking into the cushion more in these five rows than elsewhere in the three non-significant results and doing the reverse in the three significant results.

| *Pterygopappus lawrencii* | | First 3 Rows | | First 5 Rows | |
| | | Chi-test | | Chi-test | |
Date		p-value	%	p-value	%
27.5.07	edge	0.32	22	0.27	21
	remainder		17		14
29.6.07	edge	0.58	33	0.55	30
	remainder		25		21
9.3.09	edge	0.14	75	0.77;	62
	remainder		53		57
13.2.10	edge	0.75	25	<0.001	07
	remainder		21		35
22.5.10	edge	0.01	38	0.01	25
	remainder		24		41
3.7.10	edge	<0.001	67	<0.001	36
	remainder		37		6

Table 5-3 Variation in percentage soaking of droplets by *P. lawrencii* for the first 3 and 5 westward rows compared to the remainder of the cushion surface. Chi-squared test p-values and percentage (%) for water soak against species. Edge-leading edge of surface, remainder-remainder of surface

13.2.10 1st 5 rows vs. remainder		Soak	Bead	22.5.10 1st 3 rows vs. remainder		Soak	Bead
	Edge	5 (15.4)	67 (56.6)		Edge	42 (33.0)	68 (77.0)
	Remainder	27 (16.6)	51 (61.4)		Remainder	33 (42.0)	107 (98.0)
22.5.10 1st 5 rows vs. remainder		Soak	Bead	3.7.10 1st 3 rows vs. remainder		Soak	Bead
	Edge	42 (51.0)	128 (119.0)		Edge	40 (26.0)	20 (34.0)
	Remainder	33 (24.0)	47 (56.0)		Remainder	77 (91.0)	133 (119.0)
3.7.10 1st 5 rows vs. remainder		Soak	Bead				
	Edge	69 (82.3)	121 (107.7)				
	Remainder	48 (34.7)	32 (45.3)				

Table 5-3-1 Original data for days with significant results. Observed counts, (expected counts).

For *A. forsteroides*, no drops formed on the surface from the mist at any stage. The water mist soaked into *P. lawrencii* on average 57% of the time, with a maximum of 85% on the 22nd May 2010 (Table 5.4).

The simulation of rain resulted in less soaking of water into the cushions than the simulation of mist for both *A. forsteroides* (Chi^2 = 13, d.f. = 1, P < 0.001) and *P. lawrencii* (2 sample t = 3.0, d.f. = 9, P = 0.015) (Table 5.5). Mist increased soaking by 123% in *A. forsteroides* and 173% in *P. lawrencii*.

Date	Species	%	Chi-squared p-value
13.2.10	a	100	< 0.001
	p	55	
13.2.10	a	100	< 0.001
	p	52	
13.2.10	a	100	< 0.001
	p	50	
13.2.10	a	100	< 0.001
	p	59	
22.5.10	a	100	< 0.001
	p	85	
22.5.10	a	100	< 0.001
	p	57	
3.7.10	a	100	< 0.001
	p	44	

Table 5-4 The percentage of points that mist soaked into cushions by species. a-*Abrotanella forsteroides*, p-*Pterygopappus lawrencii*.

species	drop	% soak mist	grand total
a	81.17	100	91.31
p	33.17	57.43	46.23
grand total	57.17	78.71	68.77

Table 5-5 Mean of daily percentage of points at which water soaked into cushions by species and application technique. a-*Abrotanella forsteroides*, p-*Pterygopappus lawrencii*.

Discussion

As the mosaic is associated with a tarn, the impact of potential water shortages is reduced (Kirkpatrick and Gibson 1984) and soil freezing is also unlikely (Gibson 1988). Therefore there is little possibility of the cushion plants experiencing a severe water shortage. There is therefore little potential advantage in adaptations that facilitate the harvest of moisture. This is in contrast to rosette scrub in Mexico, where any capture of moisture is seen as an advantage (Martorell and Ezcurra 2002). *Abrotanella forsteroides* and *P. lawrencii* have clear differences in the water repellence properties of their surfaces. The superior water repellence of *P. lawrencii* was evident with both the mist and the rain treatments.

Abrotanella forsteroides has a thick cuticle, stomata, which occur in bands up both surfaces parallel to the leaf axis, and sunken trichomes (Gibson 1988). *Pterygopappus lawrencii* has densely packed, long shaggy trichomes (Curtis 1967), and has a glaucous surface (Kirkpatrick, Minchin et al. 1985). Trichomes can be important in reducing water contacting the leaf surface (Brewer and Smith 1997), but this is partially dependent upon trichome density (Brewer and Smith 1997). The more textured the surface, the more successfully water is repelled (Brewer, Smith et al. 1991).

Beading of water on the surfaces of plants can lead to the focussing of available light onto the leaf surface. This has some possible drawbacks, as in the potential to scorch the leaf surface (Brewer, Smith et al. 1991). Depending upon the size of the water drop and the height of the water drop

above the leaf surface, there is potential for focused light to strike several cushion plant leaves at once. This could increase the chance of photosynthesis taking place. Any increase in photosynthesis under reduced light conditions would be beneficial for the highly reflective *P. lawrencii*. Beading of water upon the surface of *A. forsteroides* could be viewed as less beneficial, as the surface is less reflective and lensing of light could damage the leaves.

In general, there is a rapid increase in wax erosion with increasing proximity to the ground surface (Hadley and Smith 1989). Hadley and Smith (Hadley and Smith 1989) suggest that leaf surface wax erosion via blowing snow may be a major force in the distribution of evergreen plants in the timberline of the central Rocky Mountains (USA). Low stature and the dense leaf arrangements are both advantages in this environment (Hadley and Smith 1989; Körner 1999). Once the surface is covered by snow, the abrasion effect would be lost, again highlighting the importance of a low profile and closely packed shoots and leaves to plant survival in alpine locations. That the westward edge of the cushion section is in the path of the principal wind direction led to the theory that there would be an increase in water soaking into the surface along that edge due to the removal of the outer layers of the leaf surfaces via abrasion by rainfall and particulate matter. This proved not to be strongly the case, nor were there any consistent seasonal differences in water shedding.

Chapter 6 General discussion

Introduction

Cushion plants can occur in two-dimensional mosaics of species, which have been shown to be stable in their proportions of species, but unstable in their patterns (Gibson and Kirkpatrick 1992). Through the investigation of temperature profiles, radiation receipt and water behaviour upon the cushion surface, the factors that might contribute to the stability of cushion mosaic assemblages and this state of quasi-stability were explored. The cushion mosaic under investigation was composed of four principal species, *Pterygopappus lawrencii*, *Abrotanella forsteroides*, *Dracophyllum minimum* and *Oreobolus pumilio* at Mt Field, Tasmania.

Endeavouring to discern the factors that allow for the maintenance of the cushion mosaic, more specific questions regarding the mosaic nature of the species assemblage were asked. This began with investigating the possibility that individual species might have environment preferences within the cushion mosaic. Next, we looked for evidence that species reverse in their relative radiation receipt and temperatures in different conditions. The degree of consistency of these interactions and relationships with possible negative feedback mechanisms is assessed in the present chapter.

Are there distinct environmental ranges in the mosaic?

At first glance, there is little to distinguish the individual cushion species: they appear to occupy very similar physical space and use the same resources.

For instance, (Gibson 1988) in describing the site from which the peat core analysis was taken at Mt. Field Tasmania notes 'an intricate mosaic of three bolster species with no evidence of differential height growth by any species'.

There is an altitudinal variation of 10.08 cm on the particular cushion section on which the present study was undertaken. Variation in altitude, slope and aspect also result in variation in radiation receipt. There was a very weak tendency for species to segregate into different topographic situations.

These segregations, that of *P. lawrencii* and *A. forsteroides* to gentler slopes than *O. pumilio*, and that of *P. lawrencii* to lower elevations than *A. forsteroides*, do not appear to be consistent with their known environmental preferences. *Oreobolus pumilio* would be expected to be on the gentlest slopes and *P. lawrencii* would be expected to be dominant on the higher points of the mosaic cushion heath.

The higher propensity of *P. lawrencii* to shed water may be a neutral or non-beneficial outcome of hairiness evolved for other reasons.

Do species respond differently to different synoptic situations?

The lack of strong patterns of environmental discrimination between species in the mosaic cushion heath suggests that some other mechanism exists for maintenance of coexistence. This mechanism seems likely to result from the variability in the growth responses of different species in different synoptic

and climatic conditions being such that no species can gain a sufficient long term advantage to displace any of the others (Grime 2001).

This hypothesis is consistent with evidence of reversal between species in their relative temperatures under different light and synoptic conditions. Three of the species also reverse in their order of radiation receipt, depending on altitude and azimuth. The exception, O. *pumilio*, consistently received the least radiation.

The undulating surface of the mosaic is likely to be the product of one species gaining a growth advantage in a sequence of years when the synoptic conditions more favoured it than other species. However, such a growth advantage, in creating relative relief, would induce variability in radiation receipt that may, over part of a mound, make conditions more suitable for other cushions than the mound-forming species. Such negative feedback is associated with stability within communities (Harrison 1979).

Implications

Mosaic cushion heath has a restricted altitudinal range on and around the study area on Mt Mawson, between approximately 1200 and 1300 m, with single species of cushion largely dominating above and below this band. Even small changes in mean temperature (around 1 °C) are likely to have significant effects in cold climates (Grace 1987). It seems highly likely that the climate at Mt Field warmed during the twentieth century, as there is a ski village on the slopes of Mt Mawson that is very rarely used, because of the

lack of snow in the last thirty years. There is no indication of changes in precipitation during the same period. Increasing warmth may result in the increasing dominance of *A. forsteroides* in the cushion mosaic, and the eventual loss of *D. minimum* and *P. lawrencii* from the site.

As Gibson and Kirkpatrick (1992) have observed, the cushion mosaics present an unusual situation in which intense competition is associated with extreme environmental conditions. The cushion species are both competitors and tolerators in the classification of Grime (Grime 1977; Grime 2001). The data most closely fit a model of temporal environmental fluctuations with continuous competition (Chesson and Case 1986; Gibson 1990). It seems fitting that the most likely model to explain the coexistence of four cushion plant species is one in which apparent altruism between species prevails, in that species reciprocally create the surface conditions for each other. The below surface interaction of root systems are unknown, but may be worthy of further investigation. Repeat surveying of the same study site could eventually provide a test of the negative feedback hypothesis.

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Appendix

2	1	1	1	1	1	1	2	2	2	1	2	2	2	2	2	2	2	2
2	2	1	1	2	2	2	2	4	4	2	2	2	4	2	4	2	2	2
2	2	2	2	2	1	5	1	2	2	2	2	2	2	2	2	2	2	1
2	2	2	5	2	5	5	5	2	1	2	2	2	2	2	2	2	2	2
1	5	4	2	2	1	2	1	2	4	2	2	4	2	2	4	2	2	2
1	4	2	1	1	1	2	1	2	4	2	4	2	2	4	2	1	2	2
1	2	2	5	4	1	2	1	2	2	2	4	2	2	2	2	1	2	2
4	2	1	1	2	1	2	2	1	1	2	1	1	1	1	1	1	1	2
4	2	2	1	2	2	2	1	1	2	2	2	2	2	1	2	1	1	2
1	1	1	5	1	1	2	1	1	4	2	1	2	1	1	2	1	5	2
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4	2	5	2	2	2	2	2	1	2	2	2	2	5	5	2	2	2	2
2	2	5	4	2	2	5	2	2	2	5	2	5	1	2	2	2	2	2
2	2	5	2	2	4	2	2	4	2	2	1	1	4	2	2	1	2	4
2	5	2	2	2	2	2	1	1	2	2	2	1	2	2	2	2	1	4
2	5	4	2	4	4	2	2	2	2	2	2	2	2	2	2	5	2	2

Species	Name
1	*Pterygopappus lawrencii*
2	*Abrotanella forsteroides*
4	*Dracophyllum minimum*
5	*Oreobolus pumilio*