

**The Effects of Vertebrate Herbivore Grazing on the Alpine Vegetation
of the Eastern Central Plateau, Tasmania.**

by

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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, the thesis contains no material previously published or written by another person, except when due reference is made in the text.



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Abstract

This thesis examines the relative influences of domestic stock, rabbits and native vertebrate herbivores on alpine and treeless subalpine vegetation on the Eastern Central Plateau Tasmania, with special reference to tall alpine herbs.

Results from 25 year old grazing exclosures on Liawenee Moor indicated that domestic stock had a much greater impact on the vegetation than rabbits and native vertebrate herbivores. Vegetation cover was greatest and structure was most complex in the ungrazed exclosure, whilst vegetation cover was least in the sheep, rabbit and marsupial grazed control area. Aerial photographic analysis showed that, over a 19 year period, regeneration in these exclosures was most successful in the ungrazed exclosure, whilst bare ground increased in the sheep grazed area.

Most plant species that were present in the grazing exclosures were also present in sheep grazed areas. However, sheep grazing had a dramatic impact on flowering success of many tall alpine herbs, with significantly more herbs flowering in the rabbit and native vertebrate herbivore grazed plot and the ungrazed exclosure than the sheep grazed area. A few tall herbs were tolerant of grazing by rabbits and native herbivores as there was no significant difference in flowering success between the two exclosures (the ungrazed exclosure and the rabbit plus native herbivore grazed exclosure).

Vegetation cover in 23 year old plots at Liawenee and Augusta tended to increase at approximately 1% per year, whether grazed by domestic stock (Liawenee) or not (Augusta). Regeneration at Liawenee was dominated by shrubs and grasses. Shrubs were the most important recolonisers of bare ground at Augusta. Regeneration occurred at a slightly faster pace at Augusta, despite its higher altitude.

At other sites, where domestic stock grazing ceased 6 years before the study commenced, the average annual increment in vegetation cover was also approximately 1%. The greatest increase in vegetation cover was found in the ungrazed exclosures, followed by the rabbit grazed exclosures, whilst the rabbit plus native vertebrate herbivore grazed controls had the lowest increase in vegetation cover.

Flowering success at these sites was greater for some tall herb species in the ungrazed exclosures, but differences were less marked than at Liawenee. There were very few differences in flowering success between rabbit grazed exclosures and those areas that were open to rabbits and native vertebrate herbivores, indicating that rabbits may have a larger impact on flowering success than native herbivores.

Naturally ungrazed areas, small islands in a fast flowing stream, were dominated by tall alpine herbs and palatable grasses, which were non-existent or sparse on the native vertebrate herbivore grazed banks. Tall herbs were dominant on the upstream ends of these islands, which experienced physical disturbance from fluctuating stream levels. These islands had very little bare ground other than that created by stream erosion.

A major implication of this study is that the continuation of domestic stock grazing in treeless subalpine environments will contribute significantly to the deterioration of the landscape through a decrease in vegetation cover in exposed sites, a reduction in the structural diversity of the vegetation, a loss or reduction of some palatable plant species (mainly tall alpine herbs), the reduction of flowering of some tall herbs, and the maintenance of bare ground patches. Sheep plus rabbits and marsupial grazers have a much greater impact than rabbits and natives alone. Rabbits in their present numbers, may be considered to be an additive effect to native vertebrate herbivore grazing as recovery is slower under combined grazing (rabbits and native vertebrate herbivores) than under rabbit grazing alone. Rabbit grazing substantially affects the flowering success of some tall herb species.

It is estimated that most of the Eastern Central Plateau will regenerate naturally within 50-80 years. Tall herbs are more prevalent where bare ground is less than 20%, but are not the dominant lifeform in areas that are grazed. Tall herbs may dominate in naturally ungrazed environments (islands) but only where physical disturbance of the ground has occurred.

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Liawenee Moor January 1997

Her nostrils quivered, sensing the new surroundings. Strange scents filled the air. She stepped forward, following the sweetest aroma, head down, concentrating on finding the source. Another step and then another, the scent willing her to succeed. At last she reached the place of the alluring, mysterious perfume. She looked around, guided by her finely-tuned nostrils, and, maximising her sensory pleasure, she put out her tongue, wrapped it around the wondrous scent and ripped it out of the ground.

And so began the conquest of Daisy over daisy.

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Chapter 1

Introduction

Introduction

Few terrestrial ecosystems have evolved without the influence of vertebrate herbivores. Thus disturbance (White and Pickett 1985) caused by grazing may be considered to be endogenous and integral to the continued existence of many ecosystems. Grazing may be considered to be exogenous where exotic herbivores (e.g. domestic stock) have been introduced to a system, or where herbivores are kept at artificially high numbers.

Research into grazed ecosystems has two major motivations:

- (1) to preserve or increase the economic value of rangelands by managing or enhancing the cover and productivity of desired plant species for livestock or crop production; and
- (2) to preserve the biodiversity and other conservation values of native and semi-native vegetation.

This thesis responds to the second motivation by assessing the role of different species of vertebrate herbivores (native and introduced) on the floristics and dynamics of alpine and treeless subalpine vegetation on Tasmania's Eastern Central Plateau.

The major research questions are:

- (1) to determine the effects of different species of vertebrate herbivores (and combinations of species) on patterns of recovery in disturbed vegetation; and
- (2) to determine the effects of different species of vertebrate herbivores on the presence and flowering success of plant species found in tall alpine herbfields.

This introductory chapter reviews the literature on the influences of vertebrate herbivores on plant species and communities, and sets out the aims and structure of the thesis.

Influences of Vertebrate Herbivores on Vegetation

Plant Productivity

Grazing by vertebrate herbivores can increase, decrease or have little effect on the productivity of grazed ecosystems (Maschinski and Whitham 1989). The overall productivity of the grazed system is affected by the species of herbivore present, the numbers of animals, the length of time the system is grazed, the season of grazing and environmental conditions such as climate and soil. Plant yield may be greater in systems

that are adapted to grazing than those that are not, such as the North American prairies under bison grazing (Vinton and Hartnett 1992) or the Serengeti grasslands under native ungulate grazing (McNaughton 1985). However, in other systems, plant productivity may decrease under grazing pressure, especially where domestic stock have been introduced into a system (Harrington *et al.* 1984).

During extreme conditions such as drought, wild herbivore population booms, or overgrazing by livestock, grazed ecosystems are likely to experience a reduction in productivity which may be irreversible. Burning and stock grazing in some alpine environments results in the creation of bare ground gaps (Wimbush and Costin 1979a; Scott and Hunter 1988; Wahren *et al.* 1994; Hofstede *et al.* 1995). These gaps are self-perpetuating or may even expand, as physical processes such as frost heave, wind and water cause sheet erosion of the loose bare soil.

Productivity may be indirectly enhanced or retarded by the addition of nutrients from herbivores. The deposition of cattle faeces and urine in Victorian alpine grasslands did not directly cause an increase in bare ground due to plant death. However, urine scorched the vegetation and created patches of litter from dead plant material (van Rees 1984). Night camping of animal herds in the Himalayas created bare ground patches due to the accumulation of faeces and urine (Rikhari *et al.* 1993). The productivity of plants in Australian semi-arid grassland communities was enhanced by the decomposing bodies of drought-affected kangaroos and the deposition of cattle dung (Leigh *et al.* 1989).

Structure and physiognomy

Through selective grazing, herbivores contribute to horizontal and vertical heterogeneity in the landscape (McNaughton 1985). Grazing affects the stature of plant communities by promoting short palatable plants and both short and tall unpalatable species (Sal *et al.* 1986; Noy-Meir *et al.* 1989; Bock *et al.* 1995; McIntyre 1995; Escarre *et al.* 1996; Kiehl *et al.* 1996). Pastures which are adapted to grazing pressure are dominated by horizontal growth forms, especially among the palatable species (Sal *et al.* 1986).

Noy-Meir *et al.* (1989) describe three main responses of plants to grazing disturbance: decreasers (protection increasers) which occur only or in greater numbers in ungrazed or lightly grazed situations, and which are tall and erect and generally palatable; increasers which are small and prostrate or have a rosette form (and which are adapted to grazing); and invaders which only occur after severe disturbance. Some species are able to change their growth form in particular grazing regimes. Herb species such as *Hypochoeris radicata* may be erect in ungrazed areas but flat rosette herbs in grazed pastures (Struik 1967; McIntyre 1995).

Where sites are subjected to high grazing intensities, vegetation may be reduced to a single layer. McNaughton (1985) found that grazing by wildebeest created a patchy grassland mosaic. The tall ungrazed grasses were then targeted by zebra, resulting in a '...structurally homogeneous grazing lawn of huge plant biomass concentration' (p. 275). Intensive stock grazing of grassy ecosystems may also create homogeneous swards (Altesor *et al.* 1998).

Numerous studies have shown that the removal of herbivores from grassland habitats has created a successional sequence from grassland to heath or woodland, such as in the Oklahoma tall-grass prairies (Collins and Adams 1983), Scottish heather moorlands (Welch and Scott 1995) and Texan grasslands (Weltzin *et al.* 1997). Where grazing is introduced to a naturally ungrazed system, or where stocking rates are increased, the result may also be a shift in the dominant vegetation type (Belsky and Blumenthal 1997; Weltzin *et al.* 1997). Where grazing was introduced and then removed from systems that have evolved with light (or no) grazing pressure, palatable species, especially perennial herbs, which decreased under grazing, began to increase in importance, for example when grazing pressure was removed from the following: Australian alpine grasslands (Carr and Turner 1959b; Wimbush and Costin 1979a,b,c; Wahren *et al.* 1994); salt desert shrublands (Whisenant and Wagstaff 1991); Serengeti grasslands (Belsky 1992); subantarctic islands (Meurk 1982); and Finnish snowbeds (Virtanen 1998).

Bowers (1993) concluded that herbivores were able to speed up or slow down succession, depending on the relationship between the competitive ability, palatability and occurrence of species in particular successional sequences. For example, differences between the grazing and trampling effects of hares, sheep and cattle resulted in an increase in heather cover with hares, no change in heather cover with sheep or a decrease in heather cover with cattle (Welch and Scott 1995), indicating that trampling rather than grazing *per se* had a greater impact on the cover of the dominant vegetation.

Change in floristics

Cessation of grazing may increase or decrease species richness depending on past management practices and the presence of other natural disturbances (Persson 1984; Bergelson and Crawley 1992). Bowers (1993) adopted the description of plant responses to disturbance of Noy-Meir *et al.* (1989) and modified it to include intermediates which are those plants that have a combination of grazing tolerance/avoidance attributes. McIntyre and Lavourel (1994) created a similar classification for southeast Australian grasslands. Their 'decreasers' were 'intolerant' species, which they defined as native species that declined with severe disturbance; tolerant species were those which were

present under any disturbance regime (native and exotic) and disturbance specialists were invading exotic species which occurred under high levels of disturbance.

Where grazing by vertebrate herbivores takes place in a previously ungrazed ecosystem, or exotic herbivores have been introduced to an ecosystem, native plant species richness usually declines, such as in the temperate grasslands (McIntyre and Lavourel 1994) and eucalypt woodlands of Australia (Pettit *et al.* 1995; Yates and Hobbs 1997), Tibetan marshland vegetation (Tsuyzaki and Tsujii 1990) and European salt marshes (Kiehl *et al.* 1996). Where grazing intensities are higher than natural levels, the result may be the establishment of exotic species (Mark 1994; Rose *et al.* 1995), and/or annuals (Facelli 1988; Whisenant and Wagstaff 1991; Pettit *et al.* 1995). Total species richness may increase, this increase being due to the establishment of exotic species at the expense of natives (Hofstede 1995; Pettit *et al.* 1995). As introduced species are generally palatable and are transported by the herbivores that eat them, higher numbers of exotic species may be found in these disturbed environments (Milchunas *et al.* 1989; Altesor *et al.* 1998).

Where there has been a long history of grazing, exclusion of herbivores tends to decrease plant species richness, such as in the sand sagebrush grasslands of Oklahoma (Collins *et al.* 1987), the mixed-grass prairies (Collins and Barber 1985), the Serengeti grasslands (Belsky 1992), English haymeadows (Smith and Rushton 1994) and the oldfield grasslands of Central Germany (Milton *et al.* 1997).

The reduction in species richness in long-term grazing exclosures in grasslands is frequently directly related to an increase in height/stature of the vegetation and a decrease in bare ground (Bassett 1980; Virtanen *et al.* 1997). Many short-statured plants become depleted or locally extinct in disturbance-free environments due to their inability to compete for light. For example, short-statured plant species were eliminated from grazing exclosures in Serengeti grasslands, causing a decrease in species richness (Belsky 1992).

Intermediate levels of grazing may provide conditions where species richness is maximised in plant communities (Bowers 1993), thus supporting the intermediate disturbance hypothesis of Connell (1978). This hypothesis has been modified recently by refining the definition of what constitutes a disturbance (Milchunas *et al.* 1989; Hobbs and Huenneke 1992) and whether disturbance is a single factor such as burning or grazing or a combination of factors such as burning and grazing (Collins and Barber 1985).

Fecundity

Herbivores may affect the reproductive ability of plants, by reducing the number of individuals in a community, by reducing the number of plants which reach maturity and therefore set seed, or by directly eating the reproductive parts (Galen 1990; Prins and Nell 1990; Bergelson and Crawley 1992; Scherff *et al.* 1994; McIntyre 1995; Kiehl *et al.* 1996). Consumption of an arctic legume by muskoxen reduced the probability of flowering during the next season (Mulder and Harmsen 1995), whilst rodent peaks (lemmings and voles) in Lapland coincided with low flowering frequencies of the herb *Solidago virgaurea* due to grazing on the nutrient rich stems (Andersson and Jonasson 1986). The removal of large vertebrate herbivores (elk and deer) increased the population of *Ipomopsis aggregata* (scarlet gilia) by up to 1000 times, also increasing the density of flowering plants (Bergelson and Crawley 1992). Vertebrate herbivore grazing of *Polemonium viscosum* (alpine sky pilot) was related to a delay in the ripening of seeds on regrowth of the grazed plant parts, possibly reducing the long-term seed production of individual plants by more than 80% (Galen 1990).

Regeneration success

Herbivore grazing has impacts on the competitive relationships of plant species. If the dominant plant in a community is palatable and grazing-sensitive, its dominance is reduced (Bowers 1993), creating opportunities for other species to establish or expand. For example, rabbits created suitable niches for the establishment of *Senecio jacobaea* seedlings by grazing competitive grass species, thus opening up the sward (Prins and Nell 1990).

Grazing as an endogenous disturbance facilitates the regeneration of inter-tussock species in *Themeda* grasslands in Africa (Belsky 1992) and Australia (Gilfedder and Kirkpatrick 1994; Lunt 1997). Competition for light and space in gaps is less strong than in closed swards. Populations of *Leucochrysum albicans*, an endangered daisy in Tasmania, were found to benefit from grazing by domestic stock due to the creation of bare ground from mechanical disturbance by stock and the reduction of competition from competitive, palatable grass species (Gilfedder and Kirkpatrick 1994).

Litter build-up is often reported on ungrazed sites (Milchunas *et al.* 1989; Coughenour 1991). The impacts of litter build-up may promote or inhibit seedling establishment in gaps, by altering the microclimate and water retention abilities (Pyrke 1994; Belsky and Blumenthal 1997) or through the suppression of species that require bare ground to establish (Bullock *et al.* 1994). Cattle grazing and trampling in the Paramo grasslands removed the litter layer which provided ground cover for the germination of stem rosettes

(Hofstede *et al.* 1995). The thistle *Cirsium vulgare* recorded a greater success in seedling emergence in microsites that had no canopy or litter on the ground (Bullock *et al.* 1994).

What Influences the Impacts of Vertebrate Herbivores?

Intensity, duration and seasonality

Plant responses to grazing may depend on the number and diversity of grazers present, the length of time the community is grazed and the season in which it is grazed. Any variation in these factors creates a number of different grazing regimes with each regime having a different impact on the vegetation. Plant species which are grazed continuously throughout the season may be killed (Leigh *et al.* 1991; Grice and Barchia 1992; Hulme 1996) or they may survive, and record higher rates of productivity than if they were ungrazed (McNaughton 1985; Leigh *et al.* 1991). Some systems are adapted to high grazing pressure. For example, high intensity sheep grazing in an English grassland produced a greater number of species than light grazing (Treweek *et al.* 1997). However, the impacts of the grazing pressure varies between systems. A stocking rate that has little or no impact on plant species in one environment, may have an extreme impact in another (Welch and Scott 1995). For example, impacts of introduced vertebrate herbivores in low altitude grasslands may be considered to be beneficial to the survival of some plant species (Gilfedder and Kirkpatrick 1998). However, the same herbivores are responsible for the disappearance of some tall herb species in alpine environments (Carr and Turner 1959b; Wimbush and Costin 1979a,b,c; Wahren *et al.* 1994).

Plants may compensate for any lost tissue as a result of vertebrate herbivore grazing. Timing of grazing is important in compensation. Plants which are grazed early in the growing season (i.e. early spring) may recover lost biomass (Vinton and Hartnett 1992) and be able to flower and set seed (Escarre *et al.* 1996). Some plants may recover lost biomass but at the expense of flowering (Leigh *et al.* 1991) whilst others may not even replace lost biomass (Hulme 1996), and will degenerate (Bridge *et al.* 1983). Late defoliation may have a negative effect on sexual biomass (Escarre *et al.* 1996; Noy-Meir and Briske 1996). The removal of biomass may be more critical to plants that live in high-stress environments such as arctic and alpine areas, as their ability to replace lost tissue may be limited by the short growing season (Gauthier *et al.* 1995; Virtanen *et al.* 1997).

The interrelationship between duration of grazing and seasonality affects plant communities through the effects on individual species. Whisenant and Wagstaff (1991) found that stock grazing in late autumn was the least detrimental to the health of a salt bush shrubland, whilst early spring grazing increased the relative cover of annuals over perennials and led to degradation of the salt bush community. Treweek *et al.* (1997) found that species richness in a grassland increased after grazing in spring or winter, but stated

that if a grassland was grazed during the spring of one season, then it should not be grazed heavily during the following spring. However, studies in plant compensation have shown that the same disturbance in the next growing season may not yield the same level of productivity or response (Vinton and Hartnett 1992).

Fluctuating populations of wild (native) herbivores such as lemmings (Moen *et al.* 1997), lemmings and voles (Andersson and Jonasson 1986), and snowshoe hares (John and Turkington 1995) may directly (through preferential grazing) and indirectly (through mechanical disturbance) influence the relative abundance of plant species. Harrington *et al.* (1984) argue that herbivore populations will either crash or migrate when pasture quality is low, enabling the vegetation to recover from times of drought. For example, caribou of Southampton Island, Canada rely heavily on lichens as a food source during the winter months. As these lichen populations may be overgrazed in particular areas, and as they are slow to recover from grazing (Oullet *et al.* 1993), caribou numbers are affected.

Environmental influences

Plant species respond differently to grazing in different situations (Noy-Meir *et al.* 1989; John and Turkington 1995). The degree of influence of vertebrate herbivores on plant species/communities is often dependent on local site conditions and climatic conditions (Bassett 1980; Rawat and Unyal 1993). Site history plays an important part in the reaction of plant communities to the cessation of grazing (Milchunas and Lauenroth 1993). Where grazing has been present for a long time in a system, communities are more likely to be delineated by abiotic factors (Austin *et al.* 1981; Persson 1984; Whisenant and Wagstaff 1991). Other factors (climate, soil nutrients, topography) may be more important than grazing regime in determining community composition (John and Turkington 1995). Maschinski and Whitham (1989) concluded that microsite was an important component in determining plant responses to grazing as nutrient availability, plant association and timing of grazing were important factors affecting plant compensation. Welch and Scott (1995) found plant species richness to be more affected by soil type than grazing intensity in acidic Scottish moorlands. Gutierrez *et al.* (1997) found that species richness and community composition around grazing exclosures in shrubby vegetation in the Chilean semiarid zone were determined by abiotic factors (rainfall and soil nutrients), whereas grazing effects were restricted to the relative abundance of plant species.

Numerous studies have linked grass and forb growth with incidence and seasonality of rainfall (Wimbush and Costin 1979a,b,c; McNaughton 1985; Coughenour 1991; Leigh *et al.* 1991; Milchunas and Lauenroth 1993).

Relative Impacts of Different Vertebrate Herbivore Species

Palatability and selectivity

Herbivores are selective about the plant species they eat, which parts they eat and when they eat them. Different species of herbivores have preferences for different species and parts of plants (Harrington *et al.* 1984; McNaughton 1985; Stuth 1991). Kangaroos selectively graze sites that sheep do not graze (Andrew and Lange 1986; Grice and Barchia 1992), while the diet of goats consist of more browse than does the diet of cattle, sheep, rabbits or kangaroos (Harrington *et al.* 1984). The diets of rabbits and kangaroos (Leigh *et al.* 1989), and wallabies and wombats (Craven 1997) overlap, but preferences for particular plant species and lifeforms differ (Tiver and Andrew 1997).

Palatability may be determined by observation of what is being grazed (van Rees 1984), which species establish or dominate in grazing exclosures (Leigh *et al.* 1987; Gibson and Kirkpatrick 1989), or by crude protein and nutrient analyses of plant material (Andrighetto *et al.* 1993).

The attractiveness of any plant species depends partially on the amount and types of palatable material available (Bakker *et al.* 1983). For example, grazing of palatable herbs in grasslands may be less intense than if the same species were grazed in heath or woodlands (Harrington *et al.* 1984). Some species are only palatable during particular life-cycle phases such as new growth, seedling or seed, whilst others are only eaten in extreme situations, such as drought. Grazing during periods of drought is likely to affect more plant species than grazing in favourable times, with all vertebrate herbivores eventually grazing the same edible species down to bare soil in long dry periods (Harrington *et al.* 1984). Perez (1992) suggested that the foliage of Andean rosettes was grazed by cattle in the dry season due to a scarcity of ground cover of other more palatable species.

Grazing preferences are partially constrained by the morphology of the animal, including its bite size and ability to reach/obtain certain plants (Noy-Meir *et al.* 1989). Cattle have larger, less sensitive mouths than horses, sheep or goats, and therefore are less selective in their choice of plants (Harrington *et al.* 1984), and sheep are able to graze much more closely to the ground than horses (Negi *et al.* 1993). Therefore the structure of the plant is also important. Taller, herbaceous species appear to be particularly susceptible to grazing (Peart 1989; Ehrlen 1995). Muskoxen preferentially selected larger individuals of an arctic legume with many inflorescences (Mulder and Harmsen 1995). Tall *Molinia* grass tussocks were targeted by cattle above other broad-leaved grass species (Grant *et al.* 1996).

Some plants contain toxins or morphological adaptations that are detrimental to vertebrate herbivores (McNaughton 1985; Fenner *et al.* 1993). A biogeographic study on the effects of hares on boreal forest species indicated that where grazing pressure was low, tree species were found to contain less toxins in regions where grazing pressure was low than in densely populated areas (Bryant *et al.* 1989).

Other influences of different grazers

Physical disturbance of the ground by wallowing and digging animals provides heterogeneity at a microtopographic scale, creating conditions under which maximum species diversity may be obtained (Collins and Barber 1985). The resultant gaps may be colonised by plant species requiring bare ground for establishment, that would otherwise be outcompeted by taller, denser vegetation (Noy-Meir *et al.* 1989). The creation of bare ground or gaps in the canopy may be both positive and negative depending on the plant and animal species present, the time of year and the ecosystem involved. Boar grubbing and vole lawns caused an increase in species richness in ex-agricultural grassland in Central Germany (Milton *et al.* 1997). Variation in the animal species creating the disturbance resulted in differences in colonising plant species. Disturbance by rodents favoured wind and mammal dispersed species, disturbance by boars favoured small therophytes, whilst disturbance by mound building ants favoured creeping perennials and shrubs (Milton *et al.* 1997).

Recovery of vegetation after grazing is also influenced by the species of herbivore. Horses are thought to have less of an impact on grazing lands than sheep because more plant biomass remains standing after grazing (Negi *et al.* 1993), thus recovery is faster.

Differences in Impacts of Native and Introduced Herbivores

Wild herbivores in their natural state depend upon plant populations for their survival (McNaughton 1985; John and Turkington 1995). The free-ranging nature of wild or unrestricted herbivores means that their selectivity is not confined to one place, enabling plants to recover from loss of biomass from grazing and associated activities (digging, trampling, uprooting) (Tiver and Andrew 1997). With increases in human populations and the adoption of domestic stock for farming, grazing pressure (per unit area) has increased as herbivores become restricted in their range. Culling of hippopotamus in National Parks in Uganda has been used to preserve the overgrazed grassland food source of the animals (Lock 1972).

The introduction of exotic herbivores with different plant preferences to native grazers has been tentatively suggested as a management tool in Scottish upland moors (Fraser and Gordon 1997). Diet preferences were similar between deer, goats and South American

camelids, although guanacos actively avoided some plant species that deer and goats ate when preferred palatable species were lacking (Fraser and Gordon 1997).

Studies in Australian mainland lowland grasslands (McIntyre 1995), alpine grasslands (Carr and Turner 1959b; Wimbush and Costin 1979a,b,c; Wahren *et al.* 1994) and grassy woodlands (Pettit *et al.* 1995) identify domestic stock grazing as the main cause in the reduction of native species richness and the introduction of exotic flora, neither of which occurred under grazing pressure from native herbivores. However, in Tasmanian remnant lowland grasslands, some rare and endangered plant species, such as *Leucochrysum albicans* (Asteraceae) (Gilfedder and Kirkpatrick 1994) are found in stock grazed areas in moderate or poor condition (Kirkpatrick and Gilfedder 1995). Other endangered Tasmanian plant species e.g. *Lepidium hyssopifolium* (Brassicaceae) and *Stackhousia gunnii* (Stackhousiaceae) (Gilfedder and Kirkpatrick 1998) have particular requirements, such as the need for bare ground for seedling establishment, but also require the absence of domestic stock grazing.

The introduction of rabbits and domestic stock into Australia during the past 200 years is generally seen to be detrimental to the conservation of native plant communities (Jackson 1973; Wilson 1990). Although the dietary requirements of sheep, cattle, goats, rabbits and kangaroos overlap, each species has a different pattern of selectivity, resulting in different impacts on the vegetation (Harrington *et al.* 1984). Rabbits appear to influence plant composition more than native herbivores in Australian grasslands (Leigh *et al.* 1989). In a 6 year study, they found that the influence of kangaroos was mainly restricted to grass tussock size and cover, whereas rabbits influenced the abundance of grasses, forbs and woody species. Sheep have been found to be more influential than rabbits, kangaroos or goats in inhibiting the establishment and regeneration of woody species in Australian chenopod shrublands (Tiver and Andrew 1997).

In an Australasian context, the greatest impact of exotic herbivores (mainly domestic stock) is on the conservation value of natural ecosystems, through reductions in native species richness and the introduction of exotic plant species (Wimbush and Costin 1979a,c; Scougall *et al.* 1993; Benson 1994; Tremont and McIntyre 1994; Yates and Hobbs 1997; Whitehouse *et al.* 1988).

The Impacts of Grazing Management on Australian Grasslands

There are many examples where the removal of stock grazing from Australian ecosystems has resulted in an improvement in the conservation value of a system (Carr and Turner 1959a,b; Wimbush and Costin 1979a,b,c; Wahren *et al.* 1994; McIntyre 1995). Pastoral practices combined with the introduction of domestic stock and pests such as rabbits have been responsible for massive soil erosion across a wide range of ecological zones from the arid lands of central and northern Australia to the alpine areas in the southeast and Tasmania (Jackson 1973; Harrington *et al.* 1984; Hobbs and Huenneke 1992; Cullen 1995).

Aboriginal impacts on the environment are under debate (see Bowman 1998), but it is generally accepted that, while some grasslands exist due to Aboriginal burning practices, others are defined by climatic constraints, especially in the alpine/subalpine zone (Kirkpatrick and Duncan 1987; Thomas and Hope 1994). Lowland grasslands created by Aboriginal people predate European occupation and are likely to have been in a state of quasi-equilibrium with occasional firing in the presence of marsupial grazing.

Whilst a great deal of Australian vegetation is fire adapted, rainforest and alpine vegetation can be irreversibly damaged by infrequent fire (Balmer 1991; Cullen 1991). Fire has been used as a management tool for graziers to promote green pick in marginal rangelands (Jackson 1973; Shepherd 1973). The alpine and subalpine grasslands of southeastern Australia were grazed almost from the beginning of European occupation of the continent (Carr and Turner 1959a,b; Jackson 1973; Costin *et al.* 1979). Frequent fire became an integral part of the management of these grasslands as the native *Poa* species are relatively unpalatable (containing high levels of silica). Burning these *Poa* grasslands ensured that grass tussocks remained small and that palatable new growth was plentiful (Jackson 1973). The adoption of burning as a management tool in high altitude grasslands was noted from the mid 1800s as having a detrimental effect on alpine and subalpine vegetation and soils, especially with respect to soil erosion (Strzlecki 1845).

Early botanical records report that grassy alpine areas were dominated by tall tussocks of either *Poa* spp. or *Chionochloa frigida*, with forbs dominating the intertussock spaces. These forbs were preferentially grazed by the introduced stock and rabbits and so became relatively rare (Carr and Turner 1959a,b; Jackson 1973; Costin *et al.* 1979). In Tasmania, rabbits increased to reach plague proportions, creating even greater stress on the remaining palatable plants (Scott 1955; Jackson 1973; Shepherd 1973). The result of this pressure, combined with the climatically hostile nature of the alpine zone, caused a great deal of soil erosion in the Australian high country (Carr and Turner 1959a,b; Wimbush and Costin

1979a,b,c; Cullen 1995). This was enough for some States to act on the presence of vast numbers of rabbits, and to control grazing leases. Grazing was banned from the alpine zone in Kosciuszko National Park in 1958 (Costin *et al.* 1979), and on a large part of the Eastern Central Plateau, Tasmania in 1989 (Whinam *et al.* 1994). Cattle grazing still continues during the summer months in some parts of the Victorian High Country (Wahren *et al.* 1994) and sheep and cattle graze on private land in Tasmania at altitudes up to 1050 m.

Debates on the impacts of domestic stock in alpine and subalpine grasslands and heaths have been continuing since the 1940s (Carr and Turner 1959a,b; Carr 1977; Wimbush and Costin 1979a,b,c; Gibson and Kirkpatrick 1989; Leigh *et al.* 1991; Wahren *et al.* 1994). Initially land managers were concerned about issues of soil conservation as soil erosion increased in water-catchment areas (Costin 1958; Carr and Turner 1959a). Later, the disappearance of palatable plant species, mainly herbs, and processes of revegetation of degraded sites became issues. A series of exclosures were built in the Victorian alpine area in the 1940s. These plots have been monitored for over 50 years (Carr and Turner 1959a,b; Wahren *et al.* 1994). Similar studies have been carried out in the alpine areas of New South Wales also over decades (Wimbush and Costin 1979a,b,c). These studies found that the cessation of grazing led to: 1) an increase in vegetation cover and the consequence of this, a decrease in bare ground; 2) an increase in palatable species such as tall alpine herbs and fabaceous shrubs; and 3) an increase in catchment water yield.

Research Hypotheses

The two major research hypotheses of this thesis are:

- H₁ patterns of vegetative recovery in Tasmanian alpine/treeless subalpine areas are affected by the presence of domestic stock, feral and native vertebrate herbivores.
- H₂ there are few tall alpine herbfields in Tasmania due to the year round presence of native vertebrate grazers (and rabbits).

Suitability and Characteristics of the Study Area

The Eastern Central Plateau (Fig 1.1) is the most suitable site in Tasmania to assess the impacts of different vertebrate herbivores on grassy alpine vegetation. A variety of native and exotic herbivores are present on the Plateau (sheep, rabbits, wallabies, wombats). Cattle and sheep have been grazed in the area to the west of Great Lake from the 1820s (Jorgenson 1829), and rabbits have been common in the region since the 1920s (Jackson 1973). The Eastern Central Plateau has been a major focus of land management issues dealing with burning and grazing (Strzleki 1845; Mitchell 1962; Jackson 1973; Shepherd 1973; Pemberton 1986; Cullen 1995). The presence of existing grazing exclosures and

photographic data sets of varying ages provided a valuable opportunity to study long-term impacts of grazing over a relatively short time period.

The Eastern Central Plateau experiences the most continental climate of any region in Tasmania. Much of the Central Plateau lies 1000 m or more above sea-level. Although the climatic treeline for eastern Tasmania is approximately 1300 m (Kirkpatrick 1982), alpine grasslands and heaths, rather than woodlands, dominate many of the broad valleys (1000-1300 m). The grasslands may have been promoted due to local climatic conditions such as cold air drainage (Jackson 1973), and they have been relatively stable for the past 8000 years (Thomas and Hope 1994). The Eastern Central Plateau was not glaciated during the last glacial period (Thomas and Hope 1994; Corbett 1996). Thus, soils akin to alpine humus soils underlying the tall alpine herbfields of the Australian mainland, have developed (Jackson 1973; Kirkpatrick 1989). Species and genera classified as tall alpine herbs by Costin *et al.* (1979) are common on the Eastern Central Plateau.

Research Questions

Limited information exists on the comparative effects of native vertebrates, rabbits and domestic stock grazing on vegetation. Studies suggest that the effects of native vertebrate herbivores is very small compared to that of rabbits (Leigh *et al.* 1989), and that these grazers combined have minimal effect when compared with the impact of domestic stock grazing (Tremont and McIntyre 1994). No data are available on the effects of domestic stock versus rabbits and native vertebrate herbivores in Tasmanian alpine (*sensu* Kirkpatrick 1983) vegetation (Kirkpatrick 1986). This shortfall is addressed by the question:

Are there differences between the effects of domestic stock and native and feral herbivores on the regeneration, structure and floristics of alpine vegetation?
(Chapters 2 and 3).

Many studies have found that the ability of the community to regenerate under natural conditions was in part dependent on the type and intensity of disturbance (Wimbush and Costin 1979a,b,c; Scott and Hunter 1988). The process of recovery is exacerbated in low productivity alpine environments, where short growing seasons severely limit the opportunity for plants to recover after grazing. Therefore, intensive grazing in alpine areas may lead to a long-term decrease in vegetation cover, resulting in an increase in bare ground. Where bare ground gaps are large, shrubs are more likely to establish, but where they are small, grasses are more likely to establish (Williams and Ashton 1987a; Williams 1990, 1992).

What are the long-term and short-term patterns of regeneration in Tasmanian alpine communities?

Do these patterns differ under different grazing pressures?

Which lifeforms dominate the regeneration process in Tasmania?

(Chapter 3).

Literature from the Australian mainland and overseas describe an increase in the cover and abundance of tall herb species with the cessation of grazing (Carr and Turner 1959b; Wimbush and Costin 1979a,b,c; Wahren *et al.* 1994), resulting in an increase in the area of tall alpine herbfields (*sensu* Costin *et al.* 1979) in the alpine areas of Victoria and New South Wales. Many of the species which dominate tall alpine herbfields are present in Tasmania, but this community type has a very small range, confined to small islands in fast-flowing rivers (Kirkpatrick 1989). Kirkpatrick (1989) hypothesised that the relative absence of this community is due to the year round presence of vertebrate herbivores (native and feral) which selectively graze the tall herb species.

Mainland mountains experience a continental climate which allows for long periods of deep snow lie during the winter months, essentially excluding large vertebrate herbivores from the alpine zone (Carr and Turner 1959a; McVean 1969; Williams and Costin 1994). The Tasmanian alpine zone is much more maritime, and therefore does not experience periods of extended snowlie over much of the alpine zone, allowing vertebrate herbivores to live and graze year round in the alpine zone.

What are the effects of vertebrate herbivore grazing on tall alpine herbfield species?

(Chapters 2, 4 and 5).

Which lifeforms dominate in naturally ungrazed Tasmanian alpine vegetation?

(Chapter 5).

Carr and Turner (1959b) hypothesised that tall alpine herbfields are a disturbance community derived from grasslands. McVean (1969) supports this, stating that tall alpine herbfields require disturbance to be able to dominate in a competitive grassy environment. Such disturbance regimes can be met through snowpatches or corbie-grub (*Oncopera* spp.) grazing.

Is there evidence of disturbance on sites dominated by tall alpine herbs in Tasmania?

(Chapter 5).

Structure of Thesis

This thesis is presented as a series of papers, with themes relevant to those discussed above, namely regeneration in treeless subalpine areas under the influence of different vertebrate grazers, with special reference to tall alpine herbs. Alpine will be used as shorthand for treeless subalpine vegetation (*sensu* Kirkpatrick 1983) in Tasmania throughout this thesis.

Chapter 2 focuses on the effects of different species of vertebrate herbivores on the vegetation (floristics, structure, revegetation) of Liawenee Moor, which is grazed by sheep during the summer months, and rabbits and native vertebrate herbivores all year round. This chapter has been published in the *Australian Journal of Botany*, vol 47, pp. 817-834, 1999. Chapter 3 explores the process of regeneration of disturbed sites, the relationship between regeneration and presence of different species of vertebrate herbivore, and the dominant lifeforms involved in recovery in different plant communities. This chapter has been submitted for publication in *Arctic, Antarctic and Alpine Research*. Chapter 4 discusses the relative impacts of different species of vertebrate herbivores on the flowering success of tall alpine herbs. This chapter has been submitted for publication in the *Australian Journal of Botany*. Chapter 5 reports on the species composition and dominance of species of naturally ungrazed areas on the Eastern Central Plateau, namely islands in fast-flowing streams. This chapter has been published in the *Papers and Proceedings of the Royal Society of Tasmania*, vol. 132, pp. 9-14, 1998.

Repetition in this format is unavoidable as the papers cover related topics, but as stand alone papers, they are required to have the introduction, sometimes reviewing the same literature. The papers are tied together, and the above hypotheses and questions addressed in the concluding chapter (Chapter 6).

Plant nomenclature follows Buchanan (1995).

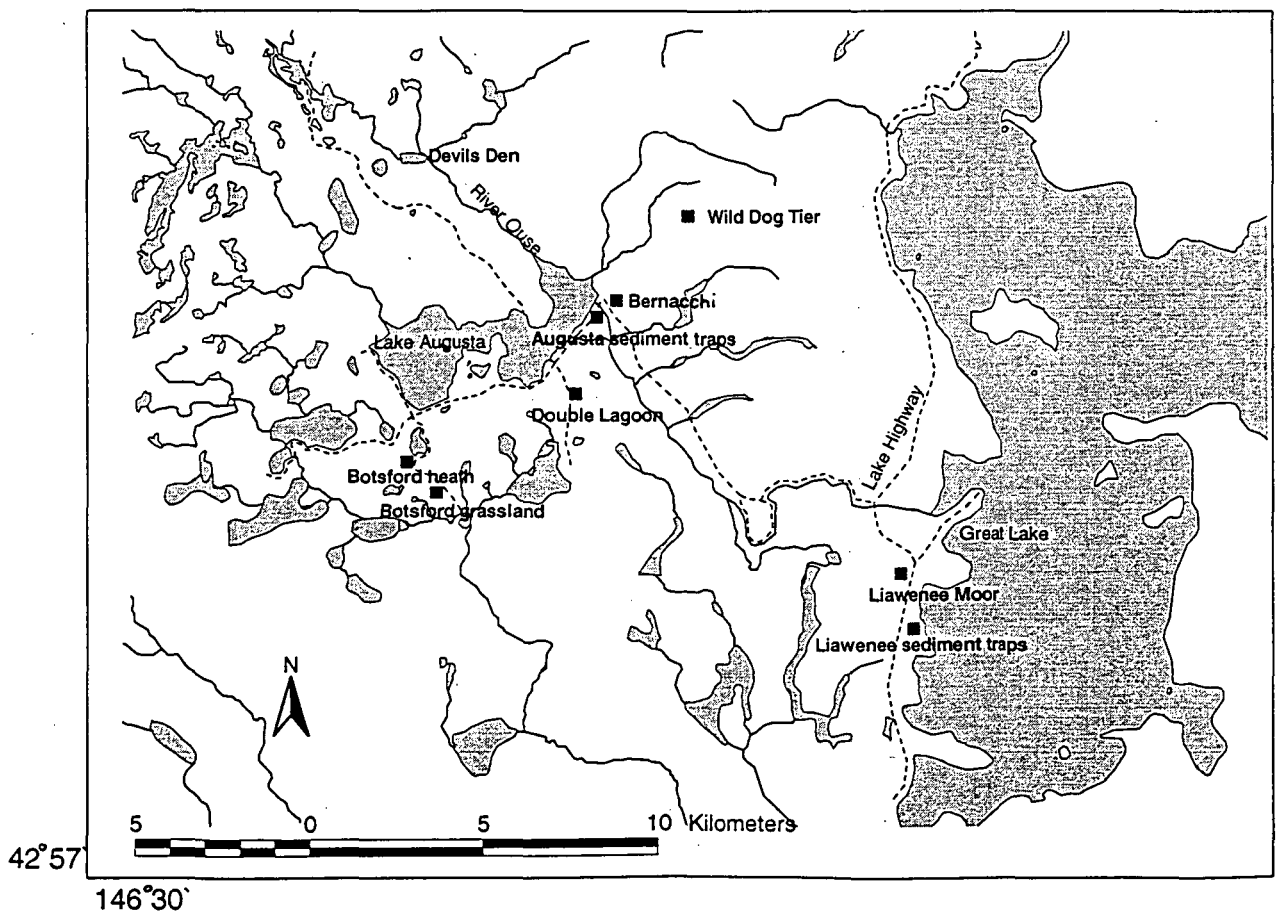
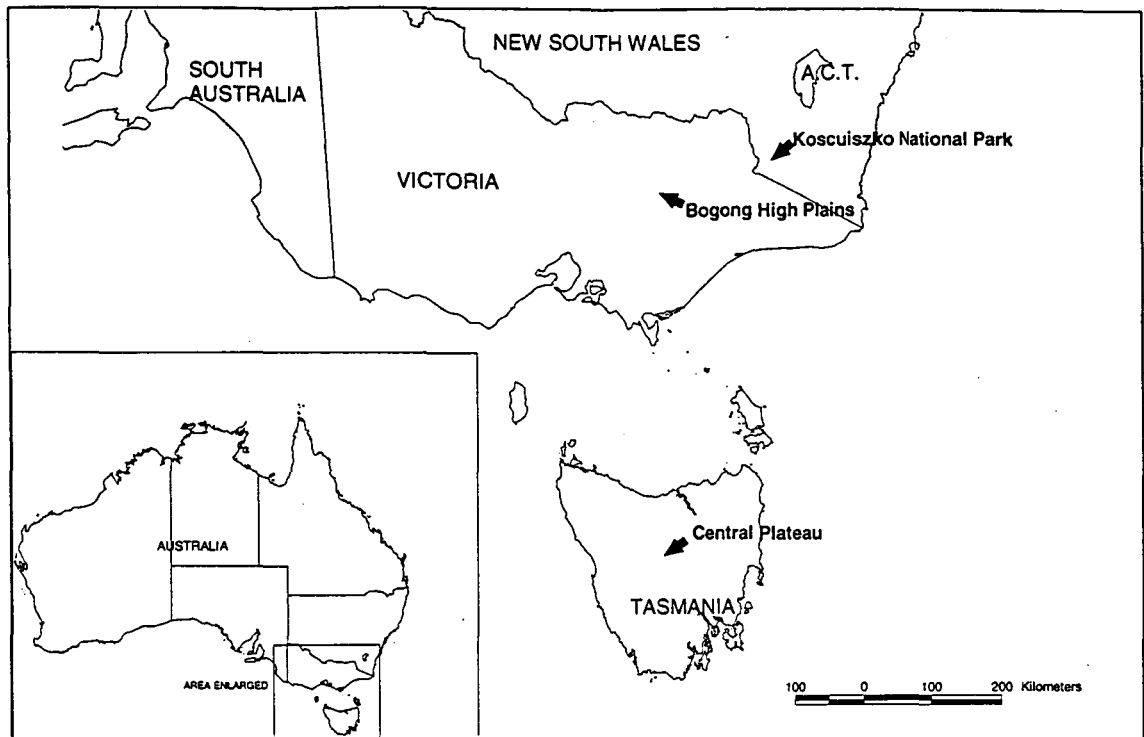


Figure 1.1 Map showing the location of the experimental sites on the Eastern Central Plateau. The regional map shows the location of mainland alpine sites mentioned in the text.

Chapter 2

The Comparative Effects of Stock and Wild Vertebrate Herbivore Grazing on Treeless Subalpine Vegetation

Introduction

Most parts of the alpine and subalpine zones of Australia that have a substantial grass or forb component in their vegetation have been grazed by domestic stock and feral rabbits during the past 200 years. This vegetation has also been grazed by wombats and wallabies, with the exception of the higher alpine areas of the Snowy Mountains and Victoria. There is a large body of evidence that exclusion of vertebrate grazers leads to dramatic changes in plant species composition and cover (Carr and Turner 1959*a,b*; Wimbush and Costin 1979*a,b,c*; Leigh *et al.* 1987; Gibson and Kirkpatrick 1989; Wahren *et al.* 1994). These changes typically include an increase in forb cover, an increase in shrub cover and an increase in overall vegetation cover.

The greater proportion of changes in vegetation cover recorded in grazing exclosures on mainland mountains are generally attributed to the exclusion of domestic stock (Wimbush and Costin 1979*c*; Leigh *et al.* 1987; Wahren *et al.* 1994). However, Kirkpatrick (1989) hypothesised that the dominance of tall forbs in Australian high alpine vegetation could be a function of the lack of wallabies and wombats. These animals are abundant in (equivalent) vegetation in Tasmania, where tall herbs are present but not dominant. Marsupial grazers and rabbits are more commonly found in the subalpine regions of mainland Australia rather than in the alpine zone. Research in these regions supports the hypothesis (Leigh *et al.* 1987).

Given the relative paucity of work differentiating between the effects of different mammalian herbivores on temperate grassy vegetation in Australia, (Leigh and Holgate 1979; Leigh *et al.* 1987), and the relative lack of data on total mammal grazing impacts on alpine/subalpine treeless vegetation in Tasmania, (Gibson and Kirkpatrick 1989;

Bridle and Kirkpatrick 1998; Chapter 5), this study was undertaken to assess the relative impacts of stock plus rabbits and native mammals, rabbits and native mammals and no mammal grazing in Tasmania. This chapter reports the impacts of stock exclosure and a total exclosure on a wide range of attributes of the treeless subalpine grassy shrubland of Liawenee Moor, Tasmania (Fig. 1.1). The following hypotheses are tested:

- (1) that alpine vegetation is differentially affected by variability in grazing pressure and type; and
- (2) that forb, shrub and total vegetation cover increase with increasing exclusion of mammals.

Tertiary basalt is the dominant rock type on Liawenee Moor (Pemberton 1986).

Average annual rainfall is 1049 mm per annum with a mean summer rainfall of 213 mm. The summer temperature varies between a mean daily minimum of 4.8°C and a mean daily maximum of 17.6°C (Bureau of Meteorology 1997). Winter temperatures vary between a mean daily minimum of -1.7°C and a mean daily maximum of 5.7°C. In January 1997 to June 1997 approximately 3000 sheep grazed on the Moor (40 square kilometres). In the 1995-1996 season a similar number of sheep grazed from November to May while approximately 20 sheep stayed on the Moor for the winter of 1997.

Liawenee Moor on the Eastern Central Plateau is the most extensive privately-owned area of alpine vegetation (*sensu* Kirkpatrick 1983) in Tasmania. Sheep usually graze on the Moor during late spring, summer and autumn (November to May). Jackson (1973) stated that, in the 19th Century, the vegetation of Liawenee Moor was a tall *Poa* tussock grassland with a rich inter-tussock herb cover. European records from the early 1800's are sparing in their descriptions of the vegetation of Liawenee Moor, despite the area being fairly well visited from very early on. The plains were covered with '... high coarse grass' (Jorgenson 1829 p. 24), '... intermixed with plantain and a species of heath' (Wedge in Crawford *et al.* 1962 p. 130). Robinson (in Plomley 1966) confirms these and other reports of the region by his comments on 'extensive plains', with the 'herbage as about Great Lake of a variety of herbs and wiry grass and occasionally moss [probably cushion plants]' (p. 542). All of the above 19th Century observers commented on the abundance of kangaroo and sightings of wild cattle in the region.

Palaeoecological studies from Camerons Lagoon, due south of Liawenee Moor, indicate that grasses were more abundant before than after European settlement (Thomas and Hope 1994). Thomas and Hope concluded that, as exotic species appeared in the pollen record approximately 150 years ago, followed by charcoal deposits in the core, the initial impact on the vegetation of the Moor was from domestic stock grazing rather than burning. Liawenee Moor was patch burned by graziers until 1978. The vegetation in an area within 300 m of the exclosures was last burnt in 1974 (as observed from aerial photographs). However there is no evidence of the exclosures being burned at this time.

Methods

The Exclosures

Two 100 x 30 m exclosures were set up on private land on Liawenee Moor by the Department of Agriculture in the late 1960s. The exclosures were set up approximately 7 m from the edge of the road and were orientated downslope from the roadside. One exclosure was built to keep out all vertebrate grazers, while the other was designed to keep out sheep and cattle only, allowing access to rabbits and native herbivores (wombats and wallabies). The exclosures are at an altitude of 1050 m and are within vegetation in which *Grevillea australis* and *Poa* spp. form a grassy shrubland. These exclosures were not kept in good repair. Despite this lack of repair, they were the only locations on the Moor where tall flowering forbs were abundant when the fences were repaired in 1995. The only baseline data available for the exclosures are interpretations of bare ground and vegetation cover from aerial photographs. There are no replicates of each exclosure treatment. Despite these problems, these exclosures are the oldest of their kind in the Tasmanian high country and were well-placed to avoid any effects of environmental heterogeneity.

After the repairs were made in 1995 the fencelines were checked regularly for signs of visiting vertebrates. The fence was raised in autumn 1996 after wallaby scats were found in the ungrazed exclosure. No new wallaby scats were found in this exclosure after this time.

Aerial Photographic Analysis

Aerial photographs of the site were obtained for 1974 (January) and 1993 (December). These photographs were enlarged to a scale of 1:1500 for 1993 and 1:2500 for 1974. The location of the exclosures was marked and the distribution of bare ground patches were mapped for the whole area. Two 15 m wide transects were located either side of the exclosures to be used as the sheep grazed plot (Fig. 2.1). The covers of bare ground and vegetation were mapped onto graph paper and their areas measured.

The shrub *Grevillea australis* was also discernible from the 1993 aerial photograph. Percentage cover was determined for each treatment.

Floristic Survey

Sixty 5 x 5 m quadrats were evenly spaced along six 100 m long transects, two in each treatment (Fig. 2.1).

Each quadrat was surveyed in January 1997. The following data were collected: treatment type consisting of - all herbivores (henceforth to be called sheep grazed), rabbits and natives without sheep (henceforth to be called rabbit plus native grazed), and no mammalian herbivores (henceforth to be called ungrazed); presence of all observable vascular plant species; species, height and cover of the dominant species in the tallest layer; species, height and cover of the dominant species in the mid-layer; species, height and cover of the dominant species in the ground layer. The following cover code was used: 1 = < 1% cover, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = 75-100%.

Environmental Data

Distance from the road (m) and percentage bare ground were recorded for each quadrat during the floristic data collection. Slope was measured with a clinometer every 10 m along the perimeter of each of the fencelines.

Mean, maximum and minimum soil depth (in cm) was taken from five probes, from the centre and midway to each of the four corners of the 5 x 5 m quadrats.

Scat data were collected from four 15 x 1m transects that were set up in the sheep grazed (s) plots (running S-N) and in the native and rabbit grazed (rn) exclosure (one running S-N, the other running E-W) (Fig. 2.1). Scats were removed when the transects

were set up and were then cleared again after identification and counting at the end of every season (end of February, end of May, end of August, end of November) over a 2-year-period. These data were used to estimate relative useage of the area by different species of vertebrate herbivover over time.

Lifeform Surveys

In March 1995 60, 50 x 50 cm quadrats adjacent to the floristic quadrats were surveyed (Fig. 2.1, Inset a) and percentage cover was recorded for all species present, bare ground, litter and rock cover. These quadrats were resurveyed in March 1996, in order to determine short term fluctuations in vegetation cover.

In March 1996 data on the cover in diameter classes and average height of grasses were measured in nested quadrats (2.5 x 2.5 m, Fig. 2.1, Inset a) which were located within the existing 5 x 5 m quadrats. Three categories were defined: small grasses with a tussock diameter of less than 5 cm; medium grasses with a tussock diameter between 5 and 15 cm; and large grasses with a tussock diameter of greater than 15 cm.

Shrub data (percentage cover over the quadrat and average height of a representative individual of each species) were also collected in the 5 x 5 m quadrats. The shrub data were also categorised into three groups: small shrubs were less than 20 cm in diameter; medium shrubs ranged from 20-50 cm in diameter; large shrubs were greater than 50 cm in diameter. For each class, percentage cover was estimated, the average height of the vegetation was measured and the dominant shrub species were identified.

Line Transect Survey of Herb Habitat

In February 1997, sixty 10 m long transects were surveyed (20 in each treatment) covering two sides of the 5 x 5 m quadrats (Fig. 2.1, Inset b). Structure of the vegetation (shrubby, grassy or non-existent overstoreys) was recorded every centimetre along the transects. Identity of the dominant in each layer and the average height of the dominant species were also recorded. The location of all tall herbs within the layers was noted.

Three vegetation classes were defined with reference to the location of the herbs: 1- where the overstorey was greater than 10 cm tall; 2 - where the overstorey was less than 10 cm tall but present; 3 - where the overstorey was bare ground, litter or lichen cover to

a depth of less than 1 cm. The frequency of occurrence of herb species was calculated for three classes of cover within each treatment.

Herb Invasion and Survival

In February 1997, populations of *Craspedia coolaminica* and *Podolepis jaceoides* were mapped across fencelines, from the rabbit plus native grazed treatment to the sheep grazed plots. At the time of the survey, damage to the vegetation by sheep grazing was limited.

Transects, 5 m in length and 50 cm apart, were located parallel to the fenceline. Any *C. coolaminica* or *P. jaceoides* rosettes located within 5 cm of the tape were noted, and the length of the longest leaf was measured. Notes were taken on the local habitat of the herb and its stage of development. Transects in the sheep grazed area were surveyed until no more rosettes of the target species were seen in the general area. Inside the rabbit plus native grazed treatment, three transects were surveyed to provide a comparison of the density of rosettes inside and outside the fenceline. The transects were resurveyed in September 1997 after sheep had grazed the area outside the exclosures and the number of disappearances of individuals was recorded.

Data Analysis

Global non-metric multi-dimensional scaling, using the default settings offered in DECODA, was considered to be the most appropriate method by which to explore gradients in the floristic data (Minchin 1987; Faith *et al.* 1987; Clarke 1993).

Ordinations were performed on the presence/absence data from the 60, 5 x 5 m quadrats and on the cover data from the 50 x 50 cm quadrats. Results in two and three dimensions were compared and if no major differences were found, then the two dimensional solution was used. These data were further analysed by the fitting of sample variables as vectors to the floristic data in ordination space (Minchin 1990).

Non-parametric statistics were used to test for any differences between plant community and environmental variables by grazing treatment (Mann-Whitney U test, Kruskal-Wallis H test, Wilcoxon-Signed Rank test) as data were not normally distributed and could not be transformed to meet the assumptions underlying the use of parametric statistics. In analyses of the structural data, the mid-points of the cover classes were used.

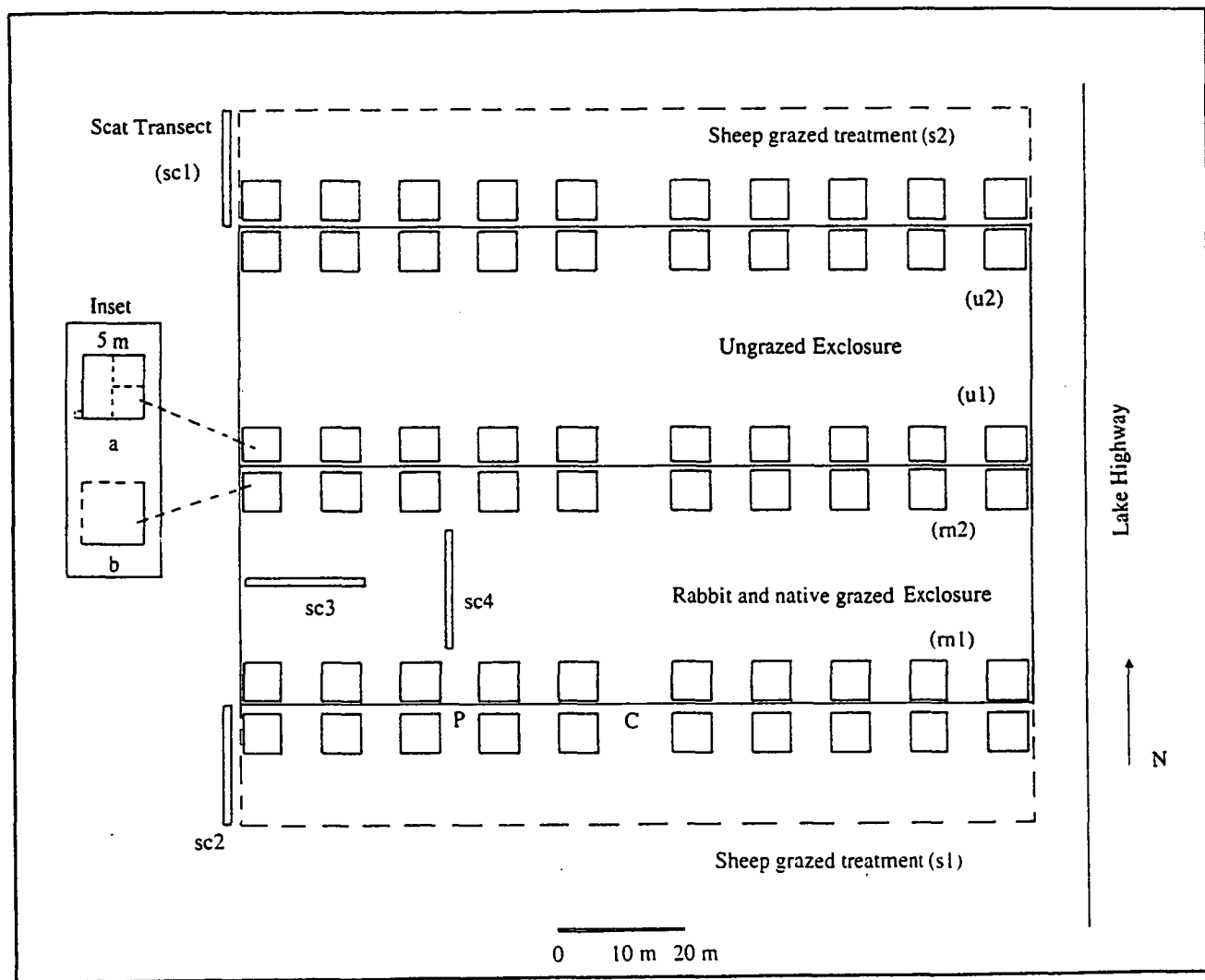


Figure 2.1 Layout of transects along fencelines and location of scat transects.

Inset shows the location of a) the 50 x 50 cm quadrats and the cover survey, and b) the line transects for the herb survey. S1, S2 = sheep plus rabbit plus native grazed transects; R/N1, R/N2 = rabbit plus native grazed transects; U1, U2 = ungrazed transects. P = site of *Podolepis jaceoides* survey, C = site of *Craspedia coolaminica* survey. SC = scat transect.

Results

Environmental Variation

Slope

The average slope of the transects was 1.6° . The slope of individual quadrats ranged from 0° to 3° . There was no significant relationship between treatment type and slope (Kruskal-Wallis $H = 0.047$, $P = 0.977$).

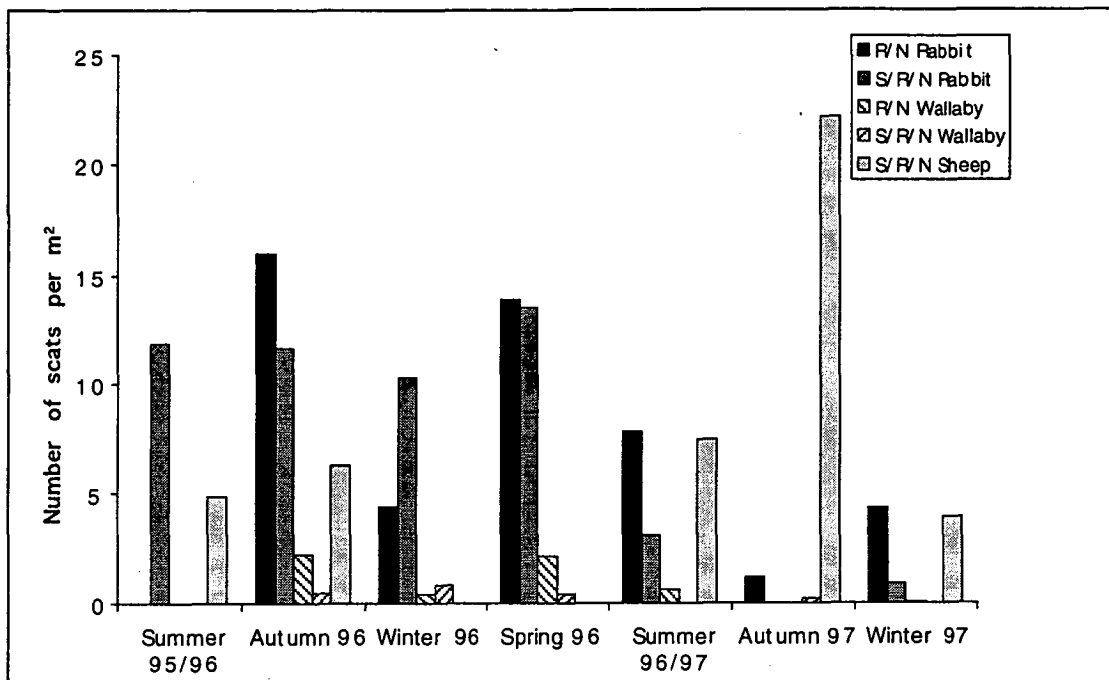


Fig. 2.2 Seasonal variation in the occurrence of scats of vertebrate grazers. Scat concentration is shown as number of scats per m^2

R/N = rabbits and native vertebrate herbivores present

S/R/N = sheep, rabbits and native vertebrate herbivores present. (Data for sheep scats are halved).

Scats

The number of scats varied from season to season. Sheep were absent during winter and spring of 1996. The majority of sheep scats counted for winter 1997 were deposited during June (Fig. 2.2).

Using the scat data from the 1 x 15 m transects, there were significantly more rabbit scats ($U = 13845$, $P = 0.011$) and more wallaby scats ($U = 14735.5$, $P = 0.034$) in the rabbit plus native vertebrate herbivore grazed enclosure than in the sheep grazed area.

The number of rabbit scats decreased dramatically over the study period, while the number of wallaby scats was relatively stable (Fig. 2.2). No wombat scats were recorded in the scat transects, but scats were seen in the rabbit plus native grazed enclosure and in the sheep grazed area.

Floristic Variation

Ordination

An ordination of the presence/absence data from the 5 x 5 m quadrats resulted in a 2-dimensional solution being accepted, with a minimum stress of 0.2388. An ordination of the cover data for the 50 x 50 cm quadrats also carried out. Again, the 2-dimensional solution was accepted with a minimum stress of 0.1167.

There are no significant differences in floristics on the ordination scores of the presence/absence data within treatments (u1 and u2, rn1 and rn2 and s1 and s2) from the 60, 5 x 5 m quadrats (Wilcoxon-Signed Rank test).

There was no significant difference between the ordination scores of the presence/absence data between the ungrazed plots (u1) and the rabbit plus native grazed enclosure (rn2) ($z = -1.376$, $P = 0.169$), nor was there any difference between the rabbit plus native grazed enclosure and the sheep grazed area ($z = -1.274$, $P = 0.203$). However there was a significant difference between the sheep grazed area (s2) and the ungrazed enclosure (u2) ($z = -2.803$, $P = 0.005$).

Vector fitting of sample variables to the ordination axes for the presence/absence data revealed distance from the road to be the strongest differentiator of the vegetation, followed by the amount of bare ground and the height and cover of the vegetation in the tallest stratum (Fig. 2.3). Presence of sheep scats was also statistically significant in ordination space, but the presence of wallaby, wombat and rabbit scats was not. Other environmental variables such as slope and soil depth were also significant.

The Kruskal-Wallis H test showed that some of the above variables were significantly different between treatments, such as: the height of the dominant species in the second

layer ($H = 10.431$, $P = 0.005$); the presence of wallaby scats ($H = 36.949$, $P < 0.001$); sheep scats ($H = 59$, $P < 0.001$); and rabbit scats ($H = 59$, $P < 0.001$).

Vector fitting of sample variables to the ordination of the 50 x 50 cm cover data supported the general results of the 5 x 5 m ordination, in that distance from the road and bare ground were the two most important vectors (Fig. 2.4). However, none of the animal scat vectors were significant and other environmental data were not collected for these quadrats.

Species Richness

There was no significant difference between treatments in the mean native species richness of the 5 x 5 m plots. However, mean total species richness was greatest in the sheep grazed plots (mean = 42.2, SE = 0.82) and least in the rabbit plus native grazed enclosure (mean = 39.5, SE = 0.67) ($H = 6.039$, $P = 0.049$).

There were significant differences in the number of exotic species between treatments ($s > u$ $z = -2.178$, $P = 0.029$, $s > rn$ $z = -1.956$, $P = 0.051$, $u > rn$ $z = -2.157$, $P = 0.031$). The rabbit plus native grazed enclosure had the least number of exotic species per 5 x 5 m quadrat. The mean values for exotic species richness were 5 per 25 m² (SE = 0.45) in the sheep grazed plots, 3.5 per 25 m² (SE = 0.34) in the ungrazed plots and 3 per 25 m² (SE = 0.29) in the rabbit plus native grazed enclosure.

Structural Variation

While there was very little difference in species composition between treatments, structurally they were very different (Plates 2.1 and 2.2). There were three distinct vegetation layers in all of the 20 ungrazed quadrats. Five of the 20 rabbit plus native grazed quadrats and 10 sheep grazed quadrats had two layers only. Where only two layers were recorded, either the shrubby tallest stratum or the grassy middle stratum were usually missing. A grassy ground layer was present in all quadrats not dominated by bare ground.

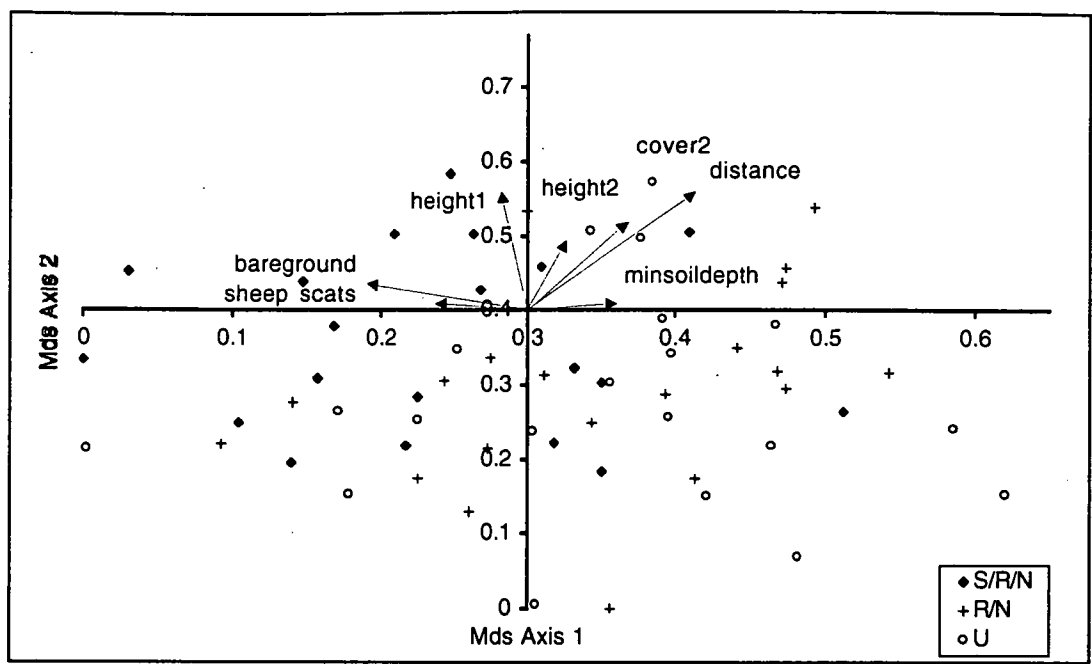


Figure 2.3 Ordination (in 2 dimensions) and vector fitting of species presence data from the 60, 5 x 5 m quadrats. Distance = distance from road; cover 2 = percentage cover of the dominant species in the middle stratum; height 1,2 = average height of the dominant species in the tallest or middle stratum, minsoildepth = minimum soil depth.

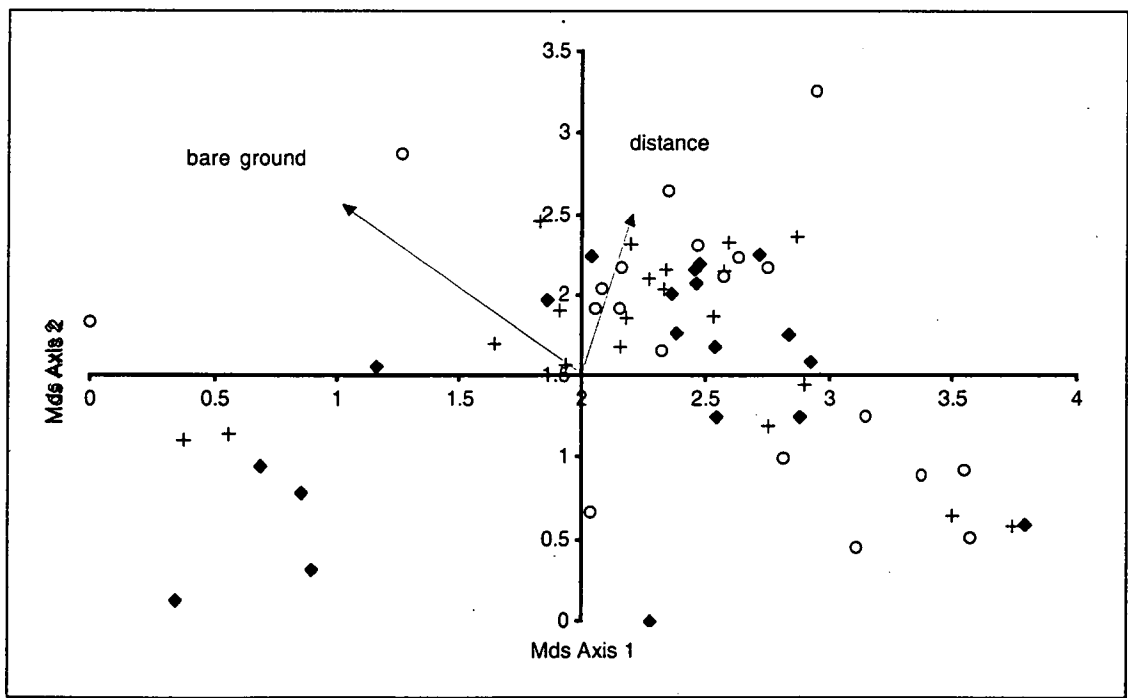


Figure 2.4 Ordination (in 2 dimensions) and vector fitting of species cover data from the 60, 50 x 50 cm quadrats. Legend and vector descriptions are the same as Fig. 2.3.



Plate 2.1 A comparison across the northern fenceline (looking East) from sheep, rabbit and native herbivore grazed vegetation (left) to ungrazed vegetation (right).



Plate 2.2 Looking East along the fenceline from the ungrazed enclosure (left) to the rabbit and native herbivore grazed enclosure (right). Yellow flowers are predominantly *Podolepis jaceoides*.

Tall herbs

The percentage frequency of tall herbs (from presence data in the 5 x 5 m quadrats) was significantly less in the sheep grazed treatment than either the rabbit plus native grazed enclosure ($z = -2.236$, $P = 0.025$) or the ungrazed plot ($z = -2.088$, $P = 0.037$). Small herbs showed the opposite effect, having greater numbers in the sheep grazed plots than both the rabbit plus native grazed enclosure ($z = -2.989$, $P = 0.003$) and the ungrazed enclosure ($z = -2.006$, $P = 0.045$). While some of the tall herbs were present in all three treatments, others showed preferences for less intensely grazed sites (e.g. *Senecio lautus* which was present in 15% of sheep grazed quadrats compared to 50-60% in the other grazing treatments, Table 2.1).

Shrubs

There was no significant difference in the percentage cover of small, medium or large shrubs between treatments (large $H = 3.711$, $P = 0.592$, medium $H = 4.19$, $P = 0.522$, small $H = 1.396$, $P = 0.925$). The average height of large shrubs was greater where grazing pressure was reduced ($H = 17.09$, $P = 0.004$). *Leucopogon montanus* was the dominant shrub species in the small category and *Olearia algida* was the most dominant shrub species in the medium category. There was no significant difference in percentage cover or average height between grazing treatments for these species (Table 2.2).

Grevillea australis was the dominant species in the large category and it was significantly taller in the ungrazed treatment than in the sheep grazed plots (Table 2.2).

The 1993 aerial photographic analysis showed that the percentage cover of *Grevillea australis* was greater inside the enclosures, covering 17% of the rabbit plus native grazed enclosure and 14% of the ungrazed plot. In contrast it covered only 9.5% of the sheep grazed area (Plate 2.3). However, there was no significant difference in cover of *Grevillea australis* between the treatments, using the plot data.

Table 2.1 Percentage frequency of species in each treatment type

U = ungrazed, R/N = rabbit and native vertebrate herbivore grazed
 S/R/N = sheep, rabbits and native vertebrate herbivores present
 tall herb > 10 cm, small herb < 5 cm, herb > 5 cm but < 10 cm
 i = introduced species, e = endemic to Tasmania

Species	Lifeform	S/R/N	R/N	U
<i>Olearia algida</i>	shrub	100	100	100
<i>Leucopogon montanus</i>	shrub	90	100	90
<i>Grevillea australis</i>	shrub	80	80	90
<i>Leucopogon stuartii</i>	shrub	50	85	35
<i>Epacris gunnii</i>	shrub	25	35	30
<i>Richea acerosa e</i>	shrub	15	-	15
<i>Leucopogon hookeri</i>	shrub	10	-	10
<i>Epacris petrophila</i>	shrub	10	10	20
<i>Hakea microcarpa</i>	shrub	5	-	-
<i>Ozothamnus hookeri</i>	shrub	-	-	5
<i>Pimelea pygmaea e</i>	mat shrub	100	90	80
<i>Coprosma moorei</i>	mat shrub	90	85	95
<i>Exocarpos nanus</i>	mat shrub	65	55	55
<i>Cryptandra alpina e</i>	mat shrub	5	30	-
<i>Craspedia glauca</i>	tall herb	100	100	90
<i>Cerastium glomeratum i</i>	tall herb	100	90	100
<i>Craspedia coolaminica</i>	tall herb	95	100	100
<i>Leptorhynchos squamatus</i>	tall herb	95	100	100
<i>Microseris lanceolata</i>	tall herb	70	80	90
<i>Ranunculus lappaceus</i>	tall herb	55	70	55
<i>Brachyscome tenuiscapa</i>	tall herb	45	50	45
<i>Hypochoeris radicata i</i>	tall herb	25	25	65
<i>Podolepis jaceoides</i>	tall herb	20	40	20
<i>Senecio lautus</i>	tall herb	15	50	60
<i>Chionogentias</i> spp.	tall herb	15	45	25
<i>Leptorhynchos elongatus</i>	tall herb	5	-	5
<i>Senecio gunnii</i>	tall herb	-	15	10
<i>Euphrasia collina</i>	tall herb	-	-	5
<i>Geranium sessiliflorum</i>	herb	100	100	95
<i>Erigeron gunnii e</i>	herb	70	90	90
<i>Taraxacum officinale i</i>	herb	70	50	35
<i>Ranunculus</i> spp.	herb	65	80	65
<i>Acaena novae-zelandiae</i>	herb	55	45	45
<i>Petrorhagia nanteuilii i</i>	herb	30	25	20
<i>Acetosella vulgaris i</i>	herb	30	5	15
<i>Ranunculus pascuinus e</i>	herb	25	25	35
<i>Epilobium</i> spp.	herb	15	25	45
<i>Cardamine</i> spp.	herb	5	15	5
<i>Plantago glabrata e</i>	herb	5	15	5
<i>Leontodon taraxacoides i</i>	herb	-	5	-
<i>Scleranthus biflorus</i>	small herb	90	90	75

Species	Lifeform	S/R/N	R/N	U
<i>Asperula gunnii</i>	small herb	90	75	90
<i>Colobanthus apetalus</i>	small herb	90	50	55
<i>Ajuga australis</i>	small herb	85	70	75
<i>Oreomyrrhis argentea</i>	small herb	80	80	95
<i>Oreomyrrhis ciliata</i>	small herb	75	55	55
<i>Erophila verna i</i>	small herb	75	45	45
<i>Viola betonicifolia</i>	small herb	70	60	70
<i>Velleia montana</i>	small herb	70	45	80
<i>Veronica gracilis</i>	small herb	50	25	40
<i>Trifolium repens i</i>	small herb	25	-	-
<i>Trifolium dubium i</i>	small herb	20	-	-
<i>Gonocarpus serpyllifolius</i>	small herb	15	5	15
<i>Hypericum japonicum</i>	small herb	-	5	5
<i>Stellaria sp.</i>	small herb	-	-	5
<i>Poa fawcettiae</i>	grass	100	100	100
<i>Poa spp.</i>	grass	100	100	100
<i>Agrostis spp.</i>	grass	100	100	95
<i>Poa hiemata</i>	grass	100	100	95
<i>Pentapogon quadrifidus</i>	grass	100	100	80
<i>Agrostis venusta</i>	grass	90	100	95
<i>Aira caryophyllaea i</i>	grass	75	40	55
<i>Danthonia spp.</i>	grass	75	30	30
<i>Danthonia nudiflora</i>	grass	75	30	25
<i>Agrostis billardiarei</i>	grass	65	95	85
<i>Poa costiniana</i>	grass	45	50	65
<i>Festuca plebeia e</i>	grass	35	20	15
<i>Vulpia myuros i</i>	grass	25	-	5
<i>Anthoxanthum odoratum i</i>	grass	10	-	5
<i>Holcus lanatus i</i>	grass	10	5	-
<i>Aira praecox i</i>	grass	5	-	-
<i>Australopyrum velutinum</i>	grass	5	-	-
<i>Deyeuxia brachyathera</i>	grass	5	-	-
<i>Poa pratense i</i>	grass	-	5	-
<i>Poa labillardierei</i>	grass	-	-	10
<i>Poa gunnii e</i>	grass	-	-	5
<i>Luzula spp.</i>	graminoid	100	100	100
<i>Luzula australasica e</i>	graminoid	90	95	100
<i>Carex breviculmis</i>	graminoid	90	90	90
<i>Luzula modesta</i>	graminoid	90	90	90
<i>Pterostylis cynocephala</i>	graminoid	55	55	30
<i>Schoenus pygmaeus e</i>	graminoid	35	10	10
<i>Juncus spp.</i>	graminoid	-	5	-
<i>Botrychium lunaria</i>	fern	10	5	20

Table 2.2 Mean values of shrub structural attributes for the three dominant species by treatments

Treatments with the same letters are paired across the fenceline

U = ungrazed, R/N = rabbits and native vertebrate herbivores present

S/R/N = sheep, rabbits and native vertebrate herbivores present

	S/R/Na	Ua	Ub	R/Nb	R/Nc	S/R/Nc
<i>Leucopogon montanus</i>						
Mean % cover	9.30	10.90	9.60	6.60	8.60	7.40
Standard error (SE)	1.36	1.34	1.11	1.42	3.22	0.51
Average height (cm)	5.20	5.20	4.50	3.70	5.40	6.40
SE	0.29	0.33	0.14	1.29	4.26	0.27
<i>Olearia algida</i>						
Mean % cover	8.30	8.10	8.60	5.90	6.80	9.20
SE	0.47	0.60	0.76	0.35	0.41	0.29
Average height (cm)	23.30	24.90	21.90	23.60	24.10	26.30
SE	0.63	0.85	1.04	1.27	0.53	0.60
<i>Grevillea australis</i>						
Mean % cover	32.50	40.10	20.40	31.60	34.20	17.80
SE	2.57	1.17	3.02	0.64	0.95	1.65
Average height (cm)	49.20	71.10	43.10	61.90	45.20	42.80
SE	1.86	2.11	2.54	0.18	0.22	1.92

Grasses

The dominant grasses were in the genus *Poa*. *Poa fawcettiae* and *Poa hiemata* occurred in nearly every quadrat. *Poa costiniana*, while present in all treatments, was more frequently observed in the ungrazed plots, where *Poa labillardierei* was exclusively found (Table 2.1, Plate 2.4).

There was a significant difference in the percentage cover of the three grass categories (small - diam. < 5 cm, medium - diam. > 5 cm but >15 cm, large - diam. > 15 cm) between the ungrazed enclosure and the sheep grazed treatment ($H = 21.967$, $P < 0.001$), but not between the rabbit plus native grazed treatment and the ungrazed enclosure ($H = 5.817$, $P = 0.055$) nor the rabbit plus native grazed treatment and the sheep grazed area ($H = 3.52$, $P = 0.172$). The percentage cover of 'small' grasses (*Poa hiemata* and *Poa fawcettiae*) was significantly greater ($z = -2.675$, $P = 0.008$) in the sheep grazed (s2) quadrats than in the ungrazed (u2) quadrats. *Poa costiniana* ('medium' grass) had greater cover ($z = -2.539$, $P = 0.011$) in the ungrazed plot (u2) than in the sheep grazed

plot (s2). There were no 'large' (*Poa costiniana*/*Poa labillardierei*) grasses in the sheep grazed plots, and there were too few cases of 'large' grass in all treatments for attributes to be tested for statistical differences between treatments.

There were significantly more flowering heads in the ungrazed enclosure than in the rabbit plus native grazed treatment ($H = 12.223$, $P = 0.002$).

Most of the smaller grass species (mainly exotics) were more frequent in the sheep grazed plots, while the native *Agrostis billardierei* was most abundant in the enclosures (Table 2.1).

Long-term vegetation change

Over the 20-year period, percentage bare ground in the ungrazed plot increased by 17% (from 39% in 1974 to 22% in 1993). Percentage bare ground also decreased in the native plus rabbit grazed enclosure but more slowly (from 37% in 1974 to 27% in 1993). In contrast percentage bare ground in the sheep grazed area decreased by 7% (from 28% in 1974 to 35% in 1993, see Plate 2.3).

The increase in vegetation cover in the ungrazed enclosure averaged 0.9% per year. The native plus rabbit grazed enclosure had a lower average change of 0.5% per year, while the sheep grazed area recorded a decrease in vegetation cover of 0.4% per year.

Climatic records from two stations at Liawenee suggest that the three month period before the photographs were taken, was slightly wetter in 1974 than in 1993 (Bureau of Meteorology 1997). While no temperature data were available for Liawenee, in 1974 the State as a whole experienced slightly higher maximum and minimum temperatures than normal (Lakin 1975), while they were slightly cooler than normal in 1993 (Bureau of Meteorology 1997).

Short-term vegetation change

The percentage cover of tall herbs ($z = -4.55$, $P < 0.001$) and small herbs ($z = -2.243$, $P = 0.025$) decreased across all treatments from March 1996 to March 1997 (Table 2.3). Shrub cover increased overall (tall shrubs $z = -2.232$, $P = 0.026$; mat shrubs $z = -2.074$, $P = 0.038$). Bare ground decreased over the 2-year-period ($z = -2.965$, $P = 0.003$) and the cover of monocotyledons increased ($z = -2.363$, $P = 0.018$).

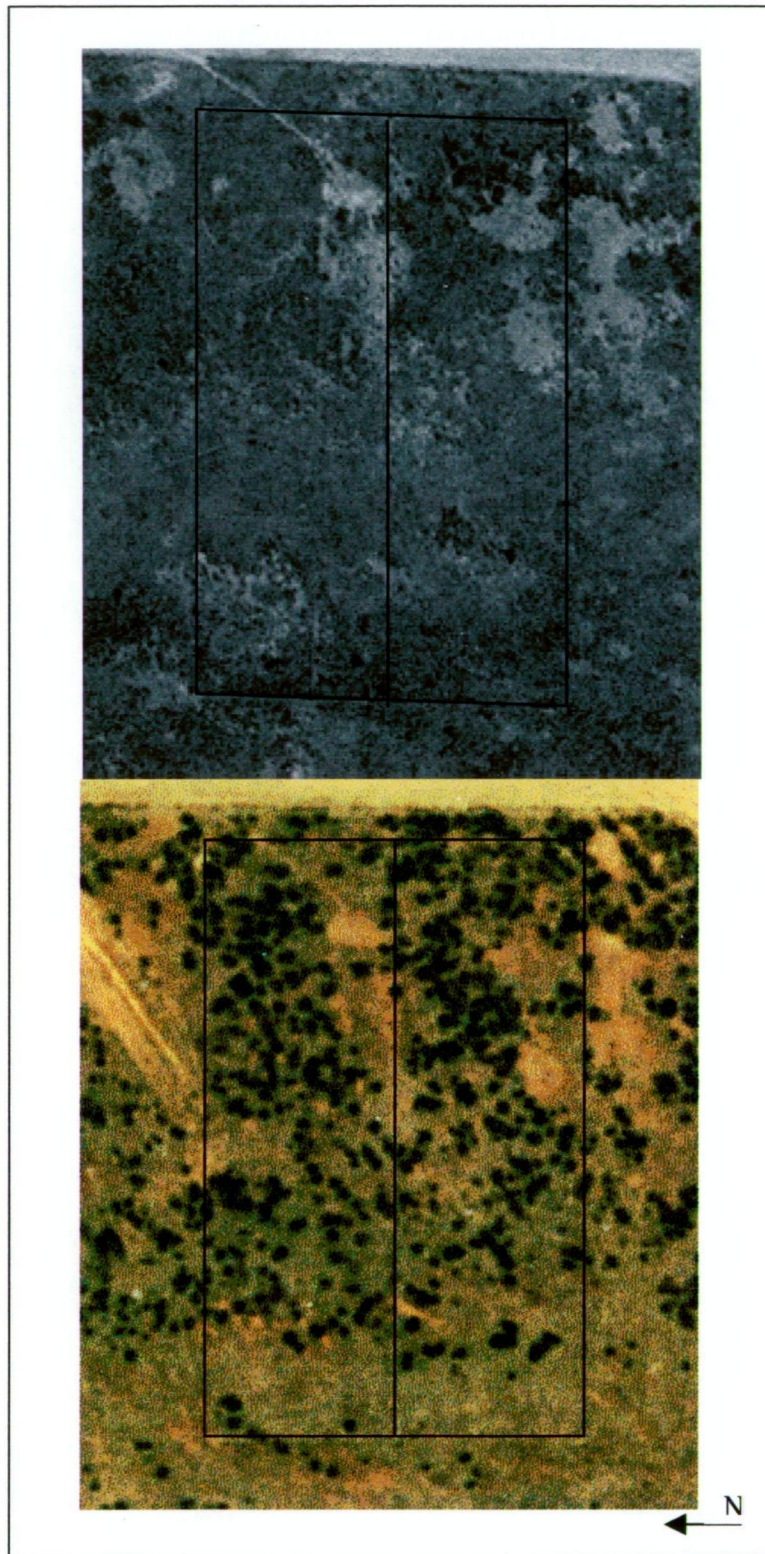


Plate 2.3 Aerial photograph of the Liawenee grazing exclosures in 1974 (above) and 1993 (below). (Scale –each exclosure is 100 x 30m. Rabbit plus native grazed exclosure on the right/South and ungrazed exclosure on the left/North, sheep plus rabbit plus native grazed area surrounding the exclosures).



Plate 2.4 *Poa costiniana* and *Poa labillardierei* tussocks amongst *Grevillea australis* in the ungrazed enclosure.



Plate 2.5 Flowering stems of *Podolepis jaceoides* and *Leptorhynchos squamatus* in the ungrazed enclosure.

Within treatments, there was a significant increase in the shrub *Olearia algida* ($z = -2.239$, $P = 0.025$) and monocotyledons (dominated by grasses, mainly *Poa* spp., $z = -2.107$, $P = 0.035$) in the sheep grazed plots. There was a decrease in tall herbs ($z = -3.083$, $P = 0.002$), notably *Leptorhynchos squamatus*, small herbs ($z = -2.83$, $P = 0.005$), monocotyledons ($z = -1.99$, $P = 0.047$), and bare ground ($z = -2.427$, $P = 0.015$) in the rabbit plus native grazed treatment. There was also a decrease in tall herbs ($z = -3.415$, $P < 0.001$) (especially *Leptorhynchos squamatus*) in the ungrazed exclosure (Table 2.3).

Table 2.3 Mean percentage cover of lifeform groups and tall herb species in 50 x 50 cm quadrats over a 2-year-period

* denotes a significant change in species or lifeforms, as a complete data set and within treatments, over the 2-year-period (using the Wilcoxon-Signed Rank test)

U = ungrazed, R/N = rabbits and native vertebrate herbivores present

S/R/N = sheep, rabbits and native vertebrate herbivores present

Species or Lifeform	U		R/N		S/R/N	
	1996	1997	1996	1997	1996	1997
small herbs*	1.7	1.0	2.5	1.7*	1.6	1.9
<i>Leptorhynchos squamatus</i> *	9.9	7.3*	7.0	5.0*	7.1	6.8
<i>Craspedia coolaminica</i>	0.7	0.8	0.7	0.7	0.4	0.2
<i>Erigeron gunnii</i>	0.4	0.3	0.2	0.4	0.0	0.0
<i>Brachyscome tenuiscapa</i>	0.1	0.1	0.1	0.1	0.0	0.0
<i>Ranunculus</i> spp.	0.1	0.0	0.1	0.0	0.0	0.0
tall herbs total*	12.6	9.6*	9.2	6.9*	8.2	7.3
mat shrubs*	2.2	2.9	2.3	1.7	1.3	1.4
<i>Grevillea australis</i>	19.4	18.8	10.5	12.6	10.3	10.6
<i>Olearia algida</i> *	5.9	5.1	6.3	6.9	4.1	5.7*
<i>Leucopogon montanus</i>	5.5	6.4	6.5	7.0	6.8	7.0
tall shrubs*	37.4	37.4	27.2	29.6	25.9	27.8
monocotyledons*	28.1	28.4	23.8	22.1*	19.5	24.0*
litter, moss, lichen	7.9	11.1	10.5	9.9	10.9	8.4
rocks and bare ground*	10.5	10.0	23.8	22.1*	32.8	29.5

Herb occurrence by other vegetation and treatment

Individuals of *Craspedia coolaminica* and *Podolepis jaceoides* (Plate 2.5) were predominantly located in vegetated areas in the sheep grazed transects, i.e. with some cover from grasses or small shrubs less than 10 cm in height. This was also the case in the rabbit plus native grazed enclosure. However, there was a greater proportion of individuals in unprotected areas growing amongst litter, mat shrubs and herbs or in bare ground than was found in the sheep grazed area. Plants in the ungrazed transects were more abundant in the open areas and those with low cover (Table 2.4, *Craspedia coolaminica* ($\chi^2 = 68.498$, $P = 0.001$, *Podolepis jaceoides* ($\chi^2 = 32.177$, $P < 0.001$). Individuals of *Microseris lanceolata* did not show any significant habitat differences between treatments (Table 2.5, $\chi^2 = 4.613$, $P = 0.329$).

Table 2.4 Percentage of *Craspedia coolaminica*, *Podolepis jaceoides* and *Microseris lanceolata* within different microhabitats

Low cover = overstorey < 10 cm tall, tall cover = overstorey > 20 cm tall,

no cover = bare ground or < 1 cm lichen or litter

U = ungrazed, R/N = rabbits and native vertebrate herbivores present

S/R/N = sheep, rabbits and native vertebrate herbivores present

	S/R/N	R/N	U
<i>Craspedia coolaminica</i>	$n = 102$	$n = 481$	$n = 702$
Overstorey < 1 cm tall	7	28	41
Overstorey < 10 cm tall	74	47	38
Overstorey > 10 cm tall	19	25	21
<i>Podolepis jaceoides</i>	$n = 8$	$n = 16$	$n = 35$
Overstorey < 1 cm tall	13	50	26
Overstorey < 10 cm tall	0	19	69
Overstorey > 10 cm tall	87	31	5
<i>Microseris lanceolata</i>	$n = 33$	$n = 27$	$n = 18$
Overstorey < 1 cm tall	21	37	33
Overstorey < 10 cm tall	64	52	39
Overstorey > 10 cm tall	15	11	28
Proportion (%) of transect covered by the three classes			
Proportion < 1 cm tall	24.7	30.0	32.5
Proportion < 10 cm tall	53.4	40.5	33.8
Proportion > 10 cm tall	21.9	29.5	33.7

Invasion and survival

There were no *C. coolaminica* plants found further than 550 cm from the fence in the sheep grazed area. Individuals of *P. jaceoides* were only found within 300 cm of the fenced population (Table 2.5). Both species were far greater in number and size inside the rabbit plus native grazed enclosure than outside in the sheep grazed area.

When the site was revisited in September 1997, one of the 20 *P. jaceoides* plants from outside the enclosure was no longer there while all of the plants inside the enclosure could still be located. Forty-three per cent (12 individuals) of the *C. coolaminica* plants found outside had disappeared while 32% (14 plants) were missing inside the enclosure.

Table 2.5 Distribution and average leaf length of two tall herbs, *Craspedia coolaminica* and *Podolepis jaceoides*, in sheep grazed and sheep exclusion (rabbit/native vertebrate grazed) plots

R/N = rabbits and native vertebrate herbivores present

S/R/N = sheep, rabbits and native vertebrate herbivores present

Distance from Fence (cm)	<i>Craspedia coolaminica</i>				<i>Podolepis jaceoides</i>			
	S/R/N		R/N		S/R/N		R/N	
	#	Mean size (cm)	#	Mean size (cm)	#	Mean size (cm)	#	Mean size (cm)
50	7	4.6	13	5.0	4	2.1	3	3.7
100	8	3.8	16	5.5	4	2.4	25	2.9
150	1	1.5	15	6.0	4	2.5	28	2.8
200	3	3.5			1	2.5		
250	2	3.3			3	2.2		
300	3	3.7			4	2.6		
350	1	8.0			0	-		
400	0	-			0	-		
450	1	9.5			0	-		
500	1	4.5			0	-		
550	1	3.0			0	-		

Discussion

The conclusions presented here rest on the assumption that the environmental conditions of the exclosures and control areas were similar when the exclosures were created. This assumption is supported by present day similarities in environmental conditions. Environmental variables (such as slope, aspect and soil depth) were found to be consistent for all treatments across the site, and there was no significant differences in variables related to the structure and composition of the vegetation between the sheep grazed areas that were situated on either side of the treatments (60 m apart).

The relative numbers of wallaby and rabbit scats on Liawenee Moor were low compared to other high altitude environments in Tasmania (Table 2.6) even in other locations on Liawenee Moor (Gibson and Kirkpatrick 1989). Numbers of rabbit scats were most similar to, but slightly higher than, those noted by Leigh *et al.* (1987) for unburnt frost hollows (heathy grasslands) on the mainland. The Liawenee scat data were collected every 3 months, while the apparently more densely populated sites of Fensham and Kirkpatrick (1992) were collected on a monthly basis. Pilot studies on Liawenee Moor indicated that very little gain was to be made in collecting scats on a more frequent basis, and that scat decay was not a concern over a period of three months. The scat transect method is inappropriate for measuring the relative populations of wombats as they have 'toilets' marking their territory.

In other studies bare ground has been found to cover a significantly larger area in grazed plots than ungrazed exclosures (Wahren *et al.* 1994), whether the grazers are predominantly domestic stock (Wahren *et al.* 1994; Wimbush and Costin 1979c), rabbits (Leigh *et al.* 1987) or native vertebrates (Gibson and Kirkpatrick 1989; Leigh *et al.* 1987). To date, there have been no data on the relative effects of sheep, rabbits and native vertebrates versus rabbits and native vertebrates. The exclusion of sheep but not other animals results in a decrease in cover of bare ground. The increase in percentage bare ground in the sheep grazed plots at Liawenee over 20 years (in the absence of periodic burning) indicates that the additional grazing pressure created by sheep has the greatest impact in degrading this environment.

Table 2.6 A comparison of scat counts for Liawenee Moor and other Australian alpine environments

* = native vertebrate grazers only

Source	Altitude (m)	Location	Habitat	Rabbits per m ²	Wallabies per m ²	Total
Fensham and Kirkpatrick 1992 (12 months data)	1000	Central Plateau	Grassland	74	90	163
Authors data	1050	Central Plateau (Liawenee)	Grassland	42	5	47
Gibson and Kirkpatrick 1989 (1 summer season)	1150	Central Plateau	Grassy woodland			22*
Authors data	1050	Central Plateau (Liawenee)	Grassland	8	1	9
Leigh <i>et al.</i> 1987 (1 year non-winter months)	1370 - 1410	Kosciuszko National Park	Grassland / Frost hollow	28	0	28
Authors data	1050	Central Plateau (Liawenee)	Grassland	38	5	43

A decrease in grazing pressure usually leads to an increase in vegetation cover (Gibson and Kirkpatrick 1989; Leigh *et al.* 1987; Carr and Turner 1959b; Wahren *et al.* 1994; Wimbush and Costin 1979b). The success of the recovery is largely dependent on the impact of the initial disturbances (Wimbush and Costin 1979a,b), and the scale of continuing disturbance (Wahren *et al.* 1994; Wimbush and Costin 1979b). As recovery rates in alpine environments are extremely slow, it may be many years before any differences in grazing treatments become evident (Carr and Turner 1959b; Leigh *et al.* 1987; Wahren *et al.* 1994; Wimbush and Costin 1979a). Where sites are in a disturbed state but the native vegetation is relatively intact, the recovery rate of tall herbs when protected from grazing is reported to be relatively fast (6-8 years) (Wimbush and Costin 1979a). However, it has taken nearly 50 years for 55 individuals of *Podolepis robusta* to become established on the ungrazed Pretty Valley plot on the Bogong High Plains (Wahren *et al.* 1994). The vegetation on Liawenee Moor has been severely disturbed by domestic stock grazing and burning, and has large areas of bare ground which are slowly revegetating. Differences in plant species composition were most evident

between the two extreme treatments of ungrazed and sheep grazed. The abundances of particular species or lifeforms, especially flowering tall herbs, are more distinct between all treatment types.

The cover of palatable/small shrubs, grasses and tall herbs has been shown to increase with a decrease in grazing pressure (Carr and Turner 1959b; Leigh *et al.* 1987; Wimbush and Costin 1979a,b,c). The composition of species within these lifeform groups has also been shown to change, with a greater number of palatable species establishing (Wimbush and Costin 1979b; Leigh *et al.* 1987; Gibson and Kirkpatrick 1989; Wahren *et al.* 1994). While the cover of individual shrub species was not significantly different between grazing treatments at Liawenee, many grasses and tall herbs were more frequent in the exclosures than the sheep grazed plots. A decrease in grazing pressure in disturbed alpine environments is known to lead to an increase in shrub cover in the short term (Williams and Ashton 1987a; Wahren *et al.* 1994). The Liawenee data show that average height of the large shrub *Grevillea australis* was significantly greater in the two exclosures than the sheep grazed area. The cover of the medium shrub *Olearia algida* increased significantly in the sheep grazed plots over a two-year-period. While *Grevillea australis* is both palatable and highly susceptible to trampling, *Olearia algida* is neither. The increase in this species over this time period is likely to be a result of the favourable growing season and the absence of sheep grazing at the onset of the growing season. However, large-scale establishment of shrub species in gaps was not noted, possibly due to the large sizes (greater than 1 m² in many cases) of the bare ground patches.

Tall herbs are generally eaten when they are flowering (Leigh *et al.* 1987). Herbs that are known to be palatable to domestic stock and rabbits from mainland studies (Wimbush and Costin 1979c; Leigh *et al.* 1987), are also preferentially grazed by native vertebrates at Liawenee (e.g. *Podolepis jaceoides*, *Craspedia coolaminica*, *Senecio lautus*). However, the combined effects of rabbits and native grazers at Liawenee do not appear to be as strong as those reported by Leigh *et al.* (1987) for rabbits only. The ungrazed exclosure at Liawenee was grazed by cattle, rabbits and wallabies before the fences were re-erected in 1995. By comparison, there was no evidence of stock grazing in the rabbit plus native grazed exclosure. Therefore, over time, there may be stronger

differences in vegetation between these two grazing treatments, as the ungrazed enclosure fully adjusts to an absence of grazing pressure.

The distribution of herbs and their behaviour on Liawenee Moor is consistent with the hypothesis of Kirkpatrick (1989) in that the cover of tall herbs is less where grazing exists. Where grazing occurred, tall herbs were preferentially located within protective canopies. However, herbs that were wind dispersed were able to recolonise sites close to a seed source relatively quickly at Liawenee, as in other areas (Wimbush and Costin 1979a; Wahren *et al.* 1994).

The impacts of grazers on exotic species at Liawenee is consistent with the hypothesis of Kirkpatrick (1989), and the results of Leigh *et al.* (1987), Whinam *et al.* (1994) and Wimbush and Costin (1979b) in that palatable exotics such as *Hypochoeris radicata* (Struik 1967; Leigh *et al.* 1987) were more frequent in the ungrazed enclosure.

Short-term fluctuations in vegetation cover may mask the long-term effects of different grazing pressures. The literature suggests that these short-term fluctuations are strongly related to seasonal climatic conditions (Wimbush and Costin 1979a,b,c). This hypothesis is supported by the short-term data presented here, where grass cover fluctuates rapidly with the onset of good versus poor growing seasons. Grass cover in the sheep plus rabbit plus native grazed area on Liawenee Moor during 1996-1997 was greater than 1995-1996, coinciding with a more favourable growing season (Bureau of Meteorology 1997) and was also enhanced by the late arrival of sheep in January (two months later than normal). Increases in grass and forb cover have been related to higher than average rainfall early in the season (Wimbush and Costin 1979a; Leigh *et al.* 1991). The favourable growing season, combined with the lack of sheep grazing in late spring and early summer, and the relative abundance of small sized (< 50 cm) bare ground patches probably accounts for the 3.3% increase in vegetation cover in the sheep grazed area. In contrast, bare ground cover only decreased by 0.5% in the ungrazed enclosure, which more closely resembles the figure obtained from the aerial photographic analysis. Small bare ground patches are less common in grazing enclosures than sheep grazed areas as the gaps are relatively easily recolonised with the removal of domestic stock (Williams 1992). The gaps that are left to be colonised are usually large (> 1 m in diameter) and tend to be recolonised from the edges of the gap, rather than from the establishment of individuals in the middle of the bare ground.

The major conclusions of this study are that sheep grazing is causing continued deterioration of vegetation cover and that recovery is taking place under rabbit and marsupial grazing. However, grazing pressure from rabbits and marsupials does reduce the abundance and the flowering success (see Chapter 4) of tall herbs.

Given, the poor maintenance history of these exclosures, an assessment of the extent of the impact of rabbits and native herbivores on tall herbs is likely to be more conclusive over a longer time period, covering variations in climatic conditions and in fluctuations in rabbit populations.

Chapter 3

Recovery in Alpine Heath and Grassland

Introduction

Many ecological studies in the Australian Alps have focused on the process of natural regeneration on disturbed ground after removal of domestic stock grazing and the cessation of associated burning. Natural regeneration in these severe environments may be extremely slow, and is likely to be related to the initial condition of the disturbed site (Ellison 1949; Wimbush and Costin 1979*a,c*). Where vertebrate herbivores are present, plant growth is impeded by the effects of grazing, browsing, trampling and defaecating (Carr and Turner 1959*b*; Wimbush and Costin 1979*a,b*; van Rees 1984; Leigh *et al.* 1987; Williams and Ashton 1987*a*; Gibson and Kirkpatrick 1989; Wahren *et al.* 1994).

Alpine areas on the Central Plateau of Tasmania have suffered some of the most severe and extensive sheet erosion to occur in Australia as a result of stock grazing, the introduction of rabbits and burning (Cullen 1995). While the process of recovery has received some attention in the alpine zones of the mainland (Wimbush and Costin, 1979*a,b,c*; Williams and Ashton 1987*a*; Williams 1990, 1992; Wahren *et al.* 1994), little information exists for equivalent regions in Tasmania (Gibson and Kirkpatrick 1989; Bridle and Kirkpatrick 1999, Chapter 2). Wimbush and Costin (1979*a,b,c*) recorded a 25% absolute decrease in bare ground cover in alpine and subalpine areas at Kosciuszko National Park, over a 20 year period at sites which had 30-50% bare ground initially. Bridle and Kirkpatrick (1999) found that the percentage of bare ground was least in 25-year-old ungrazed exclosures and highest in a sheep, rabbit and native vertebrate herbivore grazed area. Where sheep were excluded, vegetation cover increased at approximately 1% per annum, a rate similar to that for Kosciuszko (Wimbush and Costin (1979*a,b,c*)).

Relationships between gap size and vegetation recovery have been documented for alpine (and subalpine) vegetation on the Australian mainland. Wimbush and Costin (1979*a,b*) observed that initial decreases in bare ground (in the first five years after the removal of stock) were relatively rapid and were related to the lateral spread of existing vegetation, usually grass tussocks. Carr (1962) studied the establishment of vegetation in bare ground gaps on the Bogong High Plains, Victoria. She found that shrubs were more likely than grasses to establish on bare ground gaps in the presence of domestic stock. Williams (1992) also found that gap size was important in determining which lifeforms would dominate the establishment process. Where gaps were large (> 1 m diam.) shrubs tended to establish in bare ground, but where gaps were small (< 15 cm diam.) then herbs and grasses established in the gaps. Wimbush and Costin (1979*c*) found that grasses and minor herbs established in gaps smaller than 60 cm in diameter, while recovery in larger gaps only occurred from the edges of the gaps. They found that shrubs were more important than grasses and herbs in establishment on bare ground in subalpine areas.

The lifeforms and species of plants that are able to colonise bare ground gaps may not be those which are dominant in the disturbed community. Grazed grasslands may become heathy grasslands, whilst grazed open heath vegetation may become closed heath (Williams 1990). On the Bogong High Plains, stock grazing reduced the amount of litter in the gaps, creating suitable sites (i.e. bare ground) for the establishment of shrub seedlings. The presence of litter enhanced grass or herb seedling establishment (Williams and Ashton 1987*a*). In the absence of grazing, the heath component of grasslands may decrease over time, as shrubs senesce and grasses and herbs become dominant (Carr and Turner 1959*b*; Wimbush and Costin 1979*b*; Williams 1990; Wahren *et al.* 1994).

Results from recovery of alpine/subalpine vegetation on the Australian mainland have shown that initial conclusions made from patterns of recovery observed in 'young' exclosures are often very different to those conclusions gleaned from the same experiments many years later (Wahren *et al.* 1994). Therefore time is an important component necessary for predicting management outcomes.

This chapter addresses the following questions. Are bare ground patches on the Eastern Central Plateau regenerating and does the initial amount of bare ground (as an indicator of the extent of the initial disturbance) have any effect on the process of recovery? Does the presence or absence of different species of vertebrate herbivores affect the success of recovery? Which lifeforms are increasing in cover over time? Is there any difference in the process of recovery between recent experimental plots and older experimental plots?

Methods

Study area

The study area is underlain by igneous rocks (dolerite and basalt, Table 3.1). The terrain is generally flat, consisting of broad valleys separated by higher remnant plateau surfaces such as Wild Dog Tier (Pemberton 1986). There is a strong rainfall gradient from east to west, with the only meteorological station in the study area being located at Liawenee (erected in 1984). The average annual rainfall for Liawenee is 1049 mm, with a mean annual daily maximum temperature of 11.9°C and a mean annual daily minimum temperature of 1.4°C. Snow falls can occur at any time of year but there is no persistent snow cover during the winter months. The mean number of frost days is 64 per annum with the majority of frosts occurring during the months of May-July (Bureau of Meteorology 1997).

Short-term (4-5 year) recovery

In 1991-1992, the Parks and Wildlife Service, Tasmania erected a series of grazing exclosures in the World Heritage Area of the Eastern Central Plateau to investigate natural establishment and erosion rates on eroded ground in alpine vegetation in the absence of grazing, with rabbit grazing only, and with unrestricted grazing (Cullen 1995). Sites were established at Botsford, Bernacchi, Double Lagoon and Wild Dog Tier (Fig. 3.1, Table 3.1, Plates 3.1-3.4), all in severely eroded areas, that is, with bare ground covering 40-70% of 1:25,000 aerial photographs (Cullen 1995). These study sites include most of the more extensive vegetation types on the eastern Central Plateau, ranging from the vegetation of well-drained sites to that of poorly-drained sites.

Table 3.1 Major environmental attributes of each of the study sites.

Site	Date of initial data collection	Altitude (m)	Geology	Dominant plant species	Community type	Major plant families present
Botsford	1991	1150	dolerite	<i>Orites acicularis</i> - <i>Grevillea australis</i>	alpine heath	Proteaceae Epacridaceae Asteraceae
Bernacchi	1991	1160	dolerite	<i>Orites acicularis</i>	alpine heath	Proteaceae Epacridaceae
Double Lagoon	1991	1150	basalt	<i>Restio australis</i> - <i>Abrotanella fosteroides</i>	alpine sedgeland	Restionaceae Asteraceae Epacridaceae
Wild Dog Tier	1992	1270	dolerite	<i>Richea scoparia</i> - <i>Abrotanella forsteroides</i>	bolster heath	Epacridaceae Asteraceae Proteaceae
Liawenee	1973	1050	basalt	<i>Grevillea australis</i> - <i>Poa</i> spp.	alpine grassland	Proteaceae Poaceae Asteraceae
Augusta	1973	1150	dolerite	<i>Orites acicularis</i>	alpine heath	Proteaceae Epacridaceae

The experimental design at each site consisted of three treatments, each with two replicates (Fig. 3.1). The treatments were located in two blocks, each consisting of an ungrazed, a rabbit grazed and a rabbit plus native herbivore (wallaby and wombat) grazed area. The plots were located randomly within severely eroded (40-70% bare ground, see Cullen 1995) areas at each of the four sites. Each site covered approximately 5000 square metres. The exclosures at Bernacchi, Double Lagoon and Wild Dog Tier were all 6 x 6 m in size. The rabbit grazed exclosures at Botsford heath were also 6 x 6 m in size, but the ungrazed exclosures were 10 x 10 m in size. Fence heights were approximately 1.5 m. However, some of the fences were raised to approximately 1.8 m when wallaby scats were discovered inside the exclosures.

Within each exclosure a 5 m line transect located across the middle of each exclosure was permanently marked with steel spikes. This transect was then divided into ten, 50 x 50 cm quadrats. The percentage canopy cover of vegetation (to lifeform level), bare ground, litter and rock was estimated, using 100, 5 x 5 cm squares. Canopy cover for

each category was estimated to the nearest 1%, by counting the number of squares in which each of the categories dominated. These measurements were taken every six months (November and May) from 1991 (1992 for the Wild Dog Tier site) to November 1996.

The percentage canopy cover data were placed in the following groups: bare ground; rock cover; mat herbs (including small herbs < 5 cm tall); tall herbs; mat shrubs; tall shrubs; grass; all other graminoids; litter; lichen; moss.

When these groups were mapped over time it was found that the relative amounts of bare ground, lichen, moss and litter depended on season. Litter and fruticose lichens (*Thamnolia* sp.) are not attached to the ground, rock or other vegetation and are easily disturbed. It was noted over the seasons that the changes in litter and lichen cover approximately equalled the decrease in bare ground. Therefore bare ground was taken to include rock cover, bare ground, lichen, litter and moss. Mat and tall herbs were also combined into a single herb category due to the low values of herbs at each of the sites.

Long-term (23 year) recovery

In 1973, researchers from the Botany Department, University of Tasmania, set up thirty-two 3 x 1.8 m sediment/erosion traps in the treeless subalpine zone of the Eastern Central Plateau, Tasmania. Sixteen of the traps were randomly located in a *Poa/Grevillea* grassy alpine heath (Liawenee), and the rest were randomly located in *Orites acicularis* alpine heath (Augusta) (Fig. 1.1, Table 3.1).

The areas had not been burned for at least eight years before the sediment traps were created, and they have not been burned since. They were highly likely to have been burned by graziers before the plots were set up. Liawenee Moor is privately owned and is leased out to a grazier. Sheep graze on the Moor from November to May every year. Numbers of stock vary, with 3000 being typical on approximately 40 km². However there were 12000 sheep on Liawenee Moor in the 1997-1998 season. Stock grazing ceased at the Augusta site around 1980. Both sites are grazed by native herbivores (mainly wallabies and wombats) and rabbits.

Photographs were taken of each of the traps in 1973. Photographs were taken of the trap as a whole (3 x 1.8 m) and as six subplots (1 x 0.9 m). These slides were projected onto

a screen, cover types were identified (tall shrubs, mat shrubs, grasses including other monocotyledons, herbs, bare ground) and the area of each of the covers was calculated for 1 x 1.8 m subplots from the 1973 photographs. Because taller lifeforms obscured much of the underlying layers, the measurements pertain to the tallest of the cover types at any point in any subplot. Note was also taken of the presences of individual tall shrub species and the ground layer surrounding each shrub species. If an individual shrub species was found to be growing in bare ground, then the distance from the middle of the shrub to the edge of the nearest vegetation was measured. If the shrub was growing in vegetation, then the distance from the middle of the shrub to the edge of the nearest patch of bare ground was measured.

In January 1997, the cover of each of the types was remeasured in the field. Data were collected from a total of 96 (48 at each site; three quadrats, each 1 x 1.8 m, per sediment trap) quadrats. Cover was measured using the same technique described for the five year old plots.

DATA ANALYSIS

The major datum used for analysis of change was the annual increment in cover (cover at time 2 - cover at time 1 / year at time 2 - year at time 1). This datum was used as it allows for ready comparisons between sites with different measurement periods.

For the short-term recovery experiment, graphs of the cover of bare ground for each year at each site were plotted. The amount of bare ground gradually decreased over time and there were no obvious peaks or troughs. Therefore data on ground cover categories were compared from 1991 (1992 for Wild Dog Tier) to 1996.

The question of recovery or not involves a comparison of initial bare ground cover within sites with final cover, with the hypothesis that there is no difference between the two cover values over time. The paired t-test is the most appropriate method of testing this hypothesis, but only where the data are parametric or can be transformed to normality. However, the data were not normally distributed even after arcsine transformations were performed (using SAS 1989). Therefore the Wilcoxon signed-rank test was used as the most appropriate nonparametric alternative to the paired-t test.

The most effective method to determine the effect of initial bare ground on cover change was by using analysis of covariance (ANCOVA) with bare ground cover at time 1 as the covariate. Arcsine transformations failed to normalise the percentage cover data (using SAS 1989), therefore non-parametric alternatives were used to test the null hypothesis that initial bare ground had no effect on change in cover of any of the lifeform categories for individual sites, using both the long-term and the short-term recovery data. The null hypothesis was addressed directly by using the Spearman rank correlation coefficient. Graphing of the relationships between bare ground at time 1 and at time 2 for the long-term experiment revealed distinct breaks in the distribution of quadrats at 50, 80 and 95% values of initial bare ground (at time 1). Therefore the hypothesis was able to be tested indirectly, using the long-term experiment data, by testing whether there was any significant difference in the change in cover values for any category (bare ground, shrub, grass, herb) between the four bare ground groups (bare ground at time 1 =: 0-50%; 50-80%; 80-95%; 95-100%). Mean values for change in bare ground, grass, shrub, herb cover were calculated for each of the bare ground groups. Overall differences were examined using the Kruskal-Wallis H test, while between group differences were determined by the Mann-Whitney U test.

Graphs of change in bare ground over the two time periods were plotted against percentage bare ground at time 1. Mean percentage change and standard error bars were plotted for every 10% interval of bare ground at time 1.

The Kruskal-Wallis H test and the Mann-Whitney U test were used on the short-term recovery data to test the hypothesis that there was no significant difference in change in cover (of bare ground, shrub, grass or herb) between grazing treatments. These tests were used to test for differences within sites. Between site treatment interactions for change in cover were tested using Friedman's test and parametrically by GLM (SAS 1989).

Results of the non-parametric tests are used in this chapter. However, parametric analyses were undertaken, and while the results from these tests generally proved to be less powerful and the non-parametric tests, they generally indicated the same tendencies and differences.

Descriptive statistics on the percentage of quadrats that were dominated (i.e. had > 50% cover) by any of the lifeform groups were calculated from individual quadrats (and treatments) for each site.

From the 1973 photographs it was possible to record the ground cover underneath some of the dominant shrub species. A Chi-squared test on the most common shrub species was used to determine whether species were preferentially located in a particular ground cover category (bare, litter, vegetated).

For both data sets, subsets of the grazing exclosures (the 50 x 50 cm quadrats) and the sediment traps (the 1 x 1.8 m sections) were used for some parts of the data analysis. Strictly speaking this constitutes pseudoreplication (Hurlbert 1984). However, it would have been impractical for those who established the exclosures to individually fence each of the 60, 50 x 50 cm quadrats used in the grazing experiment. The focus on change in vegetation cover reduces the effect of initial vegetation cover in the analyses and subsequently also reduces the inadequacies of the inherited experimental design problems.

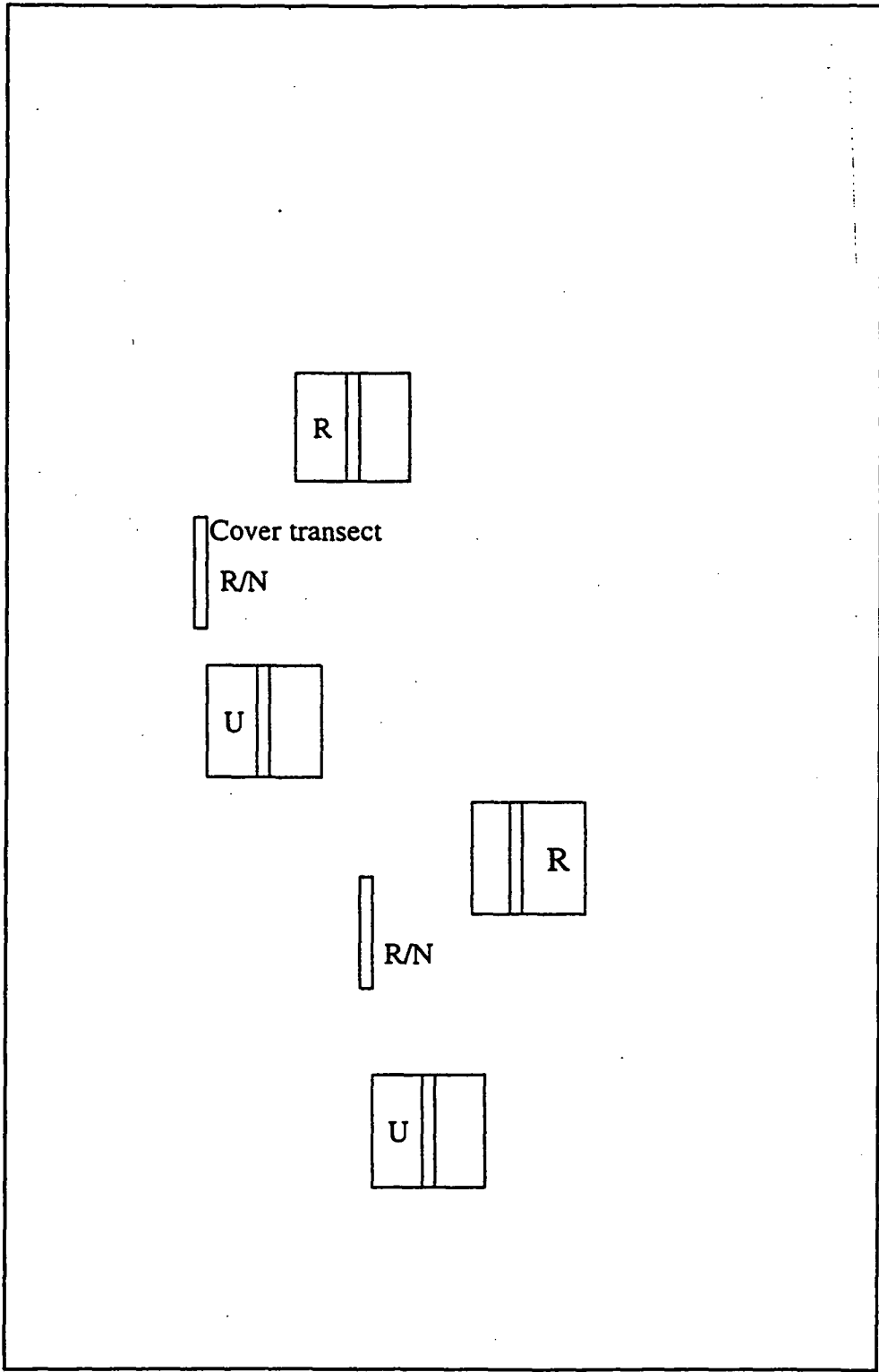


Figure 3.1 Sketch diagram of the layout of the grazing treatments at the four short-term recovery sites.
U = ungrazed, R = rabbit grazed, R/N = rabbit plus native grazed.
Cover transect refers to the 10, 50 x 50 cm quadrats used for cover data.



Plate 3.1 Botsford heath, inside the ungrazed enclosure.



Plate 3.2 Bernacchi heath, looking towards a rabbit grazed enclosure. The dominant shrubs are *Orites acicularis* (yellow bush).



Plate 3.3 Double Lagoon sedgeland, looking towards an ungrazed enclosure.



Plate 3.4 Wild Dog Tier, with a rabbit grazed enclosure in the background.

RESULTS

Short-term (4-5 year) recovery

Most of the 240 quadrats had less bare ground in 1996 than at first measurement (Fig. 3.2). Three of the four sites (Double Lagoon, Wild Dog Tier, Bernacchi) showed a significant reduction in bare ground over the 4/5 year period (Table 3.2). There was no significant difference in percentage bare ground over time at Botsford. However, there was a significant difference in change in bare ground between the rabbit and rabbit plus native grazed treatments at this site. Percentage bare ground increased over time in the rabbit plus native grazed treatment, but decreased in the rabbit grazed enclosure (Table 3.2). There was no significant difference in percentage change in bare ground by grazing treatment within the other three sites. Overall there was no site by grazing treatment interaction (Friedman's test, $S = 1.50$, $P = 0.472$, GLM $df\ 6$, $F = 0.21$, $P = 0.965$). Despite a lack of significant differences between grazing treatments within sites, bare ground decreased the most in the ungrazed enclosures and least in the rabbit and native herbivore grazed areas at all sites. The probability of this configuration occurring by chance is less than one in a thousand.

Shrub cover increased significantly at all four sites (Table 3.2). There was no site by grazing interaction in the change in shrub cover over time (Friedman's test, $S = 0.50$, $P = 0.779$, GLM, $df\ 6$, $F = 1.24$, $P = 0.351$). However, change in shrub cover was significantly less in the ungrazed enclosure than in the other grazing treatments at Double Lagoon (Table 3.2).

Grass cover significantly increased at Wild Dog Tier, significantly decreased at Botsford and showed no significant change over time at the other two sites. Change in grass cover was significantly differentiated by treatment at Double Lagoon, where cover increased in the ungrazed enclosure while decreasing in the rabbit grazed and the rabbit plus native grazed treatments (Table 3.2). Grass cover decreased least in the rabbit plus native grazed area at Botsford, but decreased most in the rabbit grazed enclosures. No significant differences in change in grass cover were recorded between treatments for the other two sites (Table 3.2), nor was there any significant site by treatment interaction ($S = 1.20$, $P = 0.549$, GLM, $df\ 6$, $F = 1.30$, $P = 0.329$).

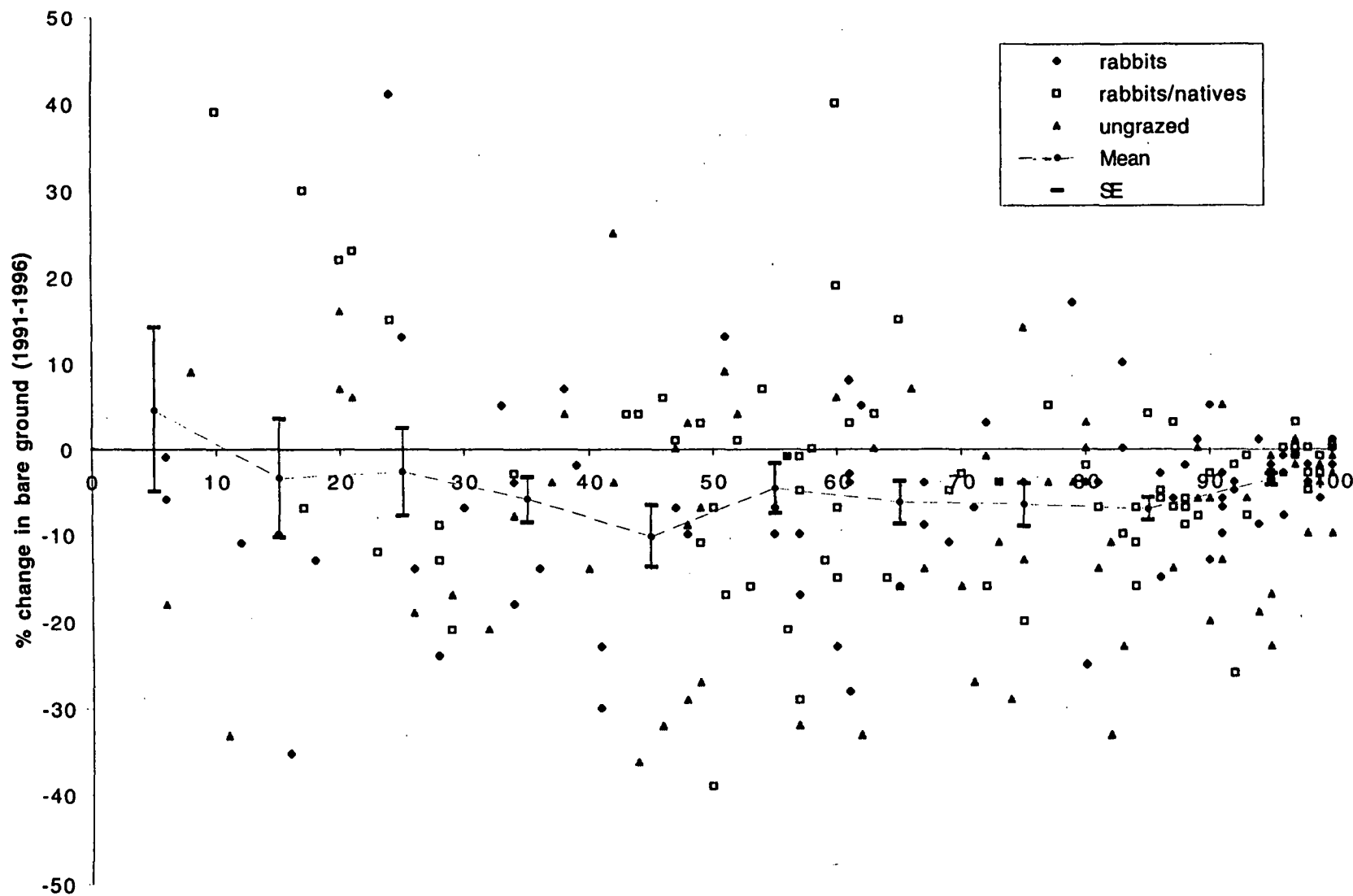


Figure 3.2 Percentage change in bare ground from 1991 to 1996 by percentage bare ground in 1991 for the four short-term recovery sites.

Mean values and standard error (SE) were calculated for percentage change in bare ground for every tenth percentile of x axis (percentage bare ground in 1991).

Table 3.2 Initial amount and mean annual percentage change of bare ground, grass, herb and shrub herb cover for each site by grazing treatment.

Significant differences in change in bare ground, tall shrub, grass and herb cover over time was tested using the Wilcoxon Signed rank test on paired samples over time (** = $P < 0.001$, * = $P < 0.01$, * = $P < 0.05$). Differences in cover of the different lifeform groups between grazing treatments (within sites) was tested using the Kruskal-Wallis H test. The letters a and b indicate any significant differences in changes in cover values between any two grazing treatments (Mann-Whitney U test) for the short-term data (where a letter is the same, no significant difference exists). These same letters were also used to determine any differences in change in lifeform cover between the two long-term sites (Liawencee and Augusta). S/R/N = Sheep plus rabbits plus natives, R/N = rabbits plus natives, R = rabbits only, U = ungrazed.

Category and Treatment	Botsford 1991-1996		Bernacchi 1991-1996		Double Lagoon 1991-1996		Wild Dog Tier 1992-1996		All short-term sites	Augusta 1973-1997		Liawencee 1973-1997	
	Initial Value	% Change p.a.	Initial Value	% Change p.a.	Initial Value	% Change p.a.	Initial Value	% Change p.a.		Initial Value	% Change p.a.	Initial Value	% Change p.a.
Bare ground	48.4	-0.56 NS	74.6	-1.35***	75.9	-1.34***	81.7	-1.20***					
U	53.0	-1.08ab	71.3	-1.44a	86.1	-1.80a	76.2	-2.03a	-1.59				
R	41.7	-1.02a	81.7	-1.36a	67.5	-1.20a	88.0	-0.85a	-1.1				
R/N	50.4	+0.42b	70.9	-1.26a	74.3	-1.02a	78.5	-0.73a	-0.65	60.7	-1.38***	55.6	-1.18*** (=S/R/N)
Shrub cover	32.7	+1.46**	10.9	+1.23***	2.5	+1.42***	0.0	+0.14**					
U	27.4	+1.64a	16.9	+1.24a	0.1	+0.38a	0.1	+0.33a	+0.9				
R	40.6	+2.64a	8.5	+1.14a	5.2	+2.38b	0.1	+0.10a	+1.07				
R/N	30.0	+0.10a	7.5	+1.32a	2.3	+1.50b	0.0	0.00a	+0.73	26.8	+1.23***	7.7	+0.97*** (=S/R/N)
Grass cover	8.3	-0.45**	12.4	+0.05 NS	18.7	-0.71 NS	17.1	+1.20 ***					NS
U	10.0	-0.30ab	10.3	-0.02a	11.5	+0.54a	20.8	+1.60a	+0.46				
R	7.8	-0.80a	8.0	+0.18a	23.4	-1.72b	14.4	+1.43a	-0.23				
R/N	7.1	-0.24b	18.9	-0.02a	21.4	-0.96b	16.3	+0.58a	-0.16	11.3	+0.11**	35.7	+0.11 (=S/R/N)
Herb cover	4.5	-0.19 NS	0.7	+0.04 NS	1.9	+0.25 ***	1.1	+0.39***					
U	5.5	-0.38a	1.1	+0.14a	1.1	+0.42a	1.1	+0.68a	+0.22				
R	3.8	-0.30a	0.6	-0.02a	3.2	+0.10a	0.6	+0.25a	+0.01				
R/N	4.3	+0.12a	0.4	0.00a	1.6	+0.22a	1.6	+0.25a	+0.15	1.1	+0.05**	1.0	+0.11*** (=S/R/N)

Herb cover significantly increased over time at the two grassy sites (Wild Dog Tier and Double Lagoon) but there was no significant difference in herb cover over time at the other two sites (Table 3.2). There was no significant difference in change in herb cover between grazing treatments at any site (Table 3.2), nor was there any significant interaction between site and treatment ($S = 2.80$, $P = 0.247$, GLM, $df\ 6$, $F = 0.43$, $P = 0.845$).

There were no significant relationships between percentage bare ground at time 1 (1991) and change in bare ground from 1991 to 1996 for three of the four sites. However, percentage bare ground in 1992 was found to be weakly and inversely related to change in bare ground over time at Wild Dog Tier ($r = -0.267$, $P = 0.04$).

There was little change in dominant (i.e. > 50% cover in the quadrat) cover/lifeform category over time, for the short-term plots as a whole (Table 3.3). The number of quadrats dominated by bare ground was reduced across all treatments, but disproportionately more in the ungrazed and the rabbit grazed treatments than in the rabbit plus native grazed treatments. The percentage of quadrats dominated by shrubs almost doubled in the rabbit grazed treatments, while increasing slightly in the other two treatments. The percentage of quadrats dominated by grasses decreased markedly in the rabbit grazed treatment, increased in the ungrazed treatment, and was constant in the rabbit plus native grazed treatment (Table 3.3).

Table 3.3 Percentage of quadrats with dominance (> 50% cover) of bare, shrubs and grass for the short-term recovery sites (1991 to 1996) and the long-term recovery sites (1973 to 1997).

Category	Short-term sites (combined)						Long-term sites			
							Liawenee		Augusta	
	Ungrazed		Rabbit grazed		Rabbit + Native grazed		Sheep + Rabbit + Native grazed		Rabbit + Native grazed	
	1991	1996	1991	1996	1991	1996	1973	1997	1973	1997
Bare ground	78	70	66	60	81	79	58	31	69	23
Shrubs	15	19	15	28	9	11	0	31	25	65
Grasses	7	11	19	12	10	10	42	38	6	12

Long-term (23 year) recovery

The amount of bare ground was reduced in 89 of the 96 sediment trap quadrats over the 23 year period (Wilcoxon Signed Rank test, $z = -8.171$, $P < 0.001$) (Figs. 3.3, 3.4). The average annual decrease in bare ground was 1.3%. All lifeform groups increased in cover. The largest increase was in the cover of shrubs, which almost equalled the decrease in bare ground (Table 3.3). Both shrub cover and herb cover increased significantly at both sites (Table 3.2). Grass cover increased significantly at Augusta (Table 3.2) but not at Liawenee, where 12 of the 48 quadrats recorded a decrease in grass cover. There was a significant inverse relationship between percentage bare ground in 1973 and change in bare ground from 1973 to 1997 for both sites (Liawenee, $r = -0.339$, $P = 0.02$, Augusta, $r = -0.483$, $P < 0.001$).

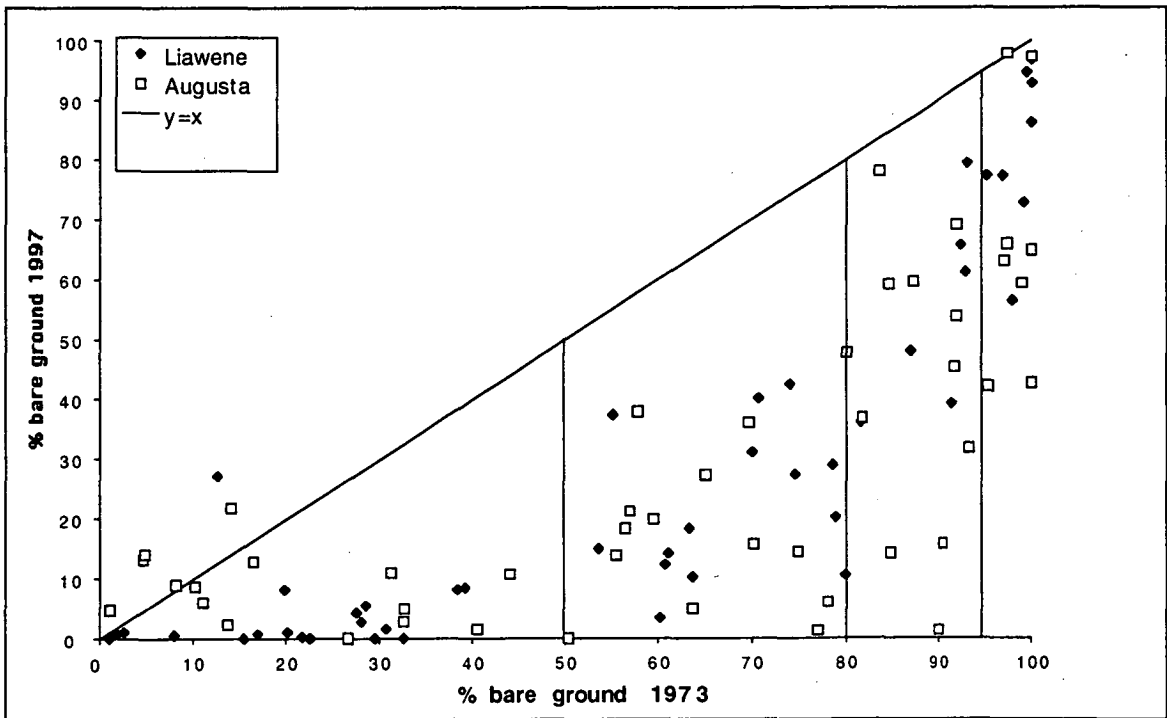


Figure 3.3. The relationship between bare ground cover in 1973 and 1997

Points above the line ($y=x$) are eroding, while those below are recovering

Horizontal lines at $x=50$, 80 and 95% highlight the thresholds used in the data analysis.

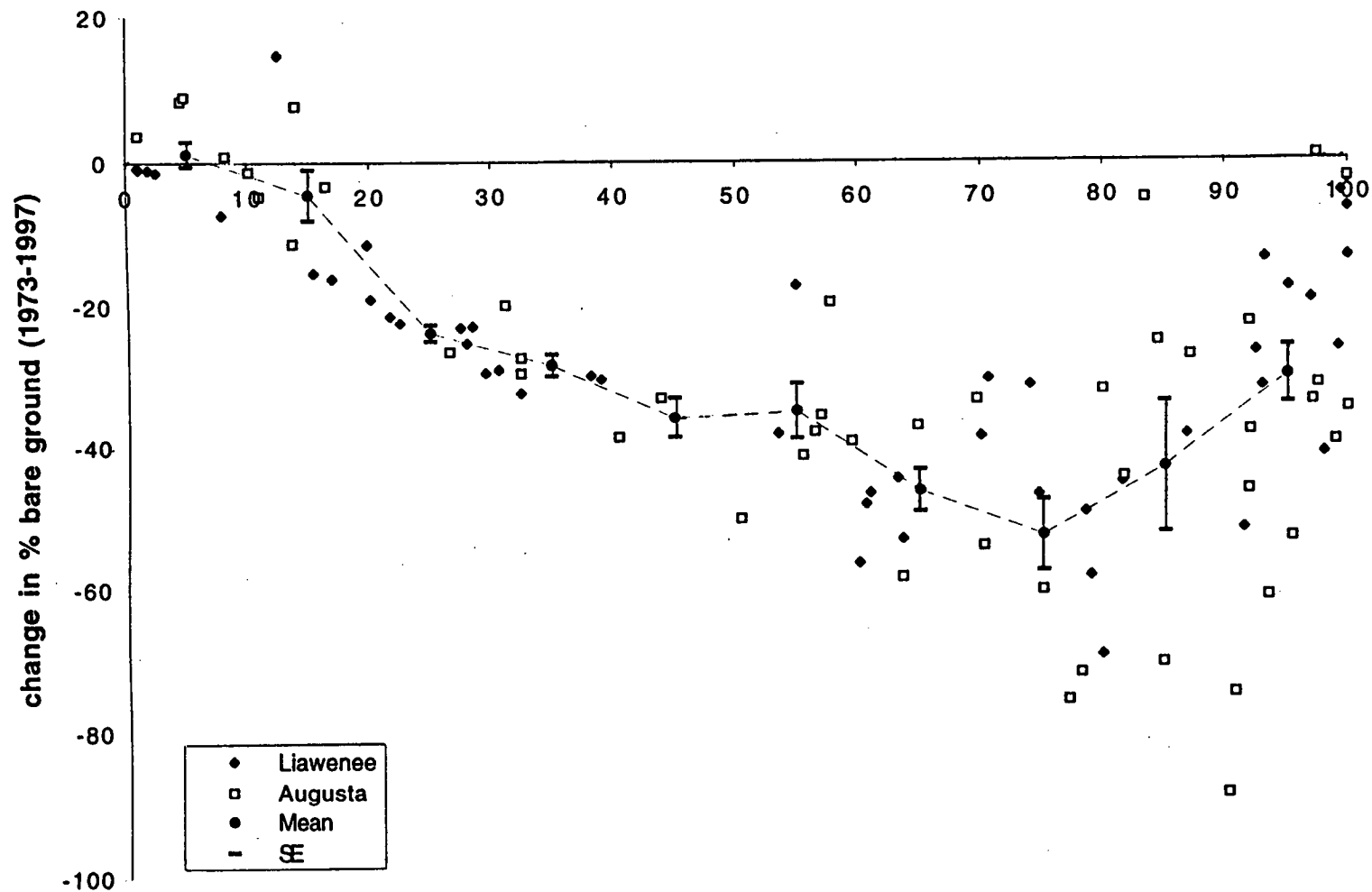


Figure 3.4 Percentage change in bare ground from 1973 to 1997 by percentage bare ground in 1973 for the two long-term recovery sites. Mean values and standard errors (SE) were calculated for percentage change in bare ground for every tenth percentile of the x axis (percentage bare ground in 1973).

In order to determine more closely the effect of initial bare ground on regeneration, four bare ground categories were defined on the basis of the stepped configuration apparent in Figure 3.3. Group 1 consisted of all quadrats that had 50% or less bare ground cover in 1973. Bare ground decreased to less than 18% for most of quadrats in this group (Fig. 3.3). However, this group also included the greatest number of quadrats where bare ground increased. Group 2 included quadrats that had more than 50% bare ground but less than or equal to 80%. All quadrats in this group recorded a reduction in bare ground. Group 3 had greater than 80% bare ground but not more than 95%. All quadrats in this group regenerated to less than 80% bare ground in 1997. Half of these quadrats recovered to less than 50% bare ground over the 23 year period. Group four consisted of all quadrats with greater than 95% bare ground cover in 1973, only one of which recorded an increase in bare ground over the time period (Fig. 3.3). Bare ground decreased on average by more than 12% (Table 3.2).

Grass cover was significantly greater at Liawenee than Augusta in 1973 ($U = 530$, $P < 0.001$), and shrub cover was significantly greater at Augusta in 1973 ($U = 591$, $P < 0.001$). There were no significant differences in herb cover ($U = 1012$, $P = 0.301$) or percentage bare ground ($U = 1043$, $P = 0.422$, Table 3.2) between the two sites at that time. There was no significant difference in the percentage increase of grass cover ($U = 940$, $P = 0.12$, ANOVA df 1, $F = 0.82$, $P = 0.37$) or shrub cover ($U = 971$, $P = 0.185$, ANOVA df 1, $F = 1.14$, $P = 0.3$) between the two sites over the 23 years (Table 3.2), nor was there any significant difference in the percentage change in bare ground ($U = 975$, $P = 0.195$, Table 3.2, ANOVA df 1, $F = 0.14$, $P = 0.71$) between the two sites. Herb cover increased significantly more at Liawenee than at Augusta over the 23 year period, ($U = 663$, $P < 0.001$, ANOVA df 1, $F = 2.99$, $P = 0.1$).

The dominant (> 50% cover) cover category at Liawenee changed from bare ground or grass in 1973 to almost equal components of grass, shrubs and bare ground in 1997 (Table 3.4, Plate. 3.5). Bare ground dominated two thirds of the quadrats at Augusta in 1973, while shrubs dominated two thirds of the quadrats in 1997 (Table 3.4, Plate 3.6).

There were significant differences in annual percentage change in cover for shrub, grass and bare ground between the four bare ground groups at Liawenee (Table 3.5). Shrub cover had significantly lower annual increases at Liawenee where bare ground exceeded

95% in 1973 than where it was less than 80% (Table 3.5). At Augusta, shrub cover increased significantly less where bare ground was less than 50% initially, than where it was greater than 50% (Table 3.5). Grass cover increased significantly more and bare ground decreased significantly more where bare ground was between 50-95% in 1973 at Liawenee, than where it was less than 50% or greater than 95% (Table 3.5). However, at Augusta there was no significant difference in change in grass cover between the four bare ground groups. At Augusta, herbs increased significantly more and bare ground decreased significantly less where bare ground was less than 50% in 1973 than where it was greater than 50%. There was no significant change in herb cover between the four bare ground groups at Liawenee. The covariate 'bare ground 1973' significantly influenced the change in cover of bare ground over time for both sites (ANCOVA, df 1, $F = 8.45$, $P = 0.01$), but did not significantly influence the change in cover of shrubs (ANCOVA, df 1, $F = 0.94$, $P = 0.34$), herbs (ANCOVA, df 1, $F = 1.78$, $P = 0.20$), or grasses (ANCOVA, df 1, $F = 2.31$, $P = 0.14$) for the two sites.

Table 3.4 Mean values for annual percentage change in canopy cover of shrubs, herbs, grasses and bare ground over the 23 year period in each bare ground group, and percentage of quadrats shifting from one lifeform dominance (> 50% cover) to another.

* Denotes significant difference in change in cover category between bare ground groups (Kruskal-Wallis H test, * = $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Significant differences between bare ground groups within cover categories occur where letters (a and b) are different (Mann-Whitney U test $P < 0.05$).

Sites		Group 1	Group 2	Group 3	Group 4
		< 50 % bare	50 – 80 % bare	80 – 95 % bare	> 95 % bare
Liawenee	shrub*	0.75a	0.5a	0.18ab	0.20b
	herb	0.05a	0.07a	0.05a	0.04a
	grass**	-0.39a	0.4b	0.31b	0.13a
	bare**	-0.41a	-0.98b	-0.53b	-0.36a
Augusta	shrub**	0.05a	0.93b	1.16b	0.66b
	herb**	0.04a	0.02b	0.01b	<0.00b
	grass	0.12a	0.06a	0.12a	0.03a
	bare***	-0.21a	-1.01b	-1.29b	-0.69b

Within the bare ground groups, shrubs were the most important colonisers of bare ground at Augusta, while both grasses and shrubs were more important at Liawenee (Table 3.5). Shrubs were important in the recovery process at both sites. However, the species composition was different (Table 3.6). The frequency of occurrence of shrub species increased over time for both sites, except for *Olearia algida*. *Ozothamnus hookeri* and *Orites acicularis* were only found at Augusta whilst *Hakea microcarpa* was only found at Liawenee. Where shrub species were found at both sites, there was a greater cover of *Olearia algida* ($z = -4.649$, $P < 0.001$) and *Grevillea australis* ($z = -5.907$, $P < 0.001$) at Liawenee in 1997 than Augusta, but no difference in the cover of *Leucopogon montanus* ($z = -1.023$, $P = 0.306$) and *Epacris gunnii* ($z = -1.892$, $P = 0.059$).

Table 3.5 Percentage change in dominance (> 50% cover) for quadrats initially dominated by bare ground, grass or shrubs by bare ground group, Liawenee and Augusta.
n.a. = not applicable

Sites	Group 1 < 50 % bare		Group 2 50 – 80 % bare		Group 3 80 – 95 % bare		Group 4 > 95 % bare	
	Lia	Aug	Lia	Aug	Lia	Aug	Lia	Aug
bare to bare	n.a.	n.a.	6	0	8	10	17	13
bare to grass	n.a.	n.a.	17	2	0	4	0	0
bare to shrub	n.a.	n.a.	10	27	0	8	0	4
grass to grass	21	4	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
grass to shrub	21	2	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
shrub to grass	0	6	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
shrub to shrub	0	19	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

The location in bare ground (no cover), grass (tall cover), and mat shrubs and litter combined (low cover) was significantly different between the three dominant shrub species (Table 3.7, $\chi^2 = 56.297$, $P = 0.001$). *Olearia algida* and *Leucopogon montanus* were usually located in grassy vegetation, with the latter also occurring regularly in mat shrubs and bare ground. *Ozothamnus hookeri* was most commonly located in bare ground and mat shrubs (Table 3.6).

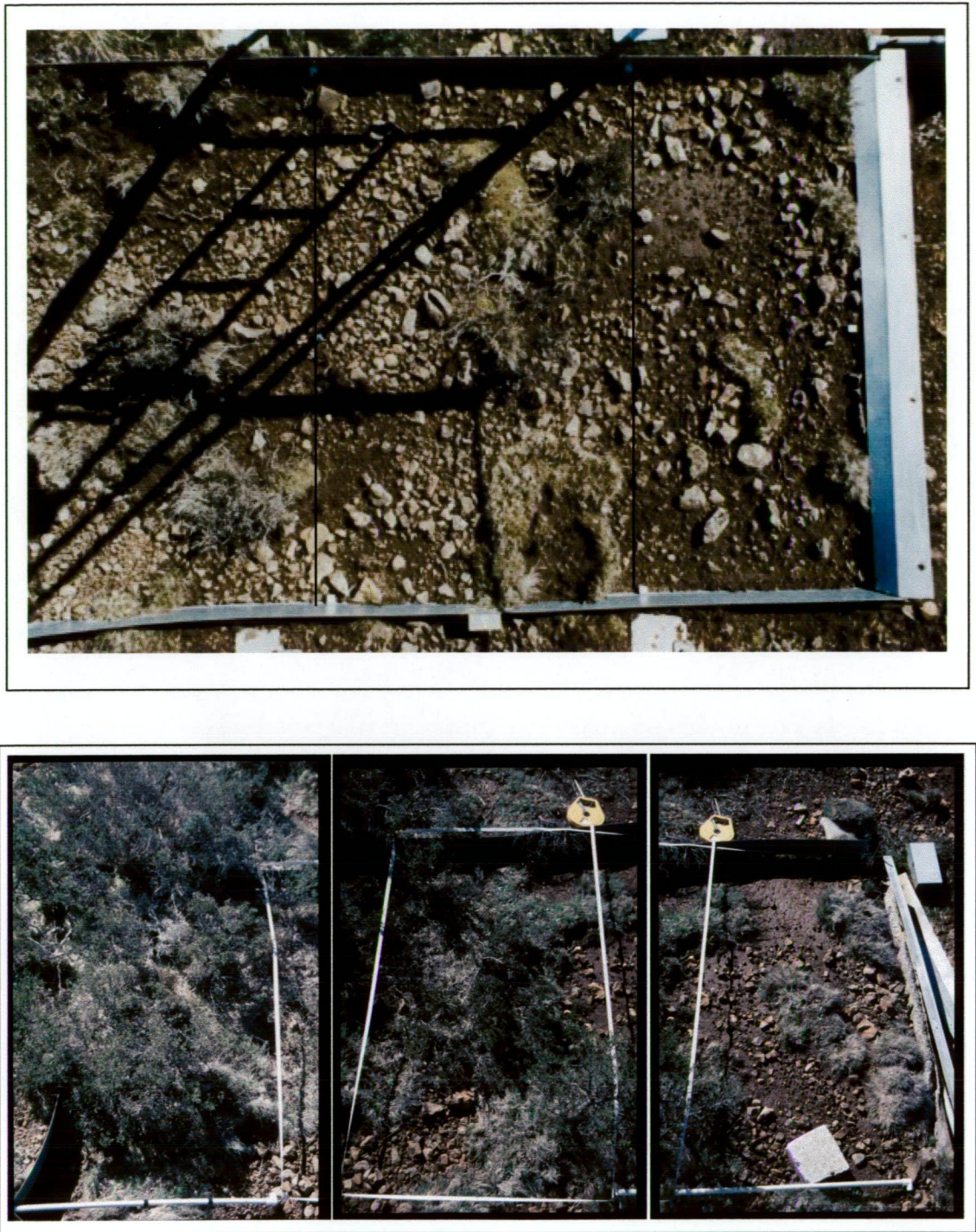


Plate 3.5 Changes in bare ground and lifeform dominance at Liawenee sediment trap No. 6 from 1973 (above) to 1998 (below).

The dominant shrub species is *Grevillea australis*.



Plate 3.6 Changes in bare ground and lifeform dominance at Augusta sediment trap No. 20 from 1973 (above) to 1998 (below).

Dominant shrubs are *Orites acicularis* (left) and *Ozothamnus hookeri* (right).

There was a significant difference between sites in the distance of *Leucopogon montanus* from bare ground ($z = -2.998$, $P = 0.003$). At Liawenee, *Leucopogon montanus* was found in vegetation, but it was found in bare ground at Augusta. There was no difference in the distance of *Olearia algida* to bare ground between the sites ($z = -1.389$, $P = 0.165$). In general, shrub species were more common in bare ground at Augusta than at Liawenee (Table 3.7).

Table 3.6 Significance of differences in frequency of shrub species between the 23 year period – within sites (Wilcoxon Signed Rank test)

Site	Species	z	P	1973	1997
Liawenee	<i>Olearia algida</i>	-3.266	= 0.001	34	18
	<i>Leucopogon montanus</i>	-4.123	< 0.001	15	32
	<i>Grevillea australis</i>	-4.262	< 0.001	1	21
	<i>Hakea microcarpa</i>	-4.359	< 0.001	0	19
Augusta	<i>Olearia algida</i>	-3.742	< 0.001	14	0
	<i>Leucopogon montanus</i>	-4.082	< 0.001	17	37
	<i>Grevillea australis</i>	-2.828	=0.005	0	8
	<i>Richea acerosa</i>	-4.600	< 0.001	10	33
	<i>Orites acicularis</i>	-4.359	< 0.001	2	21
	<i>Ozothamnus hookeri</i>	-5.099	< 0.001	17	43

Table 3.7 Frequency of ground cover classes found under dominant shrub species, and mean distance of each species to bare ground
Negative values in the distance to the edge of bare ground indicate that the shrub species is located in bare ground, whilst positive values indicate that it is located in vegetation

Species	Bare	Grass	Mat shrub	Litter	Average distance to edge of bare ground (cm)	
					Liawenee	Augusta
<i>Olearia algida</i>	10	66	3	1	7.5	-4.1
<i>Leucopogon montanus</i>	8	23	8	6	11.0	-7.1
<i>Ozothamnus hookeri</i>	13	0	8	1	-	-16.0
<i>Richea acerosa</i>	2	4	7	1	-	3.8
<i>Orites revoluta</i>	5	1	1	0	-	-19.6
<i>Orites acicularis</i>	0	0	2	0	-	-

DISCUSSION

Does bare ground decrease across all sites?

Over both long (23 years) and short (4-5 years) time scales, bare ground on the Eastern Central Plateau is decreasing. The average annual increment in vegetation cover is very similar between the two experiments (1.3% for the long-term experiment, 1.1% for the short-term experiment). These figures are also similar to those recorded by Wimbush and Costin (1979*b,c*) at Kosciuszko National Park (1.4% per year).

All sites are recovering, even in the presence of domestic stock on Liawenee Moor where there was no overall increase in bare ground for 47 of the 48 quadrats. However, recovery is greater at Augusta, where stock grazing was absent for most of the period despite being at a higher altitude. The increase in vegetation cover under domestic stock grazing at Liawenee is inconsistent with decreased covers resulting from stock grazing elsewhere on Liawenee Moor (Bridle and Kirkpatrick 1999, Chapter 2) and in similar vegetation on the Bogong High Plains (Williams and Ashton 1987*a*; Wahren *et al.* 1994). The difference in recovery between the sediment traps and the area around the exclosures on Liawenee Moor may be due to location, with the exclosures on an exposed ridge and the sediment traps on a leeward slope, sheltered from the prevailing winds.

Does the initial amount of bare ground affect regeneration success?

The nonlinear nature of the relationship between initial bare ground and annual increments of vegetation cover (Figs. 3.2, 3.3) is likely to be mathematically derived, as where bare ground is initially low opportunities for an increase in vegetation cover over time are less than where bare ground is higher. However, both data sets show a mean increase in bare ground where initial vegetation cover was high. Fluctuations in bare ground cover in well-vegetated areas may be natural in an environment where vegetation cover varies with environmental conditions such as climate and where frost heave is prevalent (Plate 3.7). Research in the Kosciuszko region found that as little as 1% bare ground may induce soil erosion in alpine environments (Costin *et al.* 1960).

The relatively low mean annual increments in vegetation cover for quadrats with very high initial bare ground cover may be related to the distance of existing vegetation to the bare patch. There is a general tendency in alpine areas for recovery to occur by lateral spread from the edges of gaps (Wimbush and Costin 1979*b,c*, see Plate 3.8). With high levels of bare ground, the area accessible to surrounding vegetation is likely to be much less than for moderate areas of bare ground. Also, large areas of bare ground are likely to occur in areas where erosion is ongoing.

Recovery in the 4-5 year experiment peaked where initial bare ground was 40-50% (Fig. 3.2). This contrasts to the 23 year study where the peak was at initial bare ground values of 70-80% (Fig. 3.3). This difference between the sites of different ages is a logical consequence of relative time elapsed since initial measurement.

Which lifeforms dominate the regeneration process?

Shrubs proved the most important colonisers of bare ground at Augusta and replaced grasses as the dominant lifeform in grassy heath vegetation at Liawenee. The role of disturbance in promoting shrub invasions of grassy vegetation types has been well documented (Williams and Ashton 1987*a*; Williams 1990). However, this dominance of shrubs over grasses generally occurs where bare ground gaps exist (Carr 1962; Williams 1990), and in sites which are not exposed (Williams 1990). Wild Dog Tier is the most exposed and high altitude site of those studied and was the only site where shrubs played a minor role in the recovery process. While the analysis of the ground cover matrix (vegetated, bare, litter) in which shrubs were present (Table 3.7) suffers from the problem that the matrix might post-date the shrub, it is apparent from the data that the different shrub species vary in their propensity to establish in bare ground.

Increases in herb cover over time were significant in the two 23-year-old sites and the two grassy sites from the 4- to 5-year-old plots. However, herbs constituted relatively little of the total vegetation cover and were not affected by grazing treatment in the short-term recovery experiment. The recovery of tall herbs from grazing pressure, especially stock grazing, may take much longer than five years, as records for the exclosures on the Bogong High Plains have shown (Carr and Turner 1959*b*; Wahren *et al.* 1994). It may be that tall herbs will become apparent in the future in the grazing exclosures. However, 23 year old exclosures on Liawenee Moor showed no significant

difference in total herb cover between grazing treatments (Bridle and Kirkpatrick 1999, Chapter 2, Chapter 4).

Do vertebrate herbivores have an effect on the regeneration process?

Relative grazing pressure and type has a significant impact on recovery, with the bare ground in ungrazed exclosures decreasing more than in the rabbit grazed exclosures, which in turn, decreased more than the rabbit plus native vertebrate herbivore grazed areas. The mean difference in the annual increment between the ungrazed treatments and the rabbit plus native grazed treatment is 0.94%, nearly three times the figure calculated for the same grazing treatments on Liawenee Moor (0.35%) (Bridle and Kirkpatrick 1999, Chapter 2). Rabbits and wallabies are generally more abundant at Liawenee (Bridle and Kirkpatrick 1999) than at the higher altitude sites (Chapter 4). Therefore the difference in annual incremental cover between the two treatments suggests that similar numbers of rabbits plus native herbivores have a greater impact on vegetation cover at higher altitudes than at lower altitudes.

The difference in recovery between rabbit and rabbit plus native grazed areas (0.45%) and ungrazed and rabbit grazed exclosures (0.49%) are similar, suggesting that both rabbits and native herbivores have an effect on recovery in Tasmanian alpine environments. The additive effect of rabbit grazing on native vegetation has also been documented in semi-arid grasslands (Leigh *et al.* 1989).

Is there any difference in the process of recovery between the short-term recovery experimental sites and the long-term sites?

Fifty-four (22.5%) of the 4- to 5-year-old quadrats had increased bare ground cover between 1991/2 to 1996. The majority of these (36 quadrats) were located in the heathy vegetation of Botsford and Bernacchi. By contrast only 7% of the long-term quadrats recorded an increase in bare ground. In the open heath of the long-term Augusta site, the decrease in bare ground was 1.4%. This figure is close to the 1.3% per annum recorded for the rabbit plus native grazed treatment in the environmentally similar five year old site at Bernacchi. While some quadrats at Bernacchi have eroded over the five year period, the average incremental change in vegetation cover at Bernacchi and Augusta is similar. However, change in ground cover dominance was not common in the short-

term experiment, indicating that an interval greater than five years is necessary before change in dominance becomes strongly expressed, a logical consequence of growth rates.

Management Implications

Vegetation has colonised most bare areas on the Eastern Central Plateau an annual increment of approximately 1%. Given that mean bare ground cover of the 4-5-year recovery sites ranged from 48-82% in 1991/2, almost complete recovery of these sites could be expected without any intervention, within 50-80 years. This would apply only in the absence of fire and/or additional grazing pressure. The rate of recovery could be increased through a decrease in animal grazing pressure. The removal of vertebrate herbivores will reduce the recovery time by half, but is probably both impractical and/or undesirable.



Plate 3.7 Needle ice on Liawenee Moor.



Plate 3.8 Vegetation in the sheep grazed area on Liawenee Moor.

Chapter 4

Impacts of Grazing by Vertebrate Herbivores on the Flower Stem Production of Tall Alpine Herbs

Introduction

It is generally accepted that vertebrate grazers affect the cover of herbs in alpine and subalpine regions of Australia (Carr and Turner 1959*a,b*; Wimbush and Costin 1979*a,b,c*; Leigh and Holgate 1979; Leigh *et al.* 1987, 1991; Gibson and Kirkpatrick 1989; Kirkpatrick 1989; Wahren *et al.* 1994; Bridle and Kirkpatrick 1999), whilst very little information is published on the relative impacts of domestic stock, rabbits and native herbivores (Leigh *et al.* 1987; Bridle and Kirkpatrick 1999). Leigh *et al.* (1987) concluded that rabbits had a greater effect on subalpine vegetation than native herbivores, whilst Bridle and Kirkpatrick (1999, Chapter 2) observed that sheep had much greater impacts than rabbits and native herbivores.

Many authors have observed that tall alpine herbs are preferentially grazed by vertebrate herbivores (Carr and Turner 1959*a,b*; van Rees 1984; Leigh *et al.* 1987; Wimbush and Costin 1979*a,b, c*; Wahren *et al.* 1994). Kirkpatrick (1989) hypothesised that the relative absence of tall alpine herbfields in Tasmania, was largely due to the year round presence of rabbits and native herbivores. This hypothesis has gained some support from observations of tall herb dominance on small ungrazed islands in a fast-flowing stream on the Eastern Central Plateau (Bridle and Kirkpatrick 1998, Chapter 5).

Clipping experiments have been used to simulate vertebrate grazing in controlled environments. The development of the plant at time of cutting, and the intensity and severity of clipping can affect the growth, fecundity and mortality of herb species (Escarre *et al.* 1996; Bergelson and Crawley 1992; Bock *et al.* 1995). Some plants compensate for this reduction in biomass by diverting energy into the production of photosynthetic parts. This may reduce the amount of resources the plant has available for reproduction (Mulder and Harmsen 1995). Other plants react to such a disturbance by producing even more flowering stems (Leigh *et al.* 1991). In Lapland, negative

correlations between rodent grazing in alpine heath and plant species flowering success and biomass have been recorded (Andersson and Jonasson 1986). In Australia, clipping experiments on alpine herbs have shown that flowering success may be retarded if plants are clipped early in the growing season or if they are cut more than once (Leigh *et al.* 1991).

Although variations in the cover of tall alpine herbs have been clearly attributed to differential grazing pressure and species composition of grazers, (see Chapters 2 and 5) it is not clear how much of this impact relates to the prevention of reproduction and how much to mortality of individuals. A step in addressing this question is to determine the impacts of vertebrate grazers on flower production in tall herbs.

This chapter addresses the impact of vertebrate herbivores on flowering of tall herbs in the alpine vegetation of the Eastern Central Plateau, Tasmania. The working hypotheses were that: grazing decreases flowering; different combinations of grazing animals have different affects on flowering; different tall herb species have different responses to grazing; the timing and intensity of grazing affects flowering.

Methods

Site Details

Four sites where pre-existing grazing exclosures had been erected were used for this study (Fig. 1.1). Exclosures at three of the sites (Double Lagoon, Botsford grassland and Botsford heath) were erected in 1990 after domestic stock grazing was discontinued. The exclosures at the fourth site (Liawenee) are 25 years old but were not in good repair until they were fixed in May 1995. Domestic stock grazing during the warmer months still occurs on the privately owned Liawenee Moor.

The Liawenee site (1050 m asl) contains two 30 x 100 m exclosures (Fig. 2.1) in open heath dominated by *Grevillea australis*. There was no replication of grazing treatments at this site. However these exclosures are probably the oldest of their kind in Tasmania (> 25 years) and for that reason, and due to the presence of domestic stock, are considered to be important, especially in the context of this study. One exclosure excluded all vertebrate herbivores whilst the other excluded sheep, allowing rabbits and native herbivores (wallabies and wombats) to graze. Sheep, rabbits and native herbivores grazed the control areas that were adjacent to the fencelines. Ten 5 x 5 m

quadrats were located in pairs across the fencelines (Fig. 2.1). This was deemed to be the most appropriate design due to the existence of a known environmental gradient (Bridle and Kirkpatrick 1999, Chapter 2) that runs parallel to the fenceline. Thus comparisons between different grazing regimes were made between the sheep grazed area and the rabbit plus native vertebrate herbivore grazed enclosure, the rabbit plus native grazed enclosure and the ungrazed enclosure, and the ungrazed enclosure and the sheep grazed area. Sheep were present on Liawenee Moor from October 1995 to June 1996 and from January 1997 to June 1997.

The Botsford *Poa* spp. grassland (*Poa hiemata*, *Poa fawcettiae*) (1150 m asl) had two treatments only – two ungrazed enclosures (both 5 x 5 m) and two controls grazed by rabbits and native herbivores adjacent to the enclosures (Fig. 4.1).

The Botsford *Orites acicularis* heath site (1150 m asl) consisted of two ungrazed enclosures (10 x 10 m) which were divided into four 5 x 5 m quadrats (Fig. 4.1). Control areas (grazed by rabbits plus native herbivores) (5 x 5 m) were established adjacent to the fencelines. In addition there were two other enclosures (6 x 6 m) that prevented wallaby and wombat grazing but allowed rabbit grazing. These two enclosures also had adjacent controls of the same size.

The Double Lagoon *Restio australis* sedgeland (1150 m asl) had the same treatments as the Botsford heath site (Fig. 4.1). However, all of the four enclosures were 6 x 6 m in size. Again the control areas were adjacent to the enclosures and were of the same size.

These three high altitude sites were not ideal for this experiment as herb cover was generally low and the sites were heterogeneous. This was an unavoidable problem due to the inherited nature of the enclosures, but it was felt that their value (in terms of age of the enclosures) outweighed the disadvantages of within site heterogeneity.

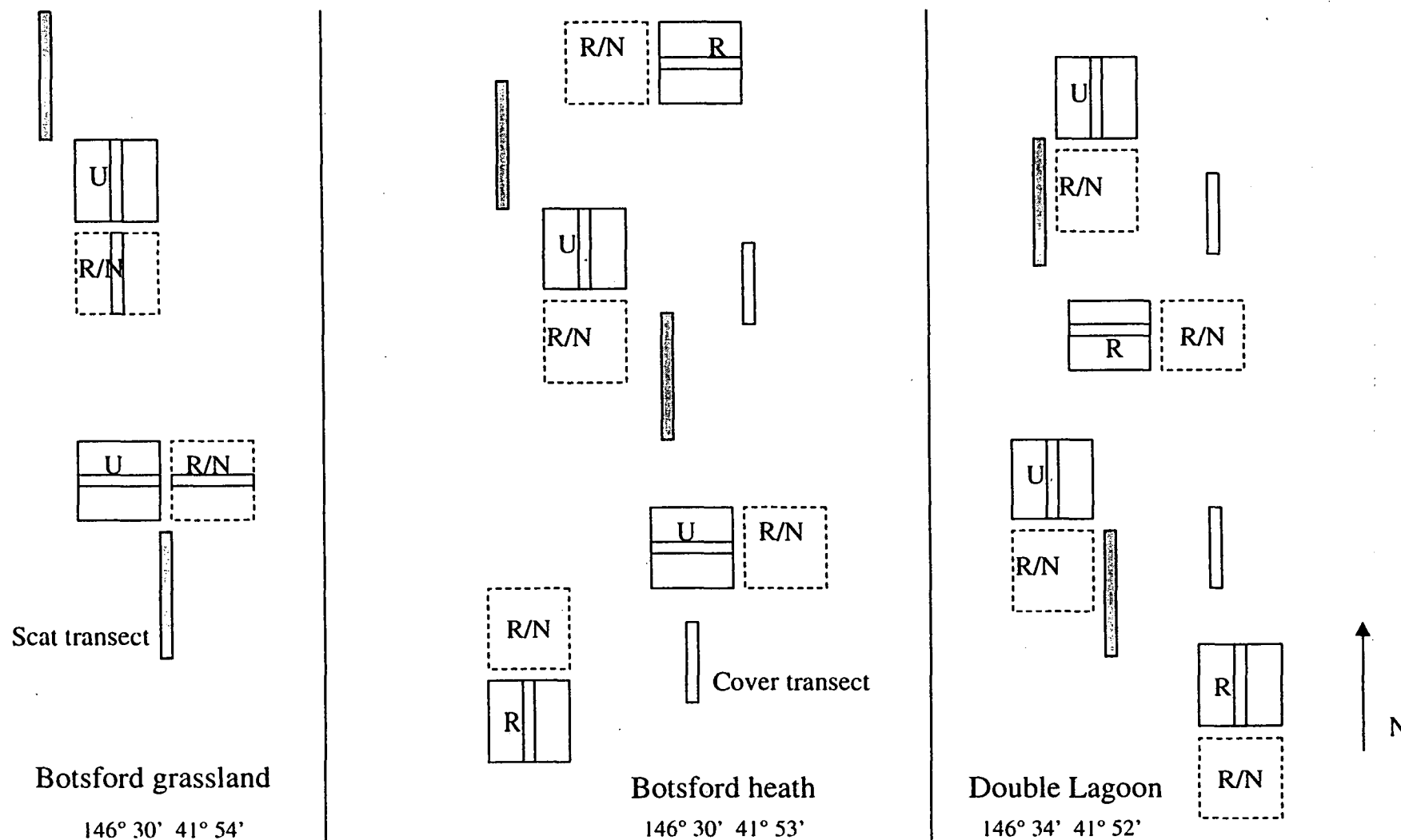


Figure 4.1 Sketch diagram of the layout of the grazing treatments at the three high altitude sites.

U = ungrazed, R = rabbit grazed, R/N = rabbit plus native grazed. Cover transect refers to the 10, 50 x 50 cm quadrats used for cover data. Scat transect refers to the 1 x 15 m transect used to collect scat data.

Sampling and Data Analysis

Flowering Survey

The number of flowering stems of tall herb species under different grazing regimes was observed over two growing seasons, December 1995 to March 1996 and November 1996 to March 1997. The number of flowering stems of each species in each treatment, their heights and their time of flowering were recorded monthly over the growing season. Any herb species which had a flowering stem averaging 10 cm or more in height was included in the survey. Data were collected for the following taxa:

Craspedia coolaminica, *C. alpina*, *C. paludicola*, *Ranunculus lappaceus*, *R. pascuinus*, *Erigeron gunnii*, *Celmisia asteliifolia*, *Euphrasia* spp., *Leptorhynchos squamatus*, *L. elongatus*, *Bracteantha subundulata*, *Chionogentias* spp., *Brachyscome tenuiscapa*, *B. spathulata*, *Podolepis jaceoides*, *Wahlenbergia ceracea*, *Microseris lanceolata*, *Linum marginale*, *Senecio lautus*, *S. gunnii*, and the exotic *Hypochoeris radicata*. At Liawenee the number of all flowering stems of tall herb species (except *Leptorhynchos squamatus*) were measured in each of 60, 5 x 5 m floristic quadrats. Individuals of *L. squamatus* were subsampled over a 2.5 x 5 m quadrat due to the large numbers present (Fig. 2.1). For each of the other sites, all flowering stems of tall herb species were measured over the whole of the quadrat.

The number of flowering stems is affected by the number of individuals present. In order to determine the relative flowering success of tall herb species between treatments, it was necessary to assess the relative cover of each species in each treatment over the two year period and across sites. Cover data for 60, 50 x 50 cm quadrats were collected for Double Lagoon, Botsford heath and Liawenee (20 for each treatment) in March 1996 and March 1997. Data from 40 such quadrats were used for the Botsford grassland site (also 20 per treatment). Quadrats were adjacent to the 5 x 5 m quadrats at Liawenee (Fig. 2.1). Quadrats at the other sites were laid out in a 5 m transect across the middle of the exclosures. Transects were also located in the controls between the grazing exclosures (Fig. 4.1). Percentage canopy cover of each species was determined by counting the number of 5 x 5 cm (equal to 1%) squares in the quadrat that a species dominated. The density for each species was expressed as number of flowering stems per m² of the cover of each species in the quadrat. This density value will subsequently be referred to as flowering stems.

There were 54 comparisons possible (see Table 4.3). A probability level of 0.05 was used for each individual comparison. Therefore one in twenty comparisons could be expected to give a significant result through chance. However, it is noted that the significance level adopted in these analyses would only result in 2-3 type I errors. It is also noted that the probability of a type I error for any single comparison does not change simply by making that comparison part of a larger set of comparisons.

Data Analysis

Across site comparisons of the number of flowering stems between ungrazed and rabbit plus native grazed treatments for the three high altitude sites (Double Lagoon, Botsford heath and Botsford grassland) were made using the General Linear Model procedure (GLM) in SAS (1989). This procedure allowed for testing of interactions. Data for this analysis were transformed ($\log(x + 1)$) to create central tendency in the data. The GLM approach was not totally appropriate to test for differences in flowering stems between rabbit and rabbit plus native grazed treatments, because of failure of transformations to satisfy the assumptions underlying the parametric tests. Nevertheless, given the insensitivity of non-parametric techniques to interactions, the parametric results are reported with the non-parametric analysis.

The preferred data analysis (and the one used to analyse the Liawenee data) used paired across fence comparisons between grazing treatments within sites. Within site analyses were preferred as plant species palatability is taken to be relative rather than absolute, depending on available forage and the number of grazers present. Across fenceline paired comparisons at Liawenee were thought to be particularly appropriate as there were no treatment replicates at this site, and because of the existence of a known environmental gradient (Bridle and Kirkpatrick 1999, Chapter 2). Total number of flowering stems for Liawenee were normalised ($\log(x + 1)$) and the paired t-test was used to test for differences in the flowering stems in paired comparisons between treatment types. All other data in the flowering survey (other sites and plant species) were analysed by the Wilcoxon Signed Rank test, a powerful non-parametric equivalent to the paired t-test for data that do not satisfy the assumptions of parametric statistics. Where any species occurred in fewer than 6 paired quadrats, insufficient data (id) were recorded and no statistics were calculated.

No direct comparisons (using non-parametric tests) were made between rabbit grazed and ungrazed exclosures at Double Lagoon and Botsford Heath as the grazing treatments were not located directly adjacent to one another. The combined data for ungrazed, rabbit grazed and rabbit and native grazed plots were not totally suitable for analysis by ANOVA as these data did not satisfy the assumptions of the test after transformation. Nevertheless, the results of the parametric tests are reported to give an indication of interactive effects.

Scat Survey

In order to assess the relative grazing pressure of different species of vertebrate herbivores across sites and over time, a scat survey was undertaken. Scat counts were taken at each site over a period of 20 months, at the end of each season (end of August - winter, November - spring, February - summer and May - autumn). Two scat transects (15 x 1 m) were set up at each of the four sites in the control area (Fig. 2.1, Fig. 4.1). An additional two transects were located in the rabbit and native grazed exclosure at Liawenee. These transects were cleared of any existing scats when they were created. Scats were identified (sheep, rabbit, wombat, wallaby), counted and cleared from the plots every three months. Log-linear models (using the CATMOD procedure in SAS 1989) were used to determine whether the distribution of scats of each species differed between site, season and year.

Clipping Experiment

Two common, palatable tall alpine herbs noted to be relatively reliable indicators of grazing pressure were chosen for this experiment; *Craspedia coolaminica* (Wahren *et al.* 1994) and *Microseris lanceolata* (McIntyre 1995). *Craspedia coolaminica* has been found to increase in abundance with the removal of domestic stock (Wahren *et al.* 1994; Wimbush and Costin 1979c). *Microseris lanceolata* has been found to stabilise in ungrazed plots, and to disappear from grazed areas (Leigh *et al.* 1987, Accessory Publication).

Craspedia coolaminica

Ninety *Craspedia coolaminica* germinants were transplanted into pots (5 x 5 cm x 12 cm deep) filled with commercial potting mix. The seedlings were taken at random from three trays of seedlings from different populations (on the Eastern Central Plateau). The

seedlings were then randomly placed into randomly allocated rows in three trays and placed in the shadehouse. After three weeks the plants were spread out into six trays (still in their original order) to provide space for them to grow. After a short time it became apparent that two of the plants were a different species of *Craspedia*. Therefore the measurements of these plants were excluded from the data analysis. Six treatments were applied to the seedlings with a row of five plants per treatment in each of the three trays. These treatments were chosen to simulate different grazing intensities and times. The treatments were: 3 rows (one per tray) of control plants (no grazing); plants that had all of their leaves cut to 1 cm in length at the beginning of the experiment (early stage of development); plants that had all of their leaves cut to 1 cm in length at the beginning of the experiment and again six weeks later (early and late stage of development); plants that had all of their leaves cut to 1 cm in length six weeks after the start of the experiment (late stage of development); plants that had half of their leaves cut to 1 cm in length at the beginning of the experiment (early stage of development, light grazing); plants that had half of their leaves cut to 1 cm in length at the beginning of the experiment and again six weeks later (early and late stage of development, light grazing).

For the last two treatments, if there was an odd number of leaves on the plant, one more than half of the leaves were clipped. Unopened leaves were not measured, nor were cotyledons. At the beginning of the experiment the number of all leaves on each plant were counted and their lengths and widths were measured.

Plants were measured after six weeks before the second round of treatments were carried out. After six weeks, width of the broadest leaf was also added to the measurements. The plants were measured again at 12 weeks. The presence of flowering stems was recorded at 11, 12 and 14 weeks. Height and stage of maturity of flowering stems was recorded at 12 weeks.

Differences between mean leaf measurements (mean leaf length, width of broadest leaf, number of leaves) and flowering stem height between treatment types were analysed using GLM and LSD (SAS 1989) (after a $\log(x + 1)$ transformation). Where data were not normally distributed and were not able to be transformed (e.g. for the percentage of plants flowering), then the Kruskal-Wallis H test and the Mann-Whitney U test were

used to test for differences in the median value of measured attributes between treatments.

Microseris lanceolata

Thirty *Microseris lanceolata* seedlings, raised from seed from several adults, were planted in pots (5 x 5 cm x 12 cm deep) with commercial potting mix, and were randomly allocated to two treatments, 15 control pots and 15 'grazed' pots. The grazed treatment consisted of clipping all leaves to 1 cm in length at the beginning of the experiment. More variations of grazing intensity could not be tested due to the limited number of plants available. The pots were randomly assigned to rows which were alternating treatment /control in two adjacent trays. Leaf number and length were measured at the beginning of the experiment. Then all of the leaves in the 'grazed' pots were cut to 1 cm in length. The plants were left for 12 weeks and were watered at least every second day. After 12 weeks, leaf number and length were again measured. The presence of flowering stems was recorded at 11 and 12 weeks. The number and height of stems were recorded at 12 weeks. Data were tested for normality and where appropriate, GLM (SAS 1989) was used to test for differences in the means of measured attributes between the two treatments. Where data were not normally distributed, the Mann-Whitney U test was used to determine differences in the median value between treatments.

Results

Flowering Survey

Flowering was most common in January and February at all sites (Table 4.1). Cover of individual species of tall herbs was not necessarily greatest in the ungrazed exclosures or least in the controls and was variable over the two year period (Chapter 2, Appendix 2). The majority of tall herbs had more flowering stems where grazing was restricted or nonexistent (Figs 4.2-4.4).

Table 4.1 Flowering times for tall herb species on the Eastern Central Plateau, 1995-1996 and 1996-1997

Species	Flowering				
	Nov	Dec	Jan	Feb	Mar
<i>Craspedia alpina</i>					
<i>Ranunculus pascuinus</i>					
<i>Brachyscome tenuiscapa</i>					
<i>Brachyscome spathulata</i>					
<i>Ranunculus lappaceus</i>					
<i>Erigeron gunnii</i>					
<i>Euphrasia collina</i>					
<i>Linum marginale</i>					
<i>Hypochoeris radicata</i>					
<i>Chionogentias</i> spp.					
<i>Senecio lautus</i>					
<i>Celmisia asteliifolia</i>					
<i>Microseris lanceolata</i>					
<i>Bracteantha subundulata</i>					
<i>Craspedia coolaminica</i>					
<i>Leptorhynchos squamatus</i>					
<i>Podolepis jaceoides</i>					
<i>Wahlenbergia ceracea</i>					

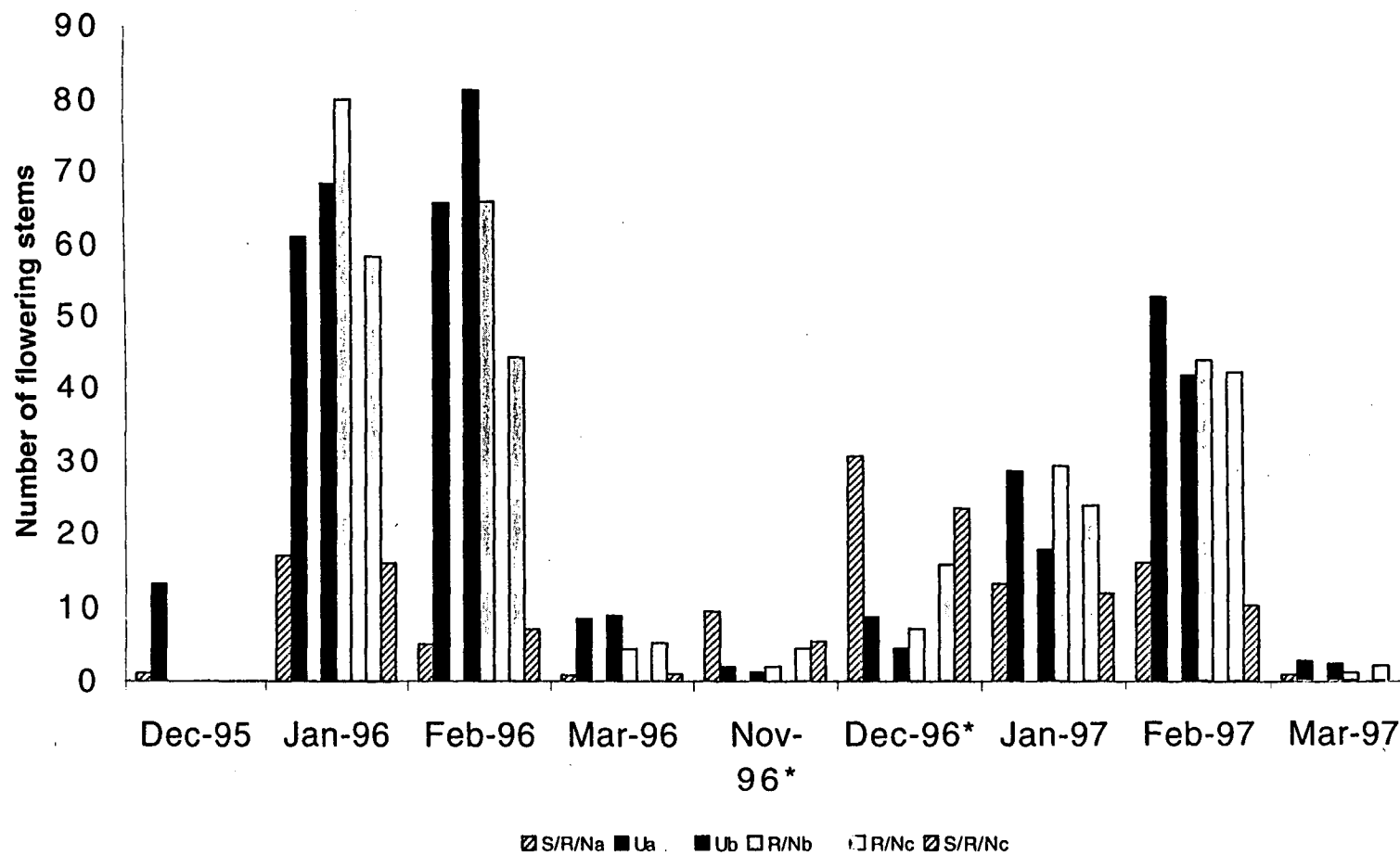


Figure 4.2 Across fence comparisons between grazing treatments of the number of flowering stems per m² on Liawenee Moor during the growing seasons of 1995-96 and 1996-7.

* = No sheep were present on the Moor in Nov and Dec 1996. S/R/N = sheep plus rabbit plus native grazed, r/n = rabbit plus native grazed, u = ungrazed. Across fence comparisons are next to one another on the graph and are denoted by the use of the same letters (a, b, c) next to the grazing treatments.

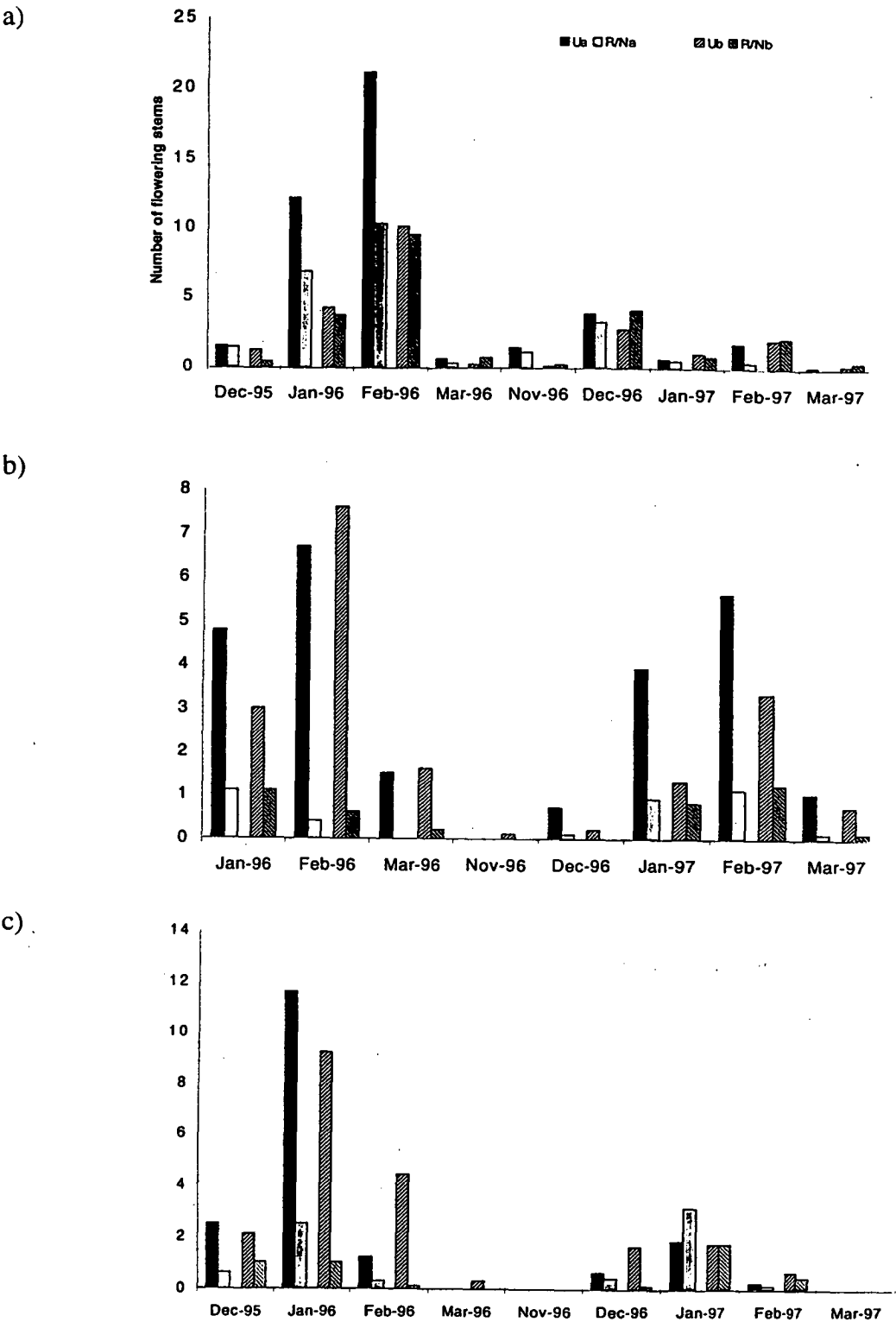
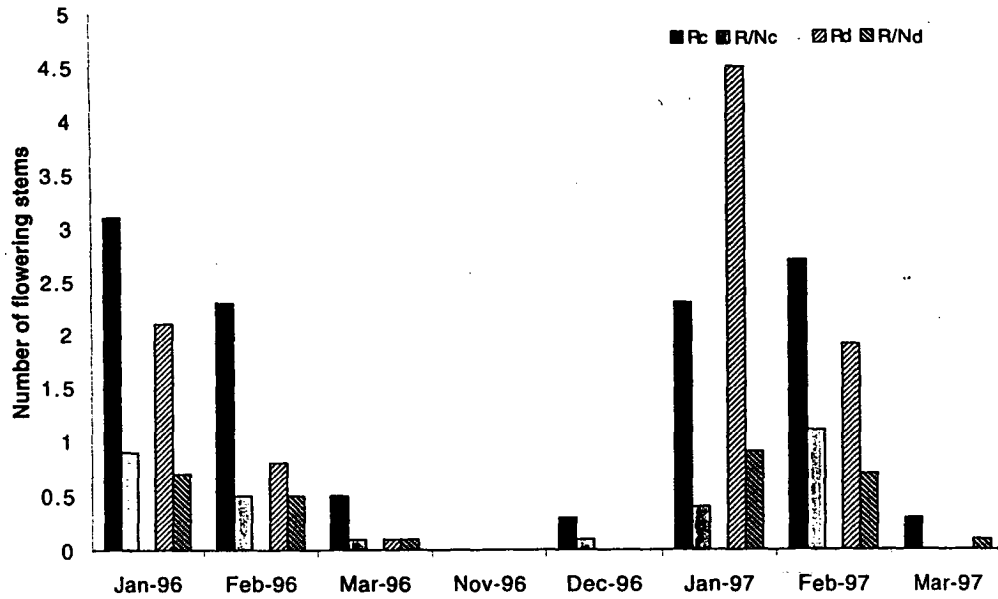


Figure 4.3 Across fence comparisons between grazing treatments (ungrazed and rabbit plus native grazed) of the number of flowering stems per m² at Botsford grassland (a), Botsford heath (b) and Double Lagoon (c) during the growing seasons of 1995-96 and 1996-7.

U = ungrazed, r/n = rabbit plus native grazed. Across fence comparisons are next to one another on the graph and are denoted by the use of the same letters (a, b) next to the grazing treatments.

a)



b)

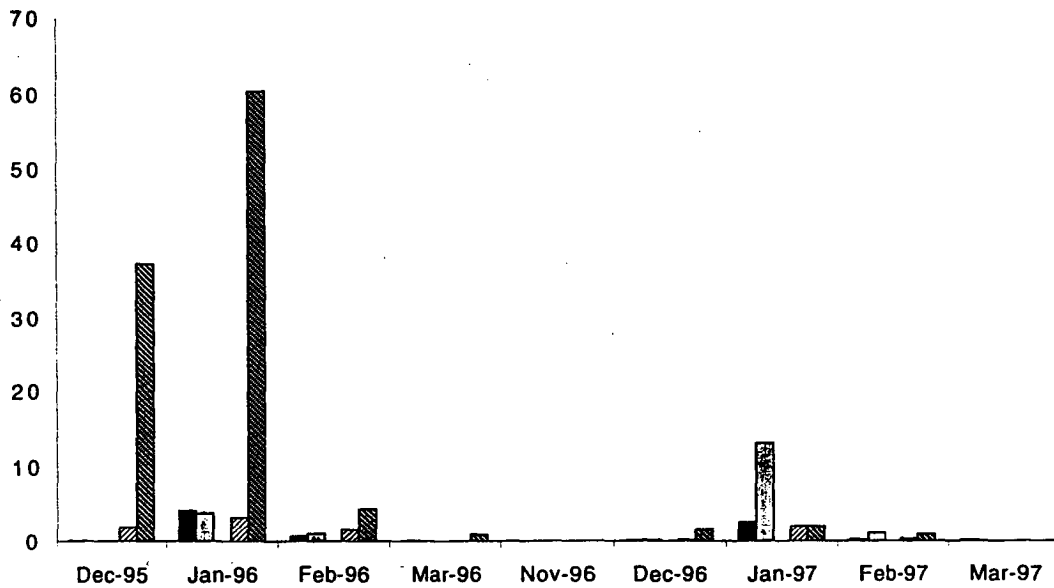


Figure 4.4 Across fence comparisons between grazing treatments (rabbit grazed and rabbit plus native grazed) of the number of flowering stems per m^2 at Botsford heath (a) and Double Lagoon (b) during the growing seasons of 1995-96 and 1996-7. R = rabbit grazed, r/n = rabbit plus native grazed. Across fence comparisons are next to one another on the graph and are denoted by the use of the same letters (a, b) next to the grazing treatments.

For the three high-altitude sites (Botsford grassland, Botsford heath and Double Lagoon) there was no overall treatment effect from the GLM analysis (Table 4.2) nor was there a site effect between the ungrazed exclosures and the rabbit plus native grazed areas. However, there were year and month effects, with significantly more flowering stems in 1996 than in 1997 and during the months of January and February.

The GLM analysis of the ungrazed, rabbit grazed and rabbit plus native grazed data for Double Lagoon and Botsford heath showed significant year and month effects and a site by treatment interaction (Table 4.2).

There was no significant difference in the number of flowering stems between the ungrazed quadrats and the rabbit plus native grazed quadrats at Liawenee (paired-t test, $T = 0.19$, $P = 0.0851$).

All species listed in Table 4.3, except *Microseris lanceolata*, showed significant differences in the number of flowering stems between different grazing treatments. At Liawenee, nine species recorded significantly fewer flowering stems in sheep grazed areas than in those where sheep were excluded. However, some species (*Brachyscome tenuiscapa*, *Craspedia alpina*) recorded significantly more flowering stems in the sheep plus rabbits plus native grazed area than in the ungrazed exclosure when sheep were absent from Liawenee Moor.

There were only three species (*Bracteantha subundulata*, *Leptorhynchus squamatus*, *Senecio lautus*) that were able to be tested for significant differences in flowering stems between the rabbit grazed exclosures and the rabbit plus native grazed areas. Only *Leptorhynchus squamatus* recorded significantly more flowering stems in the rabbit grazed exclosure than in the rabbit plus native grazed area, and this only at Botsford heath (Table 4.3).

Table 4.2 Results of Generalised Linear Model of number of flowering stems per m² of herb cover between ungrazed and rabbit plus native grazed treatments for December to March 1996 and November to March 1997 at Botsford grassland, Botsford heath and Double Lagoon, and for the ungrazed, rabbit grazed and rabbit plus native grazed treatments at Botsford heath and Double Lagoon for the same period.

Results in bold highlight significant results. R/N = rabbit plus native grazed, r = rabbit grazed, u = ungrazed.

Dependent variable: Number of Flowering Stems for Botsford heath, Double Lagoon and Botsford grassland

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	21	16.6784	0.7942	2.96	0.0048
Error	26	6.9718	0.2681		
Corrected Total	47	23.6502			
Source	DF	F Value	Pr > F		
Site	2	2.17	0.3159		
Treat	1	5.48	0.1440		
Site*Treat	2	1.42	0.2594		
Year	1	6.89	0.0143		
Month	4	6.79	0.0007		
Year*Treat	1	1.73	0.1997		
Month*Treat	4	0.34	0.8475		
Month*Year	3	1.27	0.3061		
Month*Year*Treat	3	0.20	0.8954		

Dependent variable: Number of Flowering Stems for Botsford heath and Double Lagoon
(Note the data used in the following analysis were not normal, nor were the residuals homogeneous)

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	28	27.2445	0.9730	2.35	0.0032
Error	57	23.6336	0.4146		
Corrected Total	85	50.8781			
Source	DF	F Value	Pr > F		
Site	1	0.00	0.9707		
Treat	2	0.37	0.7292		
Site*Treat	2	3.91	0.0256		
Year	1	4.72	0.0339		
Month	4	6.70	0.0002		
Year*Treat	2	0.43	0.6530		
Month*Treat	7	0.33	0.9376		
Month*Year	3	0.79	0.5072		
Month*Year*Treat	6	0.16	0.9858		
Site	Treat	N	Mean	SD	LSD
Botsford heath	rabbit/native	22	0.3351	0.2795	0.3679 (r/n v r)
	rabbits	14	0.7586	0.5866	0.4769 (r v u)
	ungrazed	8	1.0532	0.7041	0.4442 (r/n v u)
Double Lagoon	rabbit/native	21	1.0493	1.1479	0.3712 (r/n v r)
	rabbits	14	0.6376	0.5836	0.4981 (r v u)
	ungrazed	7	1.0056	0.7554	0.4442 (r/n v u)

Table 4.3 Significant differences in number of flowering stems between grazing treatments
 Probabilities in bold represent significantly more flowering stems with a decrease in grazing pressure;
 Probabilities underlined represent significantly more flowering stems with an increase in grazing pressure;
 id = insufficient data; n.a. = not applicable; NS not significant ($P > 0.05$);
 S/R/N = sheep, rabbits and native vertebrate herbivores present;
 R/N = rabbits and native vertebrate herbivores present;
 R = rabbits only; and U = ungrazed. V= versus.

Species	Site	S/R/N v. U	S/R/N v. R/N	R/N v. U	R/N v. R
<i>Brachyscome spathulata</i>	Botsford heath	n.a.	n.a.	NS	id
	Double Lagoon	n.a.	n.a.	NS	id
<i>Brachyscome tenuiscapa</i>	Liawenee (sheep)	id	0.01	NS	n.a.
	Liawenee (no sheep)	<u>0.001</u>	id	id	n.a.
	Botsford grassland	n.a.	n.a.	NS	n.a.
<i>Bracteantha subundulata</i>	Botsford heath	n.a.	n.a.	<0.001	NS
<i>Craspedia alpina</i>	Liawenee (sheep)	0.005	id	id	n.a.
	Liawenee (no sheep)	<u>0.002</u>	NS	NS	n.a.
<i>Craspedia coolaminica</i>	Liawenee (sheep)	<0.001	0.003	<0.001	n.a.
	Botsford grassland	n.a.	n.a.	NS	n.a.
	Botsford heath	n.a.	n.a.	<0.001	id
	Liawenee (sheep)	0.05	NS	0.027	n.a.
<i>Erigeron gunnii</i>	Liawenee (no sheep)	id	id	id	n.a.
	Botsford heath	n.a.	n.a.	NS	id
	Liawenee (sheep)	<0.001	<0.001	NS	n.a.
<i>Leptorhynchus squamatus</i>	Botsford grassland	n.a.	n.a.	NS	n.a.
	Botsford heath	n.a.	n.a.	<0.001	0.028
	Double Lagoon	n.a.	n.a.	0.039	NS
	Liawenee (sheep)	id	NS	id	n.a.
<i>Microseris lanceolata</i>	Botsford grassland	n.a.	n.a.	id	n.a.
	Botsford heath	n.a.	n.a.	NS	id
	Liawenee (sheep)	id	0.004	0.027	n.a.
<i>Podolepis jaceoides</i>	Liawenee (sheep)	<0.001	<0.001	NS	n.a.
	Liawenee (no sheep)	NS	NS	<u>0.049</u>	n.a.
<i>Ranunculus lappaceus</i>	Liawenee (sheep)	id	id	id	n.a.
	Liawenee (no sheep)	<u>0.039</u>	NS	NS	n.a.
<i>Ranunculus pascuinus</i>	Botsford grassland	n.a.	n.a.	NS	n.a.
	Botsford heath	n.a.	n.a.	NS	id
	Liawenee (sheep)	<0.001	0.004	<u>0.011</u>	n.a.
	Liawenee (no sheep)	id	id	id	n.a.
<i>Senecio lautus</i>	Botsford grassland	n.a.	n.a.	id	n.a.
	Botsford heath	n.a.	n.a.	<0.001	NS
	Double Lagoon	n.a.	n.a.	NS	NS
	Liawenee (sheep)	<0.001	id	NS	n.a.
<i>Wahlenbergia ceracea</i>	Botsford heath	n.a.	n.a.	NS	id
% of Significant differences between grazing treatments		91	53	37	20

Responses of some species to different mixes of vertebrate herbivores varied between sites. *Senecio lautus* recorded a greater number of flowering stems in the rabbit and native grazed enclosure than the ungrazed plot at Liawenee, but this was not the case at Botsford heath. Flowering stems of *Leptorhynchos squamatus* were significantly greater in number in the ungrazed or rabbit grazed enclosures at Botsford heath and Double Lagoon than the rabbit and native grazed area, but this difference was not significant at Botsford grassland or Liawenee. At Botsford heath there were significantly more flowering stems of *L. squamatus* in the rabbit grazed enclosures than in the rabbit and native grazed area, whilst there was no significant difference between these two treatments at Double Lagoon.

Craspedia coolaminica recorded its highest number of flowering stems in the ungrazed enclosure across all sites where it occurred (Plate 4.1), though this relationship was not significant at the Botsford grassland site. The number of flowering stems of this species was also greater in the rabbit and native grazed enclosure than the sheep grazed control at Liawenee, and greater in the rabbit grazed enclosures than the rabbit and native grazed control at Botsford heath.

Craspedia alpina occurred only at Liawenee Moor (Plate 4.2). This species is an early flowering tall herb. This species was flowering in December 1995 and November 1996. Sheep were present on Liawenee Moor in December 1995. For this month, there were more flowering stems inside the ungrazed enclosure than the sheep grazed control (Table 4.3). However, in November and December 1996, when sheep were absent, there were significantly more flowering stems in the control area than the ungrazed enclosure. There was no significant difference in the number of flowering stems of this species between the two enclosures at Liawenee.

The Botsford grassland site recorded the least number of significant differences between grazing treatments for individual plant species (Table 4.3).



Plate 4.1 *Craspedia coolaminica* and *Leptorhynchus squamatus* flowers in the ungrazed (right) and the rabbit and native herbivore grazed (left) exclosures. Very few flowers can be seen in the sheep grazed area behind.



Plate 4.2 *Craspedia alpina* flowers in the ungrazed exclosure on Liawenee Moor.

Scat Data

The log linear analysis of the scat data determined that there were interactive effects between site and year and site by season (Table 4.4). These effects were heavily influenced by the presence of large numbers of rabbits at Double Lagoon, and large numbers of wallabies at Botsford heath (Table 4.5). Rabbits were more common at Double Lagoon during the summer months, while wallabies were more common at Botsford heath during autumn or winter. No strong seasonal effects were apparent for the other sites (Table 4.5).

Botsford grassland recorded the least number of rabbit scats. There were fewer rabbit scats across all sites in 1997 than 1996. More wallaby scats were recorded in 1996 than 1997 at Liawenee but the opposite trend pertained to Botsford heath and Botsford grassland. Numbers of wallaby scats at Double Lagoon remained similar over the two year period.

At Liawenee there were more rabbit scats in the rabbit plus native grazed enclosure than in the sheep grazed area (Table 4.4). There were no scats in the ungrazed enclosure. There were more wallaby scats in the rabbit and native grazed enclosure at Liawenee than in the sheep grazed control. Sheep scats were confined to the sheep grazed control at Liawenee. There were more sheep scats on Liawenee Moor in 1997 than in 1996 (Table 4.4).

Wombats were present in the rabbit and native grazed areas at all sites, and in the sheep, rabbit and native herbivore grazed area at Liawenee.

Table 4.4. Maximum-likelihood analysis-of-variance table (log-linear model) for rabbit scats and wallaby scats

Source	DF	Chi-square	Prob.	DF	Chi-square	Prob.
Rabbit scats				Wallaby scats		
Season	3	519.91	0.0000	3	3.77	0.2869
Year	1	315.52	0.0000	1	4.47	0.0344
Season by Year*	2	124.67	0.0000	2	9.17	0.0102
Site	4	794.44	0.0000	4	56.55	0.0000
Site by season	12	422.33	0.0000	12	89.04	0.0000
Site by year	4	511.25	0.0000	4	11.94	0.0178
Likelihood ratio	7	206.08	0.0000	7	16.52	0.0024

Table 4.5 Number of scats per 30 m² for each site

No data were available for the scat transect in the Liawenee rabbit and native grazed exclosure for the summer of 1996

S/R/N = sheep, rabbit and native vertebrate herbivores present;

R/N = rabbits and native vertebrate herbivores present.

Herbivore	Season	Liawenee R/N	Liawenee S/R/N	Botsford grassland R/N	Botsford heath R/N	Double Lagoon R/N
Rabbits	Summer 96	-	357	302	243	356
	Autumn 96	480	350	134	235	302
	Winter 96	131	309	27	24	294
	Spring 96	418	405	3	90	202
	Summer 97	234	93	4	33	334
	Autumn 97	35	0	3	0	229
	Winter 97	129	59	1	4	209
Wallabies	Summer 96	-	0	5	14	23
	Autumn 96	67	16	13	18	3
	Winter 96	11	23	5	35	3
	Spring 96	63	13	8	15	3
	Summer 97	18	1	10	19	10
	Autumn 97	0	5	6	16	9
	Winter 97	4	0	19	56	11
Wombats	Summer 96	-	0	0	0	0
	Autumn 96	0	0	0	0	0
	Winter 96	0	0	1	1	0
	Spring 96	0	0	0	0	7
	Summer 97	0	4	0	4	0
	Autumn 97	0	7	0	0	0
	Winter 97	0	12	0	0	1
Sheep	Summer 96	0	291	0	0	0
	Autumn 96	0	316	0	0	0
	Winter 96	0	62	0	0	0
	Spring 96	0	0	0	0	0
	Summer 97	0	451	0	0	0
	Autumn 97	0	1329	0	0	0
	Winter 97	0	234	0	0	0

Clipping experiment

Craspedia coolaminica

Initially the plants did not significantly differ by treatment in either length of the shortest or the longest leaf, or mean leaf length. However they were significantly different in the number of leaves on each plant (ANOVA $P = 0.043$).

After 12 weeks, there was a significant difference in mean leaf length ($P = 0.002$), and the number of leaves ($P < 0.001$) between treatments (Table 4.6).

There were significant differences in the number of plants flowering per treatment (Kruskal-Wallis H test, $H = 16.157$ $P = 0.006$) and the height of flowering stems ($H = 12.745$ $P = 0.026$) after 12 weeks. The greatest flowering success was experienced in the control pots. Time of flowering was early in the control pots and late or non-existent in those treatments where all leaves had been removed (Table 4.7). Mean leaf length was significantly greater in the two treatments where all the leaves were cut after 6 weeks (all leaves cut twice at time = 0 and at 6 weeks, all leaves cut once at 6 weeks) than in all other treatments (Table 4.6), but flowering success and median height of the flowering stem was greater in the control plots than either of the two treatments (median stem height for all leaves cut twice at time = 0 and at 6 weeks, $U = 0$, $P = 0.011$, all leaves cut once at 6 weeks, $U = 3$, $P = 0.003$).

Microseris lanceolata

There were no significant differences between treatment type and plant attributes at the beginning of the experiment.

However, after 12 weeks, there were significant differences in the median height of the flowering stems (Mann Whitney U test, $U = 19$, $P = 0.013$), the median maximum height of the flowering stems ($U = 16$, $P = 0.007$) but not the presence of flower heads ($U = 90$, $P = 0.24$) between the two treatments (Table 4.8). There was no significant relationship between the number of flowering heads and treatment ($U = 69$, $P = 0.061$) (Table 4.8). Time of flowering varied between treatments, with clipped plants flowering later than the controls (Table 4.7). There were no significant affects of treatment on leaf attributes.

Table 4.6 Attributes of *Craspedia coolaminica* in the clipping experiment at 12 weeks
Values with the same letters are not significantly different at $P < 0.05$. Significant differences in leaf attributes were determined by ANOVA. Significant differences in the mean height of heads were determined by the Mann-Whitney U test.

Treatment	Percentage of Plants Flowering	Mean height of heads (cm)	Mean Number of Leaves	Mean Leaf Length (cm)	Width of Broadest Leaf (cm)
Control	71	46.6a	15.1a	4.9a	1.21a
All 1 cm @ 6 weeks	40	19.0b	6.9b	5.9b	1.01a
Half 1 cm x 2	36	36.7b	8.9b	5.0a	1.07a
Half 1 cm x 1	33	36.5b	13.9a	4.8a	1.09a
All 1 cm x 2	20	20.8b	7.5b	6.1b	1.00a
All 1 cm x 1	13	33.3b	13.1a	4.9a	1.07a

Table 4.7 Timing of flowering of *Craspedia coolaminica* and *Microseris lanceolata* during the clipping experiment

Treatment	Percentage of plants flowering				
	<i>Craspedia coolaminica</i>			<i>Microseris lanceolata</i>	
	11 weeks	12 weeks	14 weeks	11 weeks	12 weeks
Control	71	71	71	80	80
Half 1 cm x 1	20	40	40		
All 1 cm x 1	36	36	36	27	60
Half 1 cm x 2	27	33	33		
All 1 cm x 2	13	13	13		
All 1 cm @ 6 weeks	13	13	13		

Table 4.8 Attributes of *Microseris lanceolata* in the clipping experiment at 12 weeks
Values with the same letters are not significantly different at $P < 0.05$. Significant differences in leaf attributes and the mean head height were determined by ANOVA.

<i>Microseris lanceolata</i> Treatment	% of plants flowering	Mean No. heads per plant	Mean height of heads (cm)	Mean height of tallest flower (cm)
Control	80a	2.2a	17.4a	23.0a
Clipped	60a	1.8a	8.8b	11.2b

Discussion

Herbs such as *Craspedia coolaminica*, *Leptorhynchos squamatus*, *Ranunculus lappaceus* and *Senecio lautus* that occur on the Eastern Central Plateau have been shown to produce more flowering stems per unit cover of area in areas released either totally or partially from grazing by vertebrate herbivores. These species also occur in the alpine/subalpine environments of southeast Australia, where responses to a decrease in grazing pressure led to an increase in plant cover or flower stem production (Carr and Turner 1959a,b; Wimbush and Costin 1979a,b,c; Leigh *et al.* 1987; Leigh *et al.* 1991; Wahren *et al.* 1994).

Of those species occurring on the Eastern Central Plateau, a few species could be classified as grazing intolerant (*sensu* McIntyre and Lavourel 1994) as they recorded an increase in flowering success with a decrease in grazing pressure (e.g. *Craspedia coolaminica*, *Podolepis jaceoides*). Some were advantaged by a temporary decrease in grazing pressure, such as when the sheep were absent from Liawenee Moor (e.g. *Craspedia alpina*, *Ranunculus pascuinus*, *Brachyscome tenuiscapa*). However, no tall herb species recorded a greater number of flowering stems in the sheep grazed areas than other grazing treatments whilst the sheep were present.

Surprisingly, the palatable herb *Microseris lanceolata* (McIntyre 1995) recorded no significant difference in flowering success between grazing treatments at any of the sites. However, there were relatively few of these plants at any of the locations.

The effects of domestic stock on treeless subalpine vegetation are much greater than the effects of rabbits and/or natives alone (Bridle and Kirkpatrick 1999, Chapter 2). On Liawenee Moor sheep directly affect the flowering success of tall herbs by targeting the flowering stems. Where the effects of rabbits have been separated from those of rabbits and native herbivores combined, four of the five results show no significant difference in numbers of flowering heads between rabbit grazed exclosures and rabbit plus native herbivore grazed areas. This lack of a significant difference in number of flowering stems between these two treatments suggests that rabbits may have a greater effect on numbers of flowering stems than native vertebrate herbivores. Leigh *et al.* (1987) also recorded a greater impact by rabbits than native herbivores on subalpine vegetation.

However, at their study site, natural grazing pressure by native vertebrate herbivores was very light.

The number of rabbit scats in the study area declined greatly over the two year period. A possible cause for this decline may be explained by a decrease in rabbit numbers due to death by myxomatosis, which is prevalent in years of above average rainfall (Parer and Korn 1989). Throughout the 1995-1996 growing season, above average rainfall was recorded at the Liawenee weather station (Bureau of Meteorology 1997). This was followed by below average rainfall during the 1996-1997 season. However, the putative substantial decrease in rabbit numbers did not result in an increase in number of flowering stems in any plots that were subject to rabbit grazing. In fact, numbers of flowering stems decreased from the 1995-1996 season to the 1996-1997 season in most of the plots across all three high altitude sites. This decrease in rabbit numbers may be related to the lack of significant differences in the flowering success of tall herbs between grazing treatments in 1997. Whilst there was no strong treatment by year effect, differences in the flowering success of tall herbs between treatments were significant for some sites in 1996 but not in 1997. Therefore, climate is likely to have had an overriding effect on flower production, both directly (number of flowering stems) and indirectly (by affecting rabbit populations). Elsewhere, productivity of herbs in any one year has been related to precipitation patterns (Coughenour 1991; Leigh *et al.* 1991; Wimbush and Costin 1979a,b,c).

The results from the *Craspedia coolaminica* clipping experiment closely followed its behaviour in the field. It appears that *Craspedia coolaminica* is able to compensate for leaf loss from clipping as there were no significant differences in leaf length and width of broadest leaf in relation to clipping intensity. However, this compensation reduces the probability of flower production.

Microseris lanceolata also recorded a negative flowering response to clipping, although not as strong as *Craspedia coolaminica*. Data for this species were scarce in the field but it was noticeable that individuals of *Microseris lanceolata* had many flowering heads per plant in the shadehouse, but only one head per plant was ever recorded in the field.

Clipping vegetative parts affects height of the flowering stem for both *Craspedia coolaminica* and *Microseris lanceolata*, which implies that grazing may have a

reproductive impact on the dispersal opportunities of wind-dispersed species as well as their ability to attract pollinators. Both of these functions are affected by flower height. While some species of tall herbs are able to reproduce vegetatively, the impact of grazing on flowering is likely to reduce their ability to colonise beyond vegetative dispersal range, as in the case of *Podolepis jaceoides* and *Craspedia coolaminica* at Liawenee (see Chapter 2).

Disturbance is said to play a major role in the establishment of tall alpine herbfields (Carr and Turner 1959b; McVean 1969). Physical disturbance in the form of late-lying snow is not present on much of the Eastern Central Plateau. Disturbance caused by frost, wind and rain are most apparent in the degraded bare ground patches (> 1 m in diameter (Bridle and Kirkpatrick unpublished data) which inhibit the establishment of most plant species including tall herbs. Therefore small scale disturbance is provided mainly by vertebrates that graze tall herb species. These tall herbs are dominant in disturbed exclosures i.e. where gaps (caused by previous burning and grazing management) exist but grazing does not, but are less prevalent in unprotected sites (Bridle and Kirkpatrick 1998, 1999). Some species such as *Brachyscome tenuiscapa* and *Craspedia alpina* are capable of taking advantage of gaps provided by vertebrate herbivores, and flower prolifically in times of low grazing pressure.

The tall herbs *Celmisia* spp. are dominant species in the tall alpine herbfields in alpine vegetation on the Australian mainland. *C. asteliifolia* has recently been split into a Tasmanian endemic (Gray and Given 1999), occurring over a wide range on the Eastern Central Plateau including the study sites of Botsford grassland and Botsford heath, but flowering stems were only recorded in ungrazed exclosures at Botsford heath. Numbers of individuals were too few to be analysed statistically. It is possible that *Celmisia* is still recovering from the effects of stock grazing which ceased in 1989 in the Botsford area, as occurred on the mainland (Carr and Turner 1959b, Wahren *et al.* 1994). It is also possible that *Celmisia* is not potentially dominant in the Tasmanian alpine environment.

The results presented here show that the flowering success of tall alpine herbs is linked to grazing pressure, herbivore mix, and climatic conditions. These results partially support the hypothesis of Kirkpatrick (1989). However, environmental effects may have a large impact on the presence/absence of tall alpine herbs either directly, through

climatic constraints or lack of particular disturbance regimes (e.g. extended snowlie or from *Oncopera* sp. grazing), or indirectly by influencing vertebrate herbivore populations. Also a critical experimental test of the hypothesis would require comparisons between alpine environments of Tasmania and the Australian Alps.

Chapter 5

Why are Tall Herbs Rare Dominants in Tasmanian Alpine Vegetation? Evidence from Islands in the Ouse River System

Introduction

Tall alpine herbfield (*sensu* Costin *et al.* 1979) is one of the more widespread vegetation types in the Australian Alps. While many species that are found in mainland tall alpine herbfields occur in Tasmania, the community is largely absent from the Tasmanian alpine zone. One of the main ecological differences between alpine areas in mainland Australia and those in Tasmania is the lack of grazing pressure from native herbivores on the mainland. The absence of marsupial herbivores on the mainland can be accounted for by the more continental climate of the Australian Alps, resulting in extended periods of snowlie (Carr & Turner 1959a; McVean 1969). As Tasmania has a maritime climate, persistent snowlie is restricted to the highest lee slopes, allowing vertebrate herbivores to survive and feed in the relatively unprotected vegetation of the alpine zone throughout the year (Kirkpatrick 1989).

The impacts of domestic stock and rabbit grazing on tall alpine herbs has been well documented for the Australian Alps (Carr & Turner 1959b; Wimbush & Costin 1979a,b,c; Leigh & Holgate 1979; Leigh *et al.* 1987; Williams & Ashton 1987b; Wahren *et al.* 1994). However very little information is available on the effects of native vertebrate herbivores on alpine vegetation. Leigh & Holgate (1979) found that plant mortality and reproductive capacity were reduced by native vertebrates and rabbit grazing in the shrubby understorey of dry sclerophyll woodlands. Palatable forbs were considered to be the main food source of mammalian herbivores in subalpine environments (Leigh *et al.* 1991). However, the effects of native marsupial grazing have been found to be insignificant when compared to the effects of rabbits (Leigh *et al.* 1987).

In Tasmania, native herbivores (wallabies and wombats) affect the cover and heights of some shrubs and species of herbs in subalpine grassy woodlands (Gibson & Kirkpatrick 1989). Grazing by native herbivores and rabbits is considered to be the main mechanism for restricting the spread of exotic species across the Central Plateau (Kirkpatrick 1989;

Whinam *et al.* 1994; Corbett 1996). In alpine *Sphagnum* bogs, epacridaceous shrubs are subject to heavy wallaby grazing (Whinam 1990). Her study also indicated that grazing pressure was greater on individual palatable species in environments with relatively few palatable plants.

Rabbit numbers widely fluctuate on the Central Plateau and are heavily reduced during times of prolonged snowlie (Cullen 1995). Historical records detail the fluctuating numbers of kangaroo around the Great Lake area during the mid 1800's, where '...vast numbers of kangaroos perished through the cold...' and during the summer of 1845 '...one man alone killed 1 100 [kangaroos] in the vicinity of Lake Arthur...' (Breton 1846 p. 130).

Kirkpatrick (1989) postulated that the lack of tall alpine herbfield in Tasmania was due to the palatability of the herbs and the year round presence of introduced and native herbivores. He noted that tall alpine herbs were visibly abundant in places which were isolated from grazing, such as fenced plots and islands in fast-flowing, deep streams (e.g. the Ouse River system).

This chapter documents the environments, vegetation and grazing incidence on several of the islands in the Ouse River system and the adjacent banks. The working hypothesis was that the exclusion of grazing by a fast-flowing deep stream would result in a greater degree of tall herb cover than in adjacent, environmentally similar areas.

Methods

In January 1997 five islands in the upper Ouse River valley, on the eastern Central Plateau, Tasmania were surveyed (Figure 5.1). These islands were the first five seen on a traverse of the region. The closest adjacent area of the same size on the banks of the rivers was also surveyed.

The following data were recorded:

- dimensions of the island;

- minimum distance from the island to the shore;

- presence and cover of vascular plant taxa, using the following scale - 1 = <1%, 2 = 1-5%, 3 = 5-25%, 4 = 25-50%, 5 = 50-75%, 6 = 75-100%; and

- presence, identity and number of scats present.

Soil analyses were undertaken to determine whether there were any differences in soil characteristics between the islands and the shores. Three bulked samples of surface soil (<

5 cm deep) were taken from each island and adjacent shore. These were analysed for; Copper, Iron, Manganese, Zinc, Ammonium N, Nitrate N, total Nitrogen, total Phosphorus, total Calcium, extractable Phosphorus, extractable Potassium, organic Carbon, conductivity and pH, using the following methods; DTPA for Cu Fe Mn Zn; KCL extraction for NH_4/N , NO_3/N ; semimicro Kjeldahl, steam distillation for total N; ICP analysis for total P & Ca; Bicarbonate-extractable P; Bicarbonate-extractable K; organic C (Walkley & Black); $\text{pH}(\text{CaCl}_2)$ 1:5 soil/0.01M calcium chloride extract; conductivity 1:5 soil/water extract (Rayment & Higginson 1992).

Plant species were grouped according to lifeform: shrub, grass, herb (dicotyledons), graminoids (herbaceous monocotyledons other than members of the Poaceae). Herbs were further divided into three groups on the basis of stature; tall alpine herbs (*sensu* Costin *et al.* 1979), medium stature herbs (between 5-10 cm tall) and small herbs (less than 5 cm tall). All 'small herb' *Ranunculus* species were grouped under the genus.

Number of scats and species richness were calculated. The Mann-Whitney U test was used to determine whether there were any significant differences in soil characteristics between the islands and the shores. The Fisher's Exact Probability test was used to determine whether number of scats, plant species richness and presence and cover values of taxa on the shores were independent of those on the islands.

The midpoints of the cover classes were used to estimate the total cover of lifeforms for each of the island/shore plots. The Fisher's Exact Probability test was used to determine whether the cover of lifeform groups on the shores were independent of those on the islands.

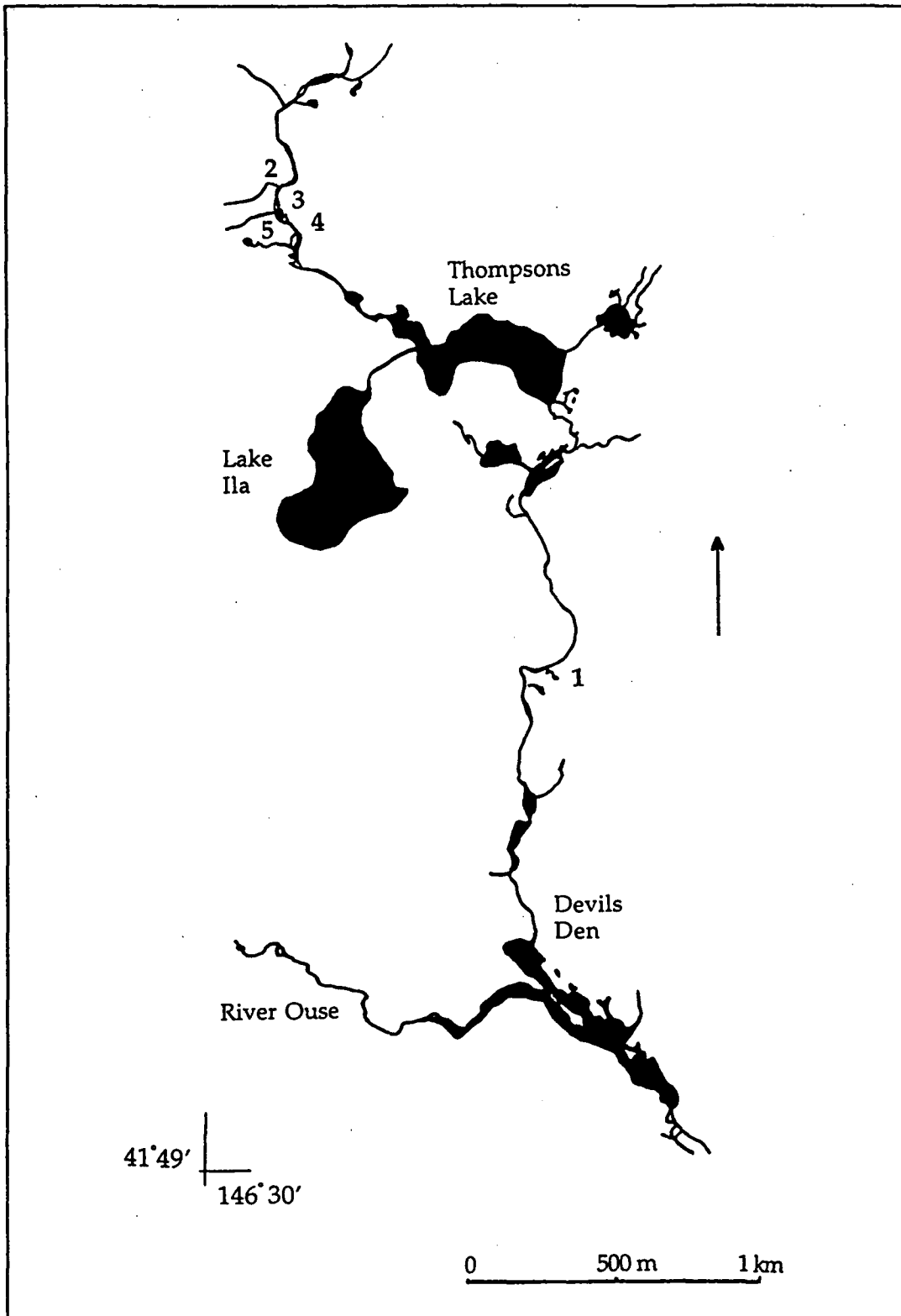


Figure 5.1 Location of the islands in the upper Ouse River system

Results

The islands varied in size from 2.25 m² to 24 m² and were from 1.5 to 12 m away from the shores (Table 5.1).

Table 5.1 Physical characteristics of the five island sites

Island	Dimensions (m)	Distance to Bank (m)	
		West	East
1	4.0 x 6.0	2.0	4.0
2	2.0 x 2.0	3.0	6.0
3	1.5 x 1.5	6.0	6.0
4	3.0 x 2.0	8.0	1.5
5	4.0 x 2.0	12.0	2.0

The number of scats recorded for the islands and the shore was significantly different ($P = 0.004$). Not surprisingly, the only scats recorded on the islands were wallaby scats, whilst both wallaby and wombat scats were recorded on the shore. Scats were only found on islands four and five which lay less than 2 m away from the river bank (Tables 5.2 and 5.3).

Table 5.2 Number of scats per m²

Site	Number of Scats		Identity of Scats on Shores
	Island	Shore	
1	0.0	0.9	Wallaby
2	0.0	9.5	Wallaby/Wombat
3	0.0	14.2	Wallaby
4	2.3	5.8	Wallaby
5	1.0	6.4	Wallaby/Wombat

Table 5.3 Results of soil analyses for the island and the shore sites

	Cu ppm	Fe ppm	Mn ppm	Zn ppm	NH ₄ ppm	NO ₃ ppm	N %	P ppm	Ca ppm	ExtP ppm	ExtK ppm	C %	Cond. dS/m	pH CaCl ₂
Shore														
Mean	2.69	328.6	441	9.44	56.8	0.05	0.84	772.6	1344.4	1.6	361	15.4	0.06	5.2
SE	1.79	237.7	274.5	6.23	52		0.04	80.8	959.3	0.9	112.7	1.56	0.01	0.6
Island														
Mean	2.47	279.4	368.6	7.56	49.4	0.05	0.86	768.2	1523.6	2.2	367	14.1	0.08	5.4
SE	0.6	72.4	122.1	2.3	16.9	0.0	0.0	30.9	479.5	0.2	68.5	0.9	0.0	0.2

There were no significant differences between the soils of the island and the shore sites (Table 5.3).

In all, 40 plant species were identified on the islands and adjacent shores. Most of the species recorded were herbs (23/40) followed by graminoids and shrubs (Table 5.4).

Only one species, *Plantago daltonii*, occurred in all ten samples, while 13 species were restricted to only one sample (Table 5.4). Species richness was significantly higher on the shores than on the islands ($P = 0.004$) (Table 5.4).

The grass *Hierochloe redolens*, the graminoid *Carpha alpina* and the tall alpine herb *Craspedia paludicola* were the only species to have significantly different frequency distributions on the islands and the shores ($P = 0.004$ for all three species).

There was no significant difference in the presence or cover of shrubs, grasses, graminoids or small herbs between the islands and the shore sites. Medium stature herbs (h) and tall herbs (tah) were significantly more abundant on the islands ($P = 0.024$, $P = 0.004$ respectively).

Seven species occurred on the islands only, while 11 species were recorded for the shore sites only (Table 5.5). Of these, small herbs made up the greater proportion of plants recorded for the shore sites only. Tall herbs and grass species were faithful only to the islands.

Table 5.4 Cover of species and lifeforms in the island/shore paired plots

life = lifeform group; gm=graminoid, gr=grass, hs=small herbs, h=medium stature herbs, tah=tall herbs, sh=shrubs, is = island; sh = shore. Species names and lifeform groups in bold type have significantly different frequency of occurrence on the islands and the shores

	life	Island		Shore	
		Mean	SE	Mean	SE
<i>Astelia alpina</i>	gm	-	-	0.5	0.5
<i>Carex gaudichaudiana</i>	gm	20.1	13.0	11.3	6.0
<i>Carpha alpina</i>	gm	2.5	-	13.7	19.5
<i>Empodisma minus</i>	gm	37.5	-	38.8	26.9
<i>Oreobolus distichus</i>	gm	-	-	0.5	0.5
<i>Restio australis</i>	gm	2.5	-	15.0	15.0
<i>Deschampsia caespitosa</i>	gr	2.5	-	-	-
<i>Hierochloa redolens</i>	gr	20.7	12.6	1.2	1.7
<i>Poa costiniana</i>	gr	19.5	9.3	19.0	15.4
<i>Acaena montana</i>	hs	-	-	0.5	0.5
<i>Acaena novae-zelandiae</i>	hs	0.5	-	0.5	0.5
<i>Asperula gunnii</i>	hs	-	-	1.2	1.4
<i>Cotula alpina</i>	hs	-	-	0.5	0.5
<i>Dichosciadeum ranunculaceum</i>	hs	0.5	-	0.5	0.5
<i>Diplaspis hdrocotyle</i>	hs	0.5	-	0.5	0.5
<i>Hydrocotyle sibthorpioides</i>	hs	-	-	1.5	2.0
<i>Hypericum japonicum</i>	hs	-	-	0.5	0.5
<i>Oreomyrrhis ciliata</i>	hs	2.5	-	1.0	1.1
<i>Ourisia integrifolia</i>	hs	0.5	-	1.0	1.3
<i>Ranunculus</i> sp.	hs	24.5	12.2	26.5	37.4
<i>Viola betonicifolia</i>	hs	-	-	0.5	0.5
<i>Viola cunninghamii</i>	hs	1.0	0.4	0.5	0.5
<i>Epilobium</i> sp.	h	-	-	0.5	0.5
<i>Geranium potentilloides</i>	h	2.5	-	0.5	0.5
<i>Plantago daltonii</i>	h	7.1	3.2	0.9	1.1
<i>Ranunculus lappaceus</i>	h	0.5	-	0.5	0.5
<i>Chinogentias</i> sp.	tah	0.5	-	-	-
<i>Craspedia coolaminica</i>	tah	0.5	-	-	-
<i>Craspedia paludicola</i>	tah	21.1	12.4	0.5	0.5
<i>Baeckea gunniana</i>	sh	2.5	-	2.5	2.5
<i>Bellendena montana</i>	sh	0.5	-	-	-
<i>Coprosma</i> sp.	sh	0.5	-	-	-
<i>Epacris gunnii</i>	sh	-	-	0.5	0.5
<i>Epacris serpyllifolia</i>	sh	-	-	0.5	0.5
<i>Olearia obcordata</i>	sh	2.5	-	0.5	0.5
<i>Orites acicularis</i>	sh	15.0	-	15.0	15.0
<i>Richea acerosa</i>	sh	2.5	-	15.0	15.0
total graminoids	gm	24.6	11.7	41.5	33.2
total grasses	gr	36.8	17.9	19.7	16.1
total small herbs	hs	27.6	12.0	31.0	42.4
total medium herbs	h	7.7	3.1	1.2	1.3
total tall herbs	tah	21.3	12.5	0.3	0.2
total all herbs	h	56.6	25.9	32.5	43.8
total shrubs	sh	4.7	4.7	6.8	1.6
species richness/m ²		12.4	1.5	15.6	2.4

Table 5.5. Lifeforms of species occurring only on either the islands or the adjacent shores.

Species	Island	Shore
<i>Astelia alpina</i>		graminoid
<i>Oreobolus distichus</i>		graminoid
<i>Deschampsia cespitosa</i>	grass	
<i>Acaena montana</i>		small herb
<i>Asperula gunnii</i>		small herb
<i>Cotula alpina</i>		small herb
<i>Epilobium</i> sp.		small herb
<i>Hydrocotyle sibthorpioides</i>		small herb
<i>Hypericum japonicum</i>		small herb
<i>Viola betonicifolia</i>		small herb
<i>Ranunculus glabrifolius</i>	small herb	
<i>Ranunculus rivularis</i>	small herb	
<i>Chinogentias</i> sp.	tall herb	
<i>Craspedia coolaminica</i>	tall herb	
<i>Bellendenia montana</i>	shrub	
<i>Coprosma</i> sp.	shrub (mat)	
<i>Epacris gunnii</i>		shrub
<i>Epacris serpyllifolia</i>		shrub

Discussion

Visually, the tall herb *Craspedia paludicola* identifies the main difference in species composition and stature between the island and the shore sites (Plate 5.1). This difference in the vegetation cannot be attributed to differences in soil fertility (Table 5.3). These islands do differ from the shores in the number of scats per unit area with several having none (Table 5.2). It was not possible to measure flood disturbance impacts. However, it appeared that these were greatest on the upstream ends of islands and least on the downstream ends. There seems little doubt that flood activity favours the establishment of tall herbs as these were concentrated on the upstream ends of islands and on the vertical banks of both the islands and the shore. However, on the shores the tall herbs are only found where the steepness of banks prevented grazing while on the islands they occurred throughout.

The dominant grass species, *Hierochloe redolens* which occurred on the downstream ends of the islands was rare on the shore. Small herbs that were absent on the highly grazed shore, were rare in the taller vegetation of the islands. Many of the species more common on the islands are reported to be palatable and/or not grazing resistant. The tall herb species on the islands are considered to be very palatable and relatively intolerant to grazing (Carr & Turner 1959a,b; Wimbush & Costin 1979a,b; Leigh *et al.* 1987; Wahren *et al.* 1994). The shrub *Bellendena montana* is also palatable to native herbivores. Of those species faithful to the shore (Table 5.5), the following are grazing resistant; *Cotula alpina* (Gibson & Kirkpatrick 1989; Leigh *et al.* 1987), *Hydrocotyle sibthorpioides* (Gibson & Kirkpatrick 1989), *Hypericum japonicum* and *Viola betonicifolia* (Gibson & Kirkpatrick 1989; Leigh *et al.* 1987). *Astelia alpina* is palatable to native vertebrates when choice of food is limited (Whinam 1990). *Asperula gunnii* (Gibson & Kirkpatrick 1989; Leigh *et al.* 1987), *Epacris gunnii* (Gibson & Kirkpatrick 1989; Whinam 1990) and *Epacris serpyllifolia* (Whinam 1990) are palatable species though they can tolerate some grazing.

Grazing can affect the overall stature of communities and individual taxa. The difference in stature of herbs that we found between the islands and shores is likely to be related to grazing pressure. Wimbush & Costin (1979a,c) found densities of minor herbs to be less in grazing exclosures over time while tall herbs increased. The dominance of small herbs on the shore sites suggests that grazing is important in creating and maintaining habitat requirements (and higher species richness) where small herbs are not outcompeted by taller species (Wimbush & Costin 1979a). Small herbs existing on the islands had suitable habitat provided for them by disturbance from the river itself, such as bank erosion and occasional flood events. Where grazing is present on the islands, the cover of *Craspedia paludicola* is less than where grazing is absent (Table 5.4 see data for islands 4 and 5).

Similar reports on community composition on ungrazed islands have been noted elsewhere on the Central Plateau. Colonel Legge (1902), on visiting the now drowned Pine Island in Great Lake, recorded a plant community dominated by ...'the tall Alpine Holy grass *Hierochloe redolens*, the *Craspedia richei* whose tall stalk and downy, button-shaped flower towered above the dwarf *Poa* grass'... [p. 141]. Other tall herbs such as '*Brachycome* sp.', '*Helichrysum bracteatum*' and '*Celmisia longifolia*' were also noted. Legge did not see any sign of vertebrate herbivores whilst he was on the island, and his companions only reported sightings of whip-snakes, echidnas and pipits. In New Zealand, tall herbs also dominated islands free from vertebrate herbivore grazing (Norton 1995). In contrast, tall herbs were only common on steep sites on the shore sites, where they were protected from feral goats.

Islands in the Ouse River system were grazed if they were in close proximity to the shore or to other islands. Where there were a series of islands linked together, scats were found on them all. While *Hierochloa redolens* was present on these grazed islands, *Craspedia paludicola* was noticeably absent or present only on the steep undercut banks (Plate 5.2). These islands were generally larger or more protected than the islands with tall herbs, due to their proximity to other islands, and they appear to be physically more stable. The dominance of *C. paludicola* on the upstream ends of the surveyed islands and along the undercut banks suggests that it is able to withstand physical disturbance and may indeed require it in order to gain dominance in a strongly competitive environment.

The dominance of tall alpine herbs in herb-rich grasslands on the mainland may be partly a result of some disturbance event(s) (Carr & Turner 1959a; McVean 1969; Costin *et al.* 1979). Tall herbs such as *Craspedia* spp. are capable of colonising bare ground (Wahren *et al.* 1994), and they are also opportunistic when gaps appear in the vegetation, such as during the senescence of *Poa* tussocks or shrubs (Carr & Turner 1959b; McVean 1969; Costin *et al.* 1979). Where exogenous disturbances (such as domestic stock grazing) have been removed, the most commonly recorded effect in the plant community is an increase in species and cover of tall alpine herbs (Carr & Turner 1959b; Wimbush & Costin 1979a,b,c; Wahren *et al.* 1994). Whether tall alpine herbfields persist in the long term appears to rely on occasional extreme climatic events such as drought or extended snowlie, or exogenous disturbance such as fire. In Tasmania, climatic events may not be so extreme, but endogenous disturbance in the form of grazing exists. While disturbance itself may be a necessary component for tall alpine herbs to dominate in grasslands, they need to be able to reproduce to do so!

Given the above reasoning, the working hypothesis is accepted. A combination of physical disturbance and an absence of marsupial grazing is necessary for tall herbs to attain dominance in Tasmanian alpine vegetation on fertile soils.



Plate 5.1 An ungrazed island in the upper Ouse River system, dominated by *Craspedia paludicola* on the upstream end. The vegetation on the opposite shores shows *C. paludicola* on the undercut banks only.



Plate 5.2 A lightly grazed island showing *Craspedia paludicola* only on the undercut banks of the island and the shore.

Chapter 6

Discussion

Data presented earlier in this thesis allow some inferences to be made on the relative effects of sheep, rabbits and native vertebrate herbivores on vegetation structure, floristics, herb fecundity and regeneration success in alpine areas of the Eastern Central Plateau, Tasmania. These data also provided a framework in which to explore the hypothesis of Kirkpatrick (1989), that the presence of vertebrate herbivores inhibits the growth of tall alpine herbfields in the Tasmanian alpine zone. This chapter integrates these results and places them in the context of previous work.

Limitations of data

Inherited grazing exclosures and photographic data from the Eastern Central Plateau have facilitated the assessment of long-term impacts of vertebrate herbivores on alpine vegetation, in a project of relatively short duration. These data have been invaluable as it is highly likely that few differences would have been discernible over a period of 2-3 years (from 1995 to 1997). However, problems were also inherited with the data and the location and experimental design of some of the exclosures.

The grazing treatments at Liawenee Moor were not replicated. Visual differences between the destocked plots and the sheep grazed area were obvious, and, while no base line data could be found (other than from aerial photographs), this site is probably the oldest grazing experiment in Tasmania, if not quite as old (c. 30 years) as similar experiments on the mainland which are more than 50 years old (see Carr and Turner 1959a). The data for the Liawenee exclosures were collected and analysed in the form of across fence comparisons between grazing treatments in order to compensate for the lack of baseline data and to accommodate a pre-existing environmental gradient along the 100 m fenceline. Bare ground was greatest in the ungrazed exclosure in 1974 and least in the stock grazed area. Therefore differences between the exclosures were apparent from the beginning of the experiment. These are likely to have had some effect on different rates of change in bare ground in the three grazing treatments. The poor condition of the northern fence when the project started in 1995 may have affected some comparisons. This fence had collapsed in places allowing stock to graze over the fence into the ungrazed exclosure.

Four of the five high altitude sites (Double Lagoon, Bernacchi, Wild Dog Tier, Botsford heath) were located in severely eroded environments because of the aims of the research that led to their establishment. While observations on regeneration at these sites indicate what may happen in the 'worst case scenario', they may not be indicative of recovery processes in less severely degraded areas.

Scat counts were made in an attempt to quantify relative grazing pressure over time and across sites. Scat counts have been used to infer animal populations in this and other studies (Andrew and Lange 1986; Leigh *et al.* 1987) While this method of measuring grazing pressure was crude, it was the most feasible method of quantifying populations and fluctuations in numbers over the two year data collection period. Vertebrate herbivore populations, as indicated by scat numbers, varied over the time period. There were significant differences in the number of rabbit scats between 1996 and 1997, indicating a decrease in grazing pressure. Sheep arrived later on Liawenee Moor in 1997 than 1996. The results on impacts on vegetation pertain only to such conditions, and could have been very different under different grazing pressures, such as an increase in wild herbivore populations or sheep grazing for longer periods. There were no direct comparisons between scat counts and vegetation cover or flowering success as the data were collected at different times and scales. The scat data were collected for the site as a whole and the vegetation data were collected for individual treatments within sites. If vegetation data had been collected for the scat transects, then comparative analyses would have been appropriate.

Non-parametric statistics were used for most of the data analyses, as the data were generally not normal, nor could they be normalised after suitable transformations were performed. Parametric statistics were used where possible to determine whether there were any interactive effects between treatments and sites and over time. However, the vegetation varied from one site to another as did the level of disturbance in terms of percentage bare ground. As vertebrate herbivores selectively graze, then their preferences must be determined by what is available at any particular site. Therefore the treatment of effects within individual sites was preferred over generalisations of effects across sites.

Are there differences between the effects of domestic stock, native and feral herbivores on the regeneration, structure and floristics of alpine/treeless subalpine vegetation?

The results presented in this thesis have shown that there are differences in vegetation characteristics which are related to the presence and/or combinations of different species of vertebrate herbivores on the Eastern Central Plateau.

Domestic stock

Sheep have had a much greater impact on plant species composition, vegetation cover, herb fecundity, and regeneration of bare areas than any other vertebrate herbivore present in the region (Bridle and Kirkpatrick 1999, Chapters 2 and 4). Impacts of domestic stock on alpine vegetation are so strong that the differences which occur between stock grazed and rabbit plus native vertebrate herbivore grazed areas (S/R/N v R/N) are generally similar to the differences between stock grazed and ungrazed areas (S/R/N v U, Table 6.1). Tiver and Andrew (1997) have shown that sheep have had a much greater effect than rabbits, goats or kangaroos on woody vegetation in eastern South Australia.

Aerial photographic analysis of bare ground at the Liawenee Moor grazing exclosures indicated that bare ground increases where stock remain, but decreases where they are excluded. Sheep grazing promotes low vegetation cover, lower mean vegetation height and an overall reduction in structural complexity. More exotic species are found in sheep grazed areas, which also have a greater frequency of small herbs. Tall herbs are less common and are less likely to flower than in the rabbit plus native grazed exclosure (Table 6.1).

Increases in vegetation cover were least for plots where sheep were present, with the exception of the Botsford heath site (Table 6.2). Other studies have recorded a decrease in bare ground with exclusion from stock grazing (Carr and Turner 1959*b*; Gibson and Kirkpatrick 1989; Wahren *et al.* 1994), although decreases in bare ground may also be recorded where stock grazing persists (Wahren *et al.* 1994). Data from the sediment trap site at Liawenee shows that recovery of bare ground may take place on the Eastern Central Plateau even in the presence of domestic stock grazing (Chapter 3). The exclosures and the Liawenee sediment trap site are less than 2 km apart (Fig. 1.1, Table 6.2). However, the sediment trap site is not as exposed to westerly and southerly weather as the grazing exclosures. Thus microclimatic effects at this site may be less severe than at the grazing exclosures, allowing recovery to take place over large areas of bare ground in the presence of sheep. Shrubs are taller at this site than at the grazing exclosures, and unpalatable shrubs such as *Hakea microcarpa* are much more abundant than in the exclosures (Table 2.2, Table 3.7).

Table 6.1 Summary of structural and floristic differences between grazing treatments at Liawenee Moor

Variable	Grazing Pressure		
	Low (U)	Intermediate (R/N)	High (S/R/N)
Structural complexity	High (3 layers)	High (3 layers)	Low (2 layers)
Mean Grass cover	High	High	Low
Mean Shrub height	Tall	Tall	Short
% Freq Tall herbs	High	High	Low
% Freq Small herbs	Low	Low	High
% Bare ground	Low	Intermediate	High
Total Species Richness	Intermediate	Low	High
Exotic Species Richness	Intermediate	Low	High
Flowering success of herbs	Tall herbs High	Intermediate/Tall herbs High	Short herbs High

Regeneration at the Liawenee sediment trap site was not as successful as at the Augusta site situated 100 m higher in altitude on a less productive soil type, and which has been free from stock grazing since 1980. Whilst these two sites are not directly comparable, one would expect productivity, and therefore recovery, to be faster at lower altitudes (Gibson and Kirkpatrick 1989). Very few quadrats recorded a decrease in vegetation cover at the Liawenee and Augusta sites, which was in direct contrast to Bernacchi, Botsford heath, Double Lagoon and Wild Dog Tier (Chapter 3). It is likely that these four sites have not yet recovered from the more severe erosional impact of domestic stock grazing, which was removed only two years before the exclosures were built.

Leigh *et al.* (1989) found that bare ground patches in subalpine grasslands were created by fire and promoted by rabbit grazing. The amount of bare ground was reduced more quickly where rabbits were absent, but increased where they were present. Bare ground was less than 5% under rabbit grazing in unburnt vegetation. The removal of fire as a management tool from the Eastern Central Plateau is likely to be the main reason for recovery under current stocking rates and in the presence of relatively low numbers of rabbits. Stock numbers and rabbit populations have also decreased over time (Shepherd 1973). It is difficult to separate the relative influences of fire and stock grazing as the site

histories are complex. However, vegetation cover at the Botsford grassland site which was formerly grazed by stock but not burnt, is close to 100%.

Table 6.2 Mean percentage bare ground and mean annual change in vegetation cover for each site

U = ungrazed

R = grazed by rabbits only

R/N = rabbits and native vertebrate herbivores

S/R/N = sheep, rabbits and native vertebrate herbivores

Site	Bare ground (%)							Annual % Change in vegetation cover			
	1973	1974	1991	1992	1993	1996	1997	U	R	R/N	S/R/N
Liawenee (S/R/N)		27.5			34.5						- 0.35
Liawenee (R/N)		37			27					+0.50	
Liawenee (U)		39			22			+0.85			
Liawenee (traps)	55.6						28.5				+1.18
Augusta (traps)	60.7						28.9			+1.38	
Botsford heath			48.4			45.5		+1.08	+1.02	- 0.42	
Bernacchi			74.6			67.9		+1.44	+1.36	+1.26	
Double Lagoon			75.9			69.3		+1.80	+1.20	+1.02	
Wild Dog Tier				81.7		76.9		+2.03	+0.85	+0.73	

Structural differences between the grazing treatments include higher covers of low statured plants in the sheep grazed area and higher covers of taller plants in the ungrazed exclosure. The general trends found here agree with results from other sites on the Eastern Central Plateau (Gibson and Kirkpatrick 1989), and elsewhere in stock grazed grasslands such as Australian temperate grasslands (McIntyre *et al.* 1995) and Mediterranean grasslands (Sal *et al.* 1986; Noy-Meir *et al.* 1989). An impact of stock grazing on shrub height has also been observed by Wahren *et al.* (1994) for sites on the Australian mainland and Primack (1978) in New Zealand.

Total species richness at the scale of 25 m² in sheep grazed areas of Liawenee Moor is greater than ungrazed or rabbit and native vertebrate herbivore grazed areas. Native species richness was not significantly different between the treatments. However, the tall tussock, *Poa labillardierei*, and another native grass *Poa gunnii*, were present in the ungrazed

enclosure only. These two species are considered to have been a major component of grassland vegetation on the Plateau before 1900 (Jackson 1973). Total species richness is greatest in the sheep grazed areas due to the presence of a number of exotic plant species. Native species richness was found to decrease in stock grazed lowland eucalypt woodland communities (Pettit *et al.* 1995). Native species richness also decreased under stock grazing in Paramo grasslands. However, total species richness increased due to the addition of exotic species (Hofstede 1995). Whilst rabbits and native herbivores are known to graze exotic herbs (Leigh *et al.* 1987; Whinam *et al.* 1994; Bridle and Kirkpatrick 1999), six exotic species which were found at Liawenee also germinated from sheep scats in the glasshouse (see Appendix 1). As the sheep themselves are a seed source for exotic species, it is not surprising that exotic species richness is greatest in the sheep grazed areas.

The presence of sheep on Liawenee Moor affects the presence and fecundity of a number of tall alpine herbs. Many of these taxa have shown an increase in cover with the removal of stock grazing in alpine areas of the mainland (Carr and Turner 1959*b*; Wimbush and Costin 1979*a,b,c*; Wahren *et al.* 1994). While limited cover data showed no significant difference between treatments, transect data indicated that there were more individuals of *Craspedia coolaminica* and *Podolepis jaceoides* in the ungrazed enclosure than in the sheep grazed area (Bridle and Kirkpatrick 1999; Chapter 2), and data on the leaf lengths of these species suggests that they are larger where grazing pressure is reduced.

Some tall herbs may easily regenerate in the absence of domestic stock. When sheep were absent from Liawenee Moor in November and December 1996, there were more flowering stems of *Craspedia alpina* outside the grazing exclosures than inside, a reversal of results of counts taken when sheep were present. The location of individuals of *Craspedia coolaminica* and *Podolepis jaceoides* under cover of vegetation in the grazed treatments, suggests that these plants are preferentially grazed in open habitats. Disseminules from populations of *Podolepis jaceoides* and *Craspedia coolaminica* spread from inside the rabbit and native vertebrate herbivore grazed enclosure into the sheep grazed area. These plants flower late in the season (January/February) and so no flowers were found in the sheep grazed area, though the rosettes did persist.

Rabbits

Recovery in the rabbit grazed exclosures was higher than recovery in the rabbit plus native grazed area but lower than the ungrazed exclosures at the four high altitude recovery sites (Botsford heath, Bernacchi, Double Lagoon, Wild Dog Tier) (Chapter 3, Table 6.2). Rabbits had a greater impact than native vertebrate herbivores on regeneration at the two grassland/sedgeland sites (Double Lagoon and Wild Dog Tier) than in the two heathy

sites (Table 6.3). No scat data were collected for Wild Dog Tier or Bernacchi. Scat numbers decreased over the 1996-1997 data collection period, but they remained relatively high at Double Lagoon. The effects of rabbits on regeneration success at Botsford heath appears to be small in comparison to the effects of native herbivores (Table 6.3). Wallaby scats were higher at Botsford heath than at any other site (Chapter 4), where rabbit numbers were relatively low, especially in 1997.

Rabbits and native vertebrate herbivores appear to have similar and relatively insignificant effects on regeneration success at Bernacchi heath (Table 6.3). This site is dominated by tall unpalatable shrubs, separated by large bare ground patches (Plate 3.2). Herb cover is minimal at this site (Chapter 3) as are changes in the cover of grasses and herbs over time (Table 3.2). It is likely that this site is lightly grazed as there is a relative lack of palatable vegetation.

The combined effects of rabbits and native herbivores at Liawenee reduced recovery by 0.35% per year in comparison with the ungrazed area (0.85%). This value is one half to two-thirds of the effect of these herbivores at higher altitudes (0.94%), despite the higher (and more consistent) numbers of rabbits and wallabies at Liawenee. Therefore, these data suggest that grazing impacts are greater at higher altitudes than at lower altitudes, under similar or lighter grazing pressures. Plant productivity is likely to be lower at higher altitudes, accounting for these differences in regeneration success across sites (Gibson and Kirkpatrick 1989).

Table 6.3 Difference in average annual increment in vegetation cover between grazing treatments

S/R/N = sheep, rabbits and native vertebrate herbivores,

R/N = rabbits and native vertebrate herbivores

R = rabbits only. U = ungrazed

(e.g. column U - R = difference in annual increment in vegetation cover from the value of the ungrazed treatment minus the value of rabbit grazed treatment)

Grazing treatment	R/N - S/R/N	U - S/R/N	U - R/N	R - R/N	U - R
Liawenee exclosures	+0.85	+1.20	+0.35		
Botsford heath			+1.50	+1.44	+0.06
Bernacchi			+0.18	+0.10	+0.08
Double Lagoon (DL)			+0.78	+0.18	+0.60
Wild Dog Tier (WDT)			+1.30	+0.12	+1.18
Mean of Botsford, Bernacchi, DL and WDT			+0.94	+0.46	+0.48

There is no real indication that rabbits affect vegetation structure in any way different to the effects of native herbivores. There is no apparent pattern in species richness between the rabbit and native grazed area and the rabbit grazed exclosures at any of the sites.

Grazing preferences of rabbits and native herbivores overlap, especially rabbits and wallabies (Appendix 1), both eating herbs and woody vegetation. However, wombats appear to avoid woody vegetation, preferring herbs (Craven 1997).

As rabbits and native vertebrate herbivores have been found to reduce the spread of exotic species across the Central Plateau (Kirkpatrick 1989; Whinam *et al.* 1994), it was not unexpected that exotic species richness is least in the rabbit and native vertebrate herbivore grazed exclosure at Liawenee Moor.

Leigh *et al.* (1987) recorded a significant difference in the cover, biomass and flowering success of palatable forbs between rabbit grazed and ungrazed in the subalpine grasslands of Kosciuszko National Park. The data collected on the Eastern Central Plateau do not directly compare the number of flowering stems between rabbit grazed and ungrazed exclosures using across fence comparisons, though the data suggest that there are differences (Chapter 4, Figs. 4.3 and 4.4). The flowering success of a few tall herb species is promoted by the absence of rabbits. The lack of a significant difference in flowering success of many of the tall herb species between rabbit grazed and rabbit plus native herbivore grazed treatments suggests that where rabbits are not the dominant herbivore at a site, their effects on plant flowering success is similar to that of native herbivores (especially wallabies). The study of Leigh *et al.* (1987) was not able to compare impacts of native herbivores on flowering with those of rabbits. It appears that the general effects of rabbits on regeneration (and flowering success) is additional to that of native herbivores, sometimes greater, sometimes less, depending on site and number of rabbits present.

Impacts of rabbits on the cover and flowering success of tall herbs are likely to be complex. Rabbit numbers fluctuate dramatically according to climatic conditions (Parer and Korn 1989; Tiver and Andrew 1997) as does the growth of herbs. Inconsistencies were recorded in the relative successes in flowering of herbs between grazing treatments over two seasons. Climatic conditions were also very different between the two growing seasons (Chapter 4). Herb growth has been related to climatic conditions (Wimbush and Costin 1979a,b,c; Leigh *et al.* 1991; Milchunas and Lauenroth 1993). It is suggested that a combination of climatic factors and variable grazing pressure resulted in the inconsistencies in plant responses to grazing on the Eastern Central Plateau.

Native vertebrate herbivores

Like rabbits, the main effect of native vertebrate herbivores on the vegetation of the Eastern Central Plateau is on the flowering success of tall alpine herbs. Limited data suggest that native herbivores affect the cover of some tall herb species (Chapter 5). Most tall herb species persist under native vertebrate herbivore grazing. However, the only evidence for the presence of the formation tall alpine herbfield is on ungrazed islands in the upper Ouse River system. It appears that native vertebrate herbivores may restrict the cover of herb species, but not their presence. Islands dominated by tall alpine herbs, which are also free from grazing have been recorded from the northwestern district of South Island, New Zealand (Norton 1995). These herbfields were only common on shore sites on steep bluffs, also protected from vertebrate herbivores. Historical records from ungrazed islands in Great Lake indicate that flowering tall herbs and palatable grasses were common (Legge 1902), and tall alpine herbfields dominate alpine environments on the Australian mainland where vertebrate herbivore grazing is absent (Kirkpatrick 1989).

To the future

It is likely with the maintenance of current rabbit and native herbivore populations, recovery will take place on the Eastern Central Plateau, but only in the absence of fire. The presence of domestic stock is likely to further decrease vegetation cover in exposed sites, but will not retard the process of recovery where sites are sheltered. An annual increase in vegetation cover of 1% is applicable to other alpine sites on the Australian mainland (Wimbush and Costin 1979b), though these authors point out that the increase is variable from year to year and depends on gap size and presence of existing vegetation.

Studies of gaps in lowland vegetation are not generally concerned with the amount of time taken for recovery to take place (Lunt 1997; Morgan 1997). In lowland environments, bare ground gaps regenerate quickly, within a year or two of the disturbance. Therefore, it appears that extreme environments such as alpine areas are controlled by very different processes. The process of continued vegetation loss, or the amount of time needed for alpine environments to recover from disturbance is controlled by plant productivity and is offset erosive forces, in which case, the size and shape of the bare ground gap will determine the length of time needed for complete recovery to occur. It is apparent that time is an important factor in the regeneration process, as it increases the likelihood of a chance event, such as a mild winter, in which shrub seedlings may establish and survive in bare ground gaps (Williams and Ashton 1987a).

Shrubs are likely to continue to increase in cover across all sites, though not necessarily in bare ground patches. As bare ground gaps are generally large (> 1 m in diameter), most of

the gaps are regenerating from existing vegetation at the perimeter rather than seedling invasion into the centre of gaps (Plate 6.1). Little shrub invasion occurs at a distance greater than 20 cm from vegetation, and then only in particular vegetation types such as tall heath (Chapter 3). Thus the establishment of shrubs in large bare ground patches as described by Williams (1992), is not evident on the Eastern Central Plateau.

Long-term data for the Bogong High Plains (over 50 years) show a shift from heathy grasslands to tall alpine herbfields (Wahren *et al.* 1994). These data initially recorded an increase in shrubs with the removal of domestic stock. However, over time the shrubs have senesced and tall herbs and grasses have invaded the gaps and increased in dominance. The lack of bare ground in these plots has retarded shrub establishment and promoted dominance by grass and tall herb species (Williams 1992). All of the Eastern Central Plateau sites show an increase in shrub cover over time. However, some *Grevillea australis* shrubs are senescing at the Liawenee grazing exclosures and tall herbs and grasses are replacing them. Many *Richea acerosa* shrubs are senescing at the relatively undisturbed Botsford grassland site (Plate 6.2). There is very little bare ground at the Botsford grassland, restricting the establishment of new shrubs. In contrast, there is still a large amount of bare ground and more open vegetation at Liawenee, where shrubs are still establishing.

Where vegetation has evolved with grazing pressure, species richness usually decreases when grazing pressure is removed (Collins *et al.* 1987; Belsky 1992; Milton *et al.* 1997). However, this is not the case on Liawenee Moor where species richness is least in the rabbit and native grazed area. Over time it is expected that native species richness will be greater in the rabbit and native grazed exclosure than in the ungrazed exclosure as existing gaps are filled. Species richness is likely to remain highest in the sheep grazed area due to the dissemination of exotics through sheep scats. If sheep were to be removed, it is expected that species richness would become, over time, similar to that for the rabbit and native grazed exclosure.



Plate 6.1 Recovery of bare ground gaps in the ungrazed enclosure on Liawenee Moor. *Grevillea australis* in a prostrate form is filling gaps from the edges. Contrast this photograph with Plate 3.8, also taken at Liawenee in the sheep grazed area.



Plate 6.2 *Poa* tussocks and tall herbs establishing in the middle of a senescent *Richea acerosa* shrub at the Botsford grassland site.

Is there any evidence to support the hypothesis that tall alpine herbfields are absent in Tasmanian alpine vegetation due to the year round presence of vertebrate herbivores (Kirkpatrick 1989)?

There is mixed support for the impacts of vertebrate herbivores on the cover of herb species (Chapter 2, Chapter 3, Chapter 4, Appendix 2), and there appears to be little impact of grazing regime on the recovery of herbs in the short-term and in the long-term (Chapter 3). Tall herbs are less common where grazing is present than where it is absent (Chapter 2, Chapter 5), whereas short herbs are common in any grazed environment. Fecundity of tall herbs is also affected by grazing. While this may not prevent some herbs from reproducing vegetatively, it will reduce the establishment of plants from seed and their dispersal range. Dispersal range and ability to attract pollinators may also be affected by height of the flowering stem.

The role of herbs in the regeneration process is small, when compared to tall shrubs and grasses. However, this is not unusual in low productivity alpine areas, especially where much of the topsoil has been removed. Increases in herb cover over a short period of time (Chapter 2, Chapter 3) were slight and may be related to climatic differences between the first and last year of data collection (Wimbush and Costin 1979a,b,c; Leigh *et al.* 1991). Most of the sites studied in this research are still recovering from extensive and extreme disturbance events, where the impact of disturbance from fire and stock grazing far outweighs lesser disturbances of year round grazing by native vertebrate herbivores and rabbits. It may take a number of years before some species re-establish in previously grazed areas (Carr and Turner 1959b; Wimbush and Costin 1979a; Wahren *et al.* 1994).

Fig. 6.1 illustrates the inverse relationship between percentage bare ground cover and percentage cover of tall herbs for some of the study sites. This relationship between bare ground cover and herb cover is a possible reason for the lack of significant differences in tall herb attributes between grazing treatments. The removal of stock from the Plateau took place less than 10 years before measurements were started at the high altitude sites. Thus tall herbs may still be in the process of re-establishment. In addition to this, many of the sites studied are severely degraded, suffering losses of topsoil up to 30 cm in depth. The herb *Leptorhynchus squamatus* was observed colonising bare ground in degraded areas of the mainland. However, these areas still had topsoil. This species is rarely seen colonising bare areas in the study site, possibly due to the lack of topsoil. A few individuals of *Celmisia asteliifolia* flower in the ungrazed exclosures at Botsford heath, but flowering stems have not been recorded in the other grazing treatments. *Celmisia* is the dominant tall alpine herb in the herbfields of Kosciuszko National Park and the

Bogong High Plains (Carr and Turner 1959b; Wimbush and Costin 1979a; Wahren *et al.* 1994).

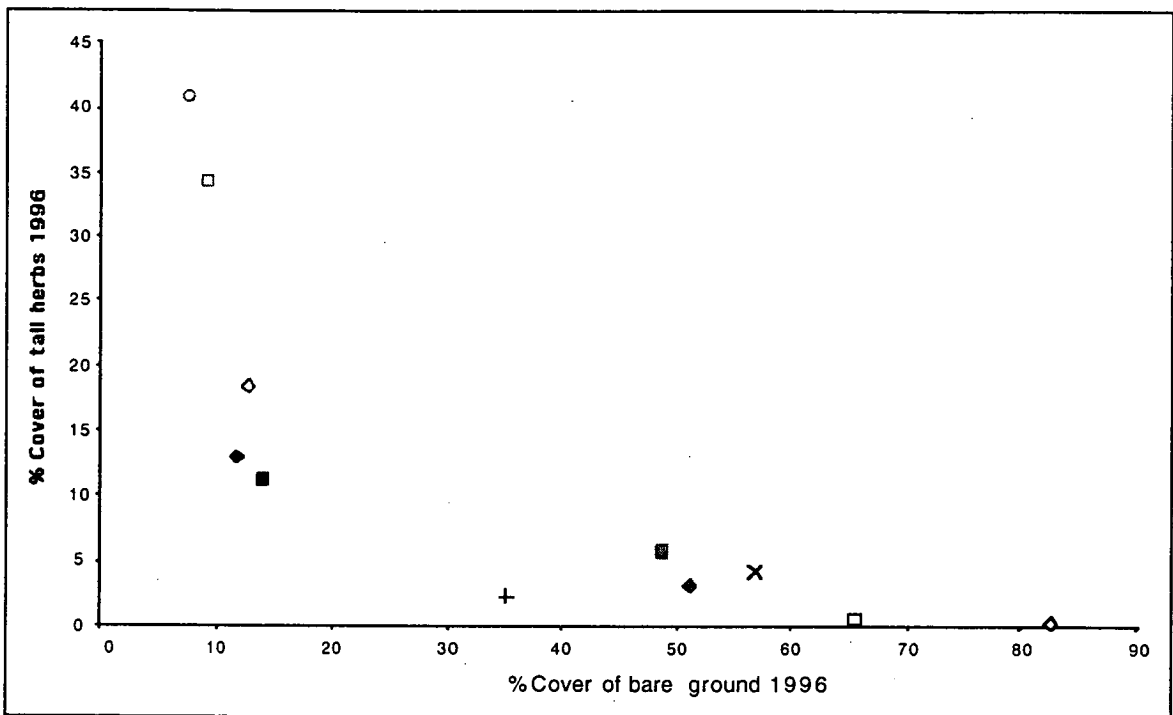


Fig. 6.1 Relationship between % cover of bare ground and % cover of tall herbs for Botsford grassland, Botsford heath, Double Lagoon and Liawenee in 1996
Diamonds represent data from ungrazed exclosures, squares represent data from rabbit plus native grazed areas, crosses represent data from rabbit grazed exclosures, circles represent data from sheep plus rabbit plus native grazed areas at Liawenee. Botsford grassland data are represented by filled black symbols, Botsford heath, filled grey symbols, Double Lagoon, open black symbols, and Liawenee, open grey symbols.

There are significant differences between climate variables of Tasmanian alpine areas and those of the mainland (Kirkpatrick and Bridle 1998). However, many tall herb taxa occur across the climatic range, including the dominant tall herb genus on the mainland *Celmisia* (see Appendix 3). It is possible that the lack of tall alpine herbfields in Tasmania may be due to a difference in soil characteristics between Tasmania and the mainland. However, a comparison between soil variables on Eastern Central Plateau and under tall alpine herbfields on the mainland determined that there was no significant difference in the nutrient status of soils from either place (Appendix 4). Tasmanian soils were slightly less acidic ($n = 13$, $U = 6.5$, $P = 0.0148$) and were deeper ($n = 13$, $U = 10$, $P = 0.0442$) than those found under tall alpine herbfields on the mainland (Appendix 4).

Other researchers have suggested that tall alpine herbfields establish as a result of disturbance (Carr and Turner 1959*b*; McVean 1969). Kirkpatrick and Bridle (1999) found that tall alpine herbfields were floristically closely related to grassland and heath in Australian alpine environments, and that disturbance factors influenced the distributions of these formations. Disturbance in the form of invertebrate grazing of tussock grasslands (Carr and Turner 1959*b*), or physical disturbance resulting from snowlie may promote tall alpine herbfields at the expense of grasslands. However, disturbance in the form of grazing is not considered to be beneficial in promoting tall alpine herbfields, as many of the dominant species are also highly palatable (Carr and Turner 1959*b*). In Tasmania, tall herbs naturally dominate small islands which are free from grazing (Bridle and Kirkpatrick 1998, Chapter 5), but which are disturbed by water erosion. Tall herbs do not dominate (i.e. have greater than 50% cover) in any of the study sites on the Eastern Central Plateau, except for the islands. However, they have relatively high cover values in the ungrazed and rabbit plus native vertebrate herbivore grazed treatments at Liawenee and Botsford grassland. Both of these sites have been disturbed by domestic stock grazing, but the Botsford grassland has not been burnt recently. As a result there are very few bare ground patches at this site, and grazing pressure is relatively low. Tall herbs such as *Craspedia* spp. occur at this site in senescent shrubs.

It seems highly likely that tall herbs will not dominate extensive areas of grassy vegetation on the Eastern Central Plateau for two reasons: 1) the year round presence of vertebrate herbivores which affect the flowering success of the tall herbs, and 2) the lack of physical disturbance (e.g. extended periods of snowlie) required to provide tall herbs with a competitive advantage over other lifeforms. The hypothesis of Kirkpatrick (1989) is therefore only validated in circumstances where disturbance is combined with lack of vertebrate herbivore grazing.

Management implications

The eroded sites on the Eastern Central Plateau are likely to recover naturally within 50-80 years. The average annual increment in vegetation cover of 1% only pertains to current conditions, namely under relatively low grazing pressure from rabbits and native herbivores, and in the absence of fire. Recovery may be accelerated by removal of vertebrate herbivores but this may be impractical and/or undesirable.

From a conservation point of view it is recommended that domestic stock grazing be removed from Liawenee Moor and that fires are also excluded and that the risk of wildfire is minimised. These actions are most likely to promote natural regeneration in the alpine environment of the Eastern Central Plateau (Plate 6.3).

The effects of rabbits should be monitored and controlled, when necessary, in order to maintain the current, relatively low, grazing pressure in environments free from stock grazing, and to be extended to Liawenee Moor after stock removal.

The existing grazing exclosures should be maintained in an attempt to monitor changes in vegetation over time, under variable grazing pressures, and variable climatic conditions.



Plate 6.3 An illustration of the effects of sheep exclusion on alpine vegetation,
Liawenee Moor

References

- Altesor, A., Di Landro, E., May, H., and Ezcurra, E. (1998) Long-term species change in a Uruguan grassland. *Journal of Vegetation Science* **9**, 173–180.
- Andersson, M., and Jonasson, S. (1986) Rodent cycles in relation to food resources on an alpine heath. *OIKOS* **46**, 93–106.
- Andrew, M. H., and Lange, R. T. (1986) The spatial distributions of sympatric populations of kangaroos and sheep: Examples of dissociation between these species. *Australian Wildlife Research* **13**, 367–373.
- Andrighetto, I., Cozzi, G., Berzaghi, P., and Zancan, M. (1993) Avoidance of degradation of alpine pasture through grazing management: investigations of change in vegetation nutrition characteristics as a consequence of sheep grazing at different periods of the growing season. *Journal of Land Degradation and Rehabilitation* **4**, 37–43.
- Austin, M. P., Williams, O. B., and Belbin, L. (1981) Grassland dynamics under sheep grazing in an Australian Mediterranean type climate. *Vegetatio* **47**, 201–211.
- Bakker, J. P., de Leeuw, J., and van Wieren, S. E. (1983) Micro-patterns in grassland vegetation created and sustained by sheep-grazing. *Vegetatio* **55**, 153–161.
- Balmer, J. (1991) Buttongrass moorlands vegetation. Pages 76–91 in J. B. Kirkpatrick, ed. *Tasmanian Native Bush: A management handbook*. Tasmanian Environment Centre, Hobart.
- Bassett, P. A. (1980) Some effects of grazing on vegetation dynamics in the Camargue, France. *Vegetatio* **43**, 173–184.
- Belsky, A. J. (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* **3**, 187–200.
- Belsky, A. J., and Blumenthal, D. M. (1997) Effects of livestock grazing on stand dynamics and soils in upland forests of the Interior West. *Conservation Biology* **11**, 315–327.
- Benson, J. S. (1994) The native grasslands of the Monaro region: Southern Tablelands of NSW. *Cunninghamia* **3**, 609–650.
- Bergelson, J., and Crawley, M. J. (1992) The effects of grazers on the performance of individuals and populations of scarlet gilia, *Ipomopsis aggregata*. *Oecologia* **90**, 435–444.

- Bock, J. H., Jolls, C. L., and Lewis, A. C. (1995) The effects of grazing on alpine vegetation: A comparison of the Central Caucasus, Republic of Georgia, with the Colorado Rocky Mountains, U.S.A. *Arctic and Alpine Research* **27**, 130–136.
- Bowers, M. A. (1993) Influence of herbivorous mammals on an old-field plant community: years 1-4 after disturbance. *OIKOS* **67**, 129–141.
- Bowman, D. M. J. S. (1998) The impact of Aboriginal landscape burning on the Australian biota. *New Phytologist* **140**, 385–410.
- Breton, W. H. (1846) Excursion to the Western Range, Tasmania. *Tasmanian Journal of Natural Science* **II**, 121–141.
- Bridge, B. J., Mott, J.J and Hartigan, R.J (1983) The formation of degraded areas in the dry savanna woodlands of Northern Australia. *Australian Journal of Soil Research* **21**, 91-104.
- Bridle, K. L., and Kirkpatrick, J. B. (1998) Why do tall herbs rarely dominate Tasmanian alpine vegetation? Evidence from islands in the Ouse River system. *Papers and Proceedings of the Royal Society of Tasmania* **132**, 9–14.
- Bridle, K. L., and Kirkpatrick, J. B. (1999) The comparative effects of stock and wild vertebrate herbivore grazing on treeless subalpine vegetation. *Australian Journal of Botany* **47**, 817-834.
- Bromham, L., Cardillo, M., Bennett, A. F., and Elgar, M. A. (1999) Effects of stock grazing in the ground invertebrate fauna of woodland remnants. *Australian Journal of Ecology* **24**, 199–207.
- Bryant, J. P., Tahvanainen, J., Sulkinoja, M., Julkunen-Thitto, R., Reichardt, P., and Green, T. (1989) Biogeographic evidence for the evolution of chemical defence by boreal birch and willow against mammal browsing. *The American Naturalist* **134**, 20–34.
- Buchanan, A. M. (1995) *A census of the vascular plants of Tasmania*. Tasmanian Herbarium Occasional Publication No. 5, Hobart.
- Bullock, J. M., Clear Hill, B., and Silvertown, J. (1994) Tiller dynamics of two grasses - responses to grazing, density and weather. *Journal of Ecology* **82**, 331–340.
- Bureau of Meteorology (1997) Monthly data for Liawenee, Climate and Consultancy Section. Tasmanian and Antarctic Regional Office, Hobart.
- Carr, S. G. M. (1962) The role of shrubs in some plant communities of the Bogong High Plains. *Proceedings of the Royal Society of Victoria* **75**, 301–311.
- Carr, S. G. M. (1977) *Report on inspection of the Bogong High Plains*. Australian National University, Canberra.
- Carr, S. G. M., and Turner, J. S. (1959a) The ecology of the Bogong High Plains. I. The environmental factors and the grassland communities. *Australian Journal of Botany* **7**, 12–33.

- Carr, S. G. M., and Turner, J. S. (1959b) The ecology of the Bogong High Plains. II. Fencing experiments in grassland c. *Australian Journal of Botany* **7**, 34–63.
- Clarke, K. R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143.
- Collins, S. L., and Adams, D. E. (1983) Succession in grasslands: Thirty-two years of change in a central Oklahoma tallgrass prairie. *Vegetatio* **51**, 181–190.
- Collins, S. L., and Barber, S. C. (1985) Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* **64**, 87–94.
- Collins, S. L., Bradford, J. A., and Sims, P. L. (1987) Succession and fluctuation in *Artemisia* dominated grassland. *Vegetatio* **73**, 89–99.
- Connell, J. H. (1978) Diversity in tropical rainforests and coral reefs. *Science* **199**, 1302–1310.
- Corbett, S. (1996) *Vegetation of the Central Plateau, Tasmanian Wilderness World Heritage Area*. Wildlife Report 95/5; Parks and Wildlife Service; Hobart.
- Costin, A. B. (1958) *The grazing factor and the maintenance of catchment values in the Australian Alps*. Division of Plant Industry Technical Paper No. 10. CSIRO Australia. .
- Costin, A. B., Gray, M., Totterdell, C. J., and Wimbush, D. J. (1979) *Kosciusko Alpine Flora*. CSIRO/Collins, Sydney.
- Costin, A. B., Wimbush, D. J., and Kerr, D. (1960) *Studies in catchment hydrology in the Australian Alps II. Surface run-off and soil loss*, Division of Plant Industry Technical Paper No. 14. CSIRO, Melbourne.
- Coughenour, M. B. (1991) Biomass and nitrogen responses to grazing of upland steppe of Yellowstone's northern winter range. *Journal of Applied Ecology* **28**, 71–82.
- Craven, B. (1997) *The subalpine grasslands of Paradise Plains, Northeast Tasmania*. B.Sc. Hons Thesis. University of Tasmania, Hobart.
- Crawford, G., Ellis, W. F., and Stancombe, G. H., eds. (1962) *The Diaries of John Helder Wedge 1824-1835*. The Queen Victoria Museum, Launceston.
- Cullen, P. (1991) Rainforest. Pages 24–34 in J. B. Kirkpatrick, ed. *Tasmanian Native Bush: A management handbook*. Tasmanian Environment Centre, Hobart.
- Cullen, P. (1995) *Land degradation on the Central Plateau, Tasmania: The legacy of 170 years of colonial exploitation*. A report to the Parks and Wildlife Service, Tasmania, Hobart.
- Ehrlen, J. (1995) Demography of the perennial herb *Lathyrus vernus*. I. Herbivory and individual performance. *Journal of Ecology* **83**, 287–295.

- Ellison, L. (1949) Establishment of vegetation on depleted subalpine range as influenced by microenvironment. *Ecological Monographs* **19**, 96–121.
- Escarre, J., Lepart, J., and Sentuc, J. J. (1996) Effects of simulated herbivory in three old field Compositae with different inflorescence architectures. *Oecologia* **105**, 501–508.
- Facelli, J. M. (1988) Response to grazing after nine years of cattle exclusion in a Flooding Pampa grassland, Argentina. *Vegetatio* **78**, 21–25.
- Faith, D. P., Minchin, P. R., and Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57–68.
- Fenner, M., Lee, W. G., and Duncan, S. J. (1993) Chemical features of *Chionochloa* species in relation to grazing by ruminants in South Island, New Zealand. *New Zealand Journal of Ecology* **17**, 35–40.
- Fensham, R. J., and Kirkpatrick, J. B. (1992) The Eucalypt forest-grassland/grassy woodland boundary in central Tasmania. *Australian Journal of Botany* **40**, 123–138.
- Fraser, M. D., and Gordon, I. J. (1997) The diet of goats, red deer and South American camelids feeding on three contrasting Scottish upland vegetation communities. *Journal of Applied Ecology* **34**, 668–686.
- Galen, C. (1990) Limits to the distributions of alpine tundra plants: herbivores and the alpine skypilot, *Polemonium viscosum*. *OIKOS* **59**, 355–358.
- Gauthier, G., Hughes, R. J., Reed, A., Beaulieu, J., and Rochefort, L. (1995) Effect of grazing by greater snow geese on the production of graminoids at an arctic site (Bylot Island, NWT, Canada). *Journal of Ecology* **83**, 653–664.
- Gibson, N., and Kirkpatrick, J. B. (1989) Effects of the cessation of grazing on the grasslands and grassy woodlands of the Central Plateau, Tasmania. *Australian Journal of Botany* **37**, 55–63.
- Gilfedder, L., and Kirkpatrick, J. B. (1994) Climate, grazing and disturbance, and the population dynamics of *Leucochrysum albicans* at Ross, Tasmania. *Australian Journal of Botany* **42**, 417–430.
- Gilfedder, L., and Kirkpatrick, J. B. (1998) Distribution, Disturbance Tolerance and Conservation of *Stackhousia gunnii* in Tasmania. *Australian Journal of Botany* **46**, 1–13.
- Gradwell, M. W. (1960) Soil frost action in snow-tussock grassland. *New Zealand Journal of Science* **3**, 580–590.
- Grant, S. A., Torvell, L., Common, T. G., Sim, E. M., and Small, J. L. (1996) Controlled grazing studies on *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on *Molinia* growth and responses of swards to controlled grazing by cattle. *Journal of Applied Ecology* **33**, 1267–1280.

- Gray, M and Given, D. R. (1999) New species and a new combination in Australian *Celmisia* (Asteraceae-Astereae). *Australian Systematic Botany* **12**, 201-206.
- Grice, A. C., and Barchia, I. (1992) Does grazing reduce survival of indigenous perennial grasses of the semi-arid woodlands of western New South Wales? *Australian Journal of Ecology* **17**, 195-205.
- Gutierrez, J. R., Meserve, P. L., Herrera, S., Contreras, L. C., and Jaksic, F. M. (1997) Effects of small mammals and vertebrate predators on vegetation in the Chilean semiarid zone. *Oecologia* **109**, 398-406.
- Harrington, G. N., Friedel, M. H., Hodgkinson, K. C., and Noble, J. C. (1984). Vegetation ecology and management in G. N. Harrington, A. D. Wilson and M. D. Young, eds. *Management of Australia's Rangelands*. CSIRO, Melbourne.
- Hobbs, R. J., and Huenneke, L. F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* **6**, 324-337.
- Hofstede, R. G. M. (1995) Effects of livestock farming and recommendations for management and conservation of Paramo grasslands (Colombia). *Journal of Land Degradation and Rehabilitation* **6**, 133-147.
- Hofstede, R. G. M., Castillo, M. X. M., and Osorio, C. M. R. (1995) Biomass of grazed, burned, and undisturbed Paramo grasslands, Colombia. I. Aboveground vegetation. *Arctic and Alpine Research* **27**, 1-12.
- Hulme, P. E. (1996) Herbivory, plant regeneration, and species coexistence. *Journal of Ecology* **84**, 609-615.
- Hurlbert, S. H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187-211.
- Jackson, W. D. (1973) Vegetation of the Central Plateau in W. D. Jackson, ed. *The Lake Country of Tasmania*.
- John, E., and Turkington, R. (1995) Herbaceous vegetation in the understorey of the boreal forest: does nutrient supply or snowshoe hare herbivory regulate species composition and abundance? *Journal of Ecology* **83**, 581-590.
- Jorgenson, J. (1829) *The history of the origin, rise and progress of the Van Diemen's Land Company*, Facsimile Edition (1979).
- Kiehl, K., Eischeid, I., Gettner, S., and Walter, J. (1996) Impact of different sheep grazing intensities on salt marsh vegetation in northern Germany. *Journal of Vegetation Science* **7**, 99-106.
- Kirkpatrick, J. B. (1982) Phytogeographical analysis of Tasmanian alpine floras. *Journal of Biogeography* **9**, 255-271.
- Kirkpatrick, J. B. (1983) Treeless plant communities of the Tasmanian high country. *Proceedings of the Ecological Society of Australia* **12**, 61-77.

- Kirkpatrick, J. B. (1986) Conservation of plant species, alliances and associations of the treeless high country of Tasmania, Australia. *Biological Conservation* **37**, 43–57.
- Kirkpatrick, J. B. (1989). The comparative ecology of mainland Australian and Tasmanian alpine vegetation. Pages 127–142 in R. Good, ed. *The Scientific Significance of the Australian Alps*. Proceedings of the First Fenner Conference on the Environment, Canberra.
- Kirkpatrick, J. B. and Bridle, K. L. (1998) Environmental relationships of floristic variation in the alpine vegetation of southeast Australia. *Journal of Vegetation Science* **9**, 251–260.
- Kirkpatrick, J. B., and Bridle, K. L. (1999) Environment and floristics of ten Australian alpine vegetation formations. *Australian Journal of Botany* **47**, 1–21.
- Kirkpatrick, J. B., and Duncan, F. (1987) Tasmanian high altitude grassy vegetation: its distribution, community composition and conservation status. *Australian Journal of Ecology* **12**, 73–86.
- Kirkpatrick, J. B., and Gilfedder, L. (1995) Maintaining integrity compared with maintaining rare and threatened taxa in remnant bushland in subhumid Tasmania. *Biological Conservation* **74**, 1–8.
- Lakin, R. (1975) Climate of Tasmania. Pages 43–54 in R. Lakin, ed. *Tasmanian Year Book*. ABS, Hobart.
- Legge, W. V. (1902) Contribution to the physiography of Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **1902**, 137–142.
- Leigh, J. H., and Holgate, M. D. (1979) The responses of the understorey of forests and woodlands of the Southern Tablelands to grazing and burning. *Australian Journal of Ecology* **4**, 25–45.
- Leigh, J. H., Wimbush, D. J., Wood, D. H., Holgate, M. D., Slee, A. V., Stanger, M. G., and Forrester, R. I. (1987) Effects of rabbit grazing and fire on a subalpine environment. I. Herbaceous and shrubby vegetation. *Australian Journal of Botany* **35**, 433–464.
- Leigh, J. H., Wood, D. H., Holgate, M. D., Slee, A., and Stanger, M. G. (1989) Effects of rabbit and kangaroo grazing on two semi-arid grassland communities in central-western New South Wales. *Australian Journal of Botany* **37**, 375–396.
- Leigh, J. H., Wood, D. H., Slee, A. V., and Holgate, M. D. (1991) The effects of burning and simulated grazing on productivity, forage quality, mortality and flowering of eight subalpine herbs in Kosciuszko National Park. *Australian Journal of Botany* **39**, 97–118.
- Lock, J. M. (1972) The effects of hippopotamus grazing on grasslands. *Journal of Ecology* **60**, 445–467.

- Lunt, I. D. (1997) A multivariate growth-form analysis of grassland and forest forbs in south-eastern Australia. *Australian Journal of Botany* **45**, 691–705.
- Mark, A. F. (1994) Effects of burning and grazing on sustainable utilisation of upland snow tussock (*Chionochloa* spp.) rangelands for pastoralism in South Island, New Zealand. *Australian Journal of Botany* **42**, 149–161.
- Maschinski, J., and Whitham, T. G. (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *The American Naturalist* **134**, 1–19.
- McIntyre, S. (1995) Comparison of a common, rare and declining plant species in the Asteraceae: possible causes of rarity. *Pacific Conservation Biology* **2**, 177–190.
- McIntyre, S., and Lavorel, S. (1994) How environmental and disturbance factors influence species composition in temperate Australian grasslands. *Journal of Vegetation Science* **5**, 373–384.
- McIntyre, S., Lavorel, S., and Tremont, R. M. (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology* **83**, 31–44.
- McNaughton, S. J. (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* **55**, 259–294.
- McVean, D. N. (1969) Alpine vegetation of the Central Snowy Mountains of New South Wales. *Journal of Ecology* **57**, 67–86.
- Meurk, C. D. (1982) Regeneration of subantarctic plants on Campbell Island following exclusion of sheep. *New Zealand Journal of Ecology* **5**, 51–58.
- Milchunas, D. G., and Lauenroth, W. K. (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* **63**, 327–366.
- Milchunas, D. G., Lauenroth, W. K., Chapman, P. L., and Kazempour, M. K. (1989) Effects of grazing, topography, and precipitation on the structure of a semiarid grassland. *Vegetatio* **80**, 11–23.
- Milton, S. J., Dean, W. R. J., and Klotz, S. (1997) Effects of small-scale animal disturbances on plant assemblages of set-aside land in Central Germany. *Journal of Vegetation Science* **8**, 45–54.
- Minchin, P. (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**, 89–107.
- Minchin, P. (1990) *DECODA- Database for Ecological Community Data, Version 2.02*. Australian National University, Canberra.
- Mitchell, A. (1962) *Report on soil conservation problems on the Central Plateau and South Esk River catchment in Tasmania*. Unpublished report for the Standing Committee on Conservation of Natural Resources of Tasmania, Hobart.

- Moen, R., Pastor, J., and Cohen, Y. (1997) A spatially explicit model of moose foraging and energetics. *Ecology* **78**, 505–521.
- Morgan, J. W. (1997) The effect of grassland gap size on establishment, growth and flowering of the endangered *Rutidosia leptorrhynchoidea* (Asteraceae). *Journal of Applied Ecology* **34**, 566–576.
- Mulder, C. P. H., and Harmsen, R. (1995) The effect of muskox herbivory on growth and reproduction in an Arctic legume. *Arctic and Alpine Research* **27**, 44–53.
- Neave, H. M., and Tanton, M. T. (1989) The effects of grazing by kangaroos and rabbits on the vegetation and the habitat of other fauna in the Tidbinbilla Nature Reserve, Australian Capital Territory. *Australian Wildlife Research* **16**, 337–351.
- Negi, G. C. S., Rikhari, H. C., and Singh, S. P. (1993) Plant regrowth following selective horse and sheep grazing and clipping in an Indian Central Himalayan alpine meadow. *Arctic and Alpine Research* **25**, 211–215.
- Norton, D. A. (1995) Vegetation on goat-free islands in a low-alpine lake, Paparoa Range, and implications for monitoring goat control operations. *New Zealand Journal of Ecology* **19**, 67–72.
- Noy-Meir, I., and Briske, D. D. (1996) Fitness components of grazing-induced population reduction in a dominant annual, *Triticum dicoccoides* (wild wheat). *Journal of Ecology* **84**, 439–448.
- Noy-Meir, I., Gutman, M., and Kaplan, Y. (1989) Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* **77**, 290–310.
- Oullet, J.-P., Heard, D. C., and Boutin, S. (1993) Range impacts following the introduction of caribou on Southampton Island, Northwest Territories, Canada. *Arctic and Alpine Research* **25**, 136–141.
- Parer, I., and Korn, T. J. (1989) Seasonal incidence of myxomatosis in New South Wales. *Australian Wildlife Research* **16**, 563–568.
- Peart, D. R. (1989) Species interactions in a successional grassland. III. Effects of canopy gaps, gopher mounds and grazing on colonisation. *Journal of Ecology* **77**, 267–289.
- Pemberton, M. (1986) *Land systems of Tasmania Region 5 - Central Plateau*. Department of Agriculture, Tasmania.
- Perez, F.L. (1992) The ecological impact of cattle on caulescent Andean rosettes in a high Venezuelan paramo. *Mountain Research and Development* **12**, 29–46.
- Persson, S. (1984) Vegetation development after the exclusion of cattle grazing in a meadow area in the south of Sweden. *Vegetatio* **55**, 65–92.
- Pettit, N. E., Froend, R. H., and Ladd, P. G. (1995) Grazing in remnant woodland vegetation: changes in species composition and life form groups. *Journal of Vegetation Science* **6**, 121–130.

- Plomley, N. J. B. (1966) *The Friendly Mission: the Tasmanian journal and papers of George Augustus Robinson*. Tasmanian Historical Research Association, Hobart.
- Primack, R. B. (1978) Effects of grazing on indigenous shrubs in tussock grassland at Cass, Canterbury, New Zealand. *New Zealand Journal of Botany* **16**, 461–469.
- Prins, A. H., and Nell, H. W. (1990) Positive and negative effects of herbivory on the population dynamics of *Senecio jacobaea* L. and *Cynoglossum officinale* L. *Oecologia* **83**, 325–332.
- Pyrke, A. (1994) *Soil disturbance by native mammals and the germination and establishment of plant species*. Ph.D. Dissertation. University of Tasmania, Hobart.
- Rawat, G. S., and Uniyal, V. K. (1993) Pastoralism and plant conservation: The Valley of the Flowers dilemma. *Environmental Conservation* **20**, 164–167.
- Rayment, G. E., and Higginson, F. R. (1992) *Australian Laboratory Handbook of Soil and Water Chemical Methods*. Inkata Press, Melbourne.
- Rikhari, H. C., Negi, G. C. S., Ram, J., and Singh, S. P. (1993) Human-induced secondary succession in an alpine meadow of Central Himalaya, India. *Arctic and Alpine Research* **25**, 8–14.
- Rose, A. B., Platt, K. H., and Frampton, C. M. (1995) Vegetation change over 25 years in a New Zealand short-tussock grassland: Effects of sheep grazing and exotic invasions. *New Zealand Journal of Ecology* **19**, 163–174.
- Sal, A. G., De Miguel, J. M., Casado, M. A., and Pineda, F. D. (1986) Successional changes in the morphology and ecological responses of a grazed pasture ecosystem in Central Spain. *Vegetatio* **67**, 33–44.
- SAS. (1989) *SAS/STAT user's guide*, Version 6. SAS Institute, Cary, NC.
- Scherff, E. J., Galen, C., and Stanton, M. L. (1994) Seed dispersal, seedling survival and habitat affinity in a snowbed plant: limits to the distribution of the snow buttercup, *Ranunculus adoneus*. *OIKOS* **69**, 405–413.
- Scott, R. D., and Hunter, G. G. (1988) Changes in the tussock grasslands in the central Waimakariri River basin, Canterbury, New Zealand, 1947–1981. *New Zealand Journal of Botany* **26**, 197–222.
- Scott, P. (1955) Transhumance in Tasmania. *New Zealand Geographer* **11**, 155–172.
- Scougall, S. A., Majer, J. D., and Hobbs, R. J. (1993). Edge effects in grazed and ungrazed Western Australian wheatbelt remnants in relation to ecosystem reconstruction. Pages 163–178 in D. A. Saunders, R. J. Hobbs and P. R. Ehrlich, eds. *Nature Conservation 3: Reconstruction of fragmented ecosystems*. Surrey Beatty & Sons.

- Shepherd, R. R. (1973) Land use on the Central Plateau with special reference to the grazing industry. Pages 161–176 in M. R. Banks, ed. *The Lake Country of Tasmania*. Royal Society of Tasmania, Hobart.
- Smith, R. S., and Rushton, S. P. (1994) The effects of grazing management on the vegetation of mesotrophic (meadow) grassland in Northern England. *Journal of Applied Ecology* **31**, 13–24.
- Struik, G. J. (1967) Growth habits of dandelion, daisy, catsear, and hawkbit in some New Zealand grasslands. *New Zealand Journal of Agricultural Research* **10**, 331–344.
- Stuth, J. W. (1991) Foraging behaviour. Pages 65–83 in R. K. Heitschmidt and J. W. Stuth, eds. *Grazing management: an ecological perspective*. Timber Press, Portland, Oregon.
- Strzlecki, P. E. de. (1845) *Physical description of New South Wales and Van Dieman's Land*. Longman, Brown, Green and Longman, London.
- Thomas, I., and Hope, G. (1994) An example of Holocene vegetation stability from Camerons Lagoon, a near treeline site on the Central Plateau, Tasmania. *Australian Journal of Ecology* **19**, 150–158.
- Tiver, F., and Andrew, M. H. (1997) Relative effects of herbivory by sheep, rabbits, goats and kangaroos on recruitment and regeneration of shrubs and trees in eastern South Australia. *Journal of Applied Ecology* **34**, 903–914.
- Tremont, R. M., and McIntyre, S. (1994) Natural grassy vegetation and native forbs in temperate Australia: Structure, dynamics and life histories. *Australian Journal of Botany* **42**, 641–658.
- Treweek, J. R., Watt, T. A., and Hambler, C. (1997) Integration of sheep production and nature conservation: experimental management. *Journal of Environmental Management* **50**, 193–210.
- Tsuyuzaki, S., and Tsujii, T. (1990) Preliminary study in grassy marshland vegetation, western part of Sichuan Province, China, in relation to yak-grazing. *Ecological Research* **5**, 271–276.
- van Rees, H. (1984) *Behaviour and Diet of free-ranging cattle on the Bogong High Plains Victoria*. Department of Conservation, Forests and Lands, Victoria.
- Vinton, M. A., and Hartnett, D. C. (1992) Effects of bison grazing on *Andropogon gerardii* and *Panicum virgatum* in burned and unburned tallgrass prairie. *Oecologia* **90**, 374–382.
- Virtanen, R. (1998) Impact of grazing and neighbour removal on a heath plant community transplanted onto a snowbed site, NW Finnish Lapland. *OIKOS* **81**, 359–367.
- Virtanen, R., Henttonen, H., and Laine, K. (1997) Lemming grazing and structure of a snowbed plant community – a long-term experiment at Kilpisjärvi, Finnish Lapland. *OIKOS* **79**, 155–166.

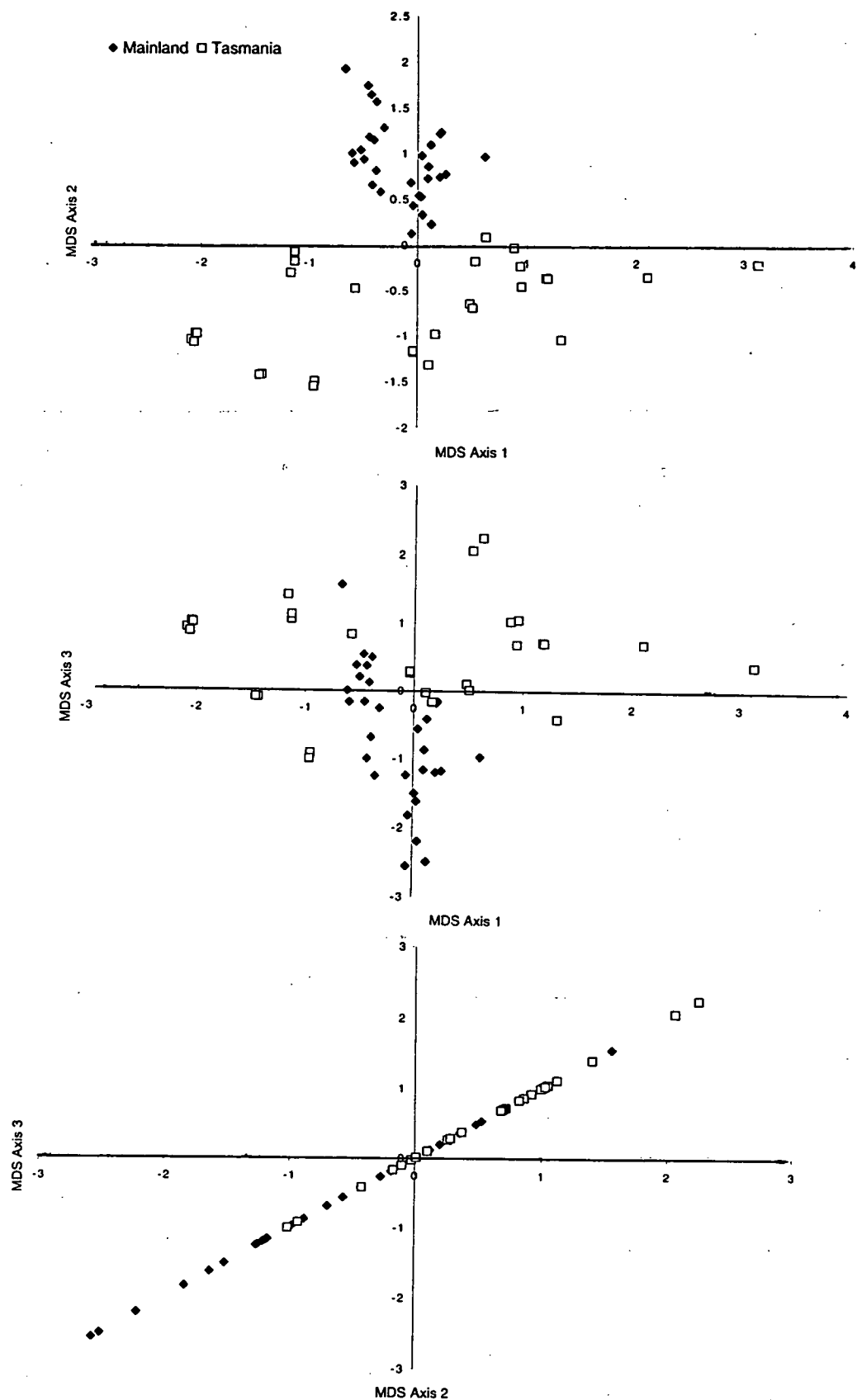
- Wahren, C.-H. A., Papst, W. A., and Williams, R. J. (1994) Long-term vegetation change in relation to cattle grazing in subalpine grassland and heathland on the Bogong High Plains: An analysis of vegetation records from 1945 to 1994. *Australian Journal of Botany* **42**, 607–639.
- Welch, D., and Scott, D. (1995) Studies in the grazing of heather moorland in north-east Scotland. VI. 20-year trends in botanical composition. *Journal of Applied Ecology* **32**, 596–611.
- Weltzin, J. F., Archer, S., and Heitschmidt R.K. (1997) Small-mammal regulation of vegetation structure in a temperate savanna. *Ecology* **78**, 751–763.
- Whinam, J. (1990) *A study of the ecology of Tasmanian Sphagnum peatlands*. Ph.D. Dissertation. University of Tasmania, Hobart.
- Whinam, J., Cannell, E. J., Kirkpatrick, J. B., and Comfort, M. (1994) Studies on the potential impact of recreational horseriding on some alpine environments of the Central Plateau, Tasmania. *Journal of Environmental Management* **40**, 103–117.
- Whisenant, S. G., and Wagstaff, F. J. (1991) Successional trajectories of a grazed salt desert shrubland. *Vegetatio* **94**, 133–140.
- White, P. S., and Pickett, S. T. A. (1985). Natural disturbance and patch dynamics: an introduction. Pages 3–13 in S. T. A. Pickett and P. S. White, eds. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida.
- Whitehouse, I. E., Cuff, J. R. I., Evans, G. R., and Jensen, C. (1988) Trend in bare ground from tussock grassland surveys, Canterbury, New Zealand. *New Zealand Journal of Ecology* **11**, 31–38.
- Williams, R. J. (1990) Cattle grazing within subalpine heathland and grassland communities on the Bogong High Plains: disturbance, regeneration and the shrub-grass balance. *Proceedings of the Ecological Society of Australia* **16**, 255–265.
- Williams, R. J. (1992) Gap dynamics in subalpine heathland and grassland vegetation in south-eastern Australia. *Journal of Ecology* **80**, 343–352.
- Williams, R. J., and Ashton, D. H. (1987a) Effects of disturbance and grazing by cattle on the dynamics of heathland and grassland communities on the Bogong High Plains, Victoria. *Australian Journal of Botany* **35**, 413–431.
- Williams, R. J., and Ashton, D. H. (1987b) The composition, structure and distribution of heathland and grassland communities in the subalpine tract of the Bogong High Plains, Victoria. *Australian Journal of Ecology* **12**, 57–71.
- Williams, R. J., and Costin, A. B. (1994) Alpine and subalpine vegetation. Pages 467–500 in R. H. Groves, ed. *Australian Vegetation*. Cambridge University Press, Melbourne.

- Wilson, A. D., and Harrington, G. N. (1984) Grazing ecology and animal production in G. N. Harrington, A. D. Wilson and M. D. Young, eds. *Management of Australia's Rangelands*. CSIRO, Melbourne.
- Wilson, A. D. (1990) The effect of grazing on Australian ecosystems. *Proceedings of the Ecological Society of Australia* **16**, 235–244.
- Wimbush, D. J., and Costin, A. B. (1979a) Trends in vegetation at Kosciusko. I. Grazing trials in the subalpine zone, 1957–1971. *Australian Journal of Botany* **27**, 741–787.
- Wimbush, D. J., and Costin, A. B. (1979b) Trends in vegetation at Kosciusko. II Subalpine range transects, 1959–1978. *Australian Journal of Botany* **27**, 789–831.
- Wimbush, D. J., and Costin, A. B. (1979c) Trends in vegetation at Kosciusko. III Alpine range transects, 1959–1978. *Australian Journal of Botany* **27**, 833–871.
- Yates, C. J., and Hobbs, R. J. (1997) Woodland restoration in the Western Australian wheatbelt: a conceptual framework using a state and transition model. *Restoration Ecology* **5**, 28–35.

Appendix 1 List of plant species which germinated from animal seats collected from the grazing exclosures on the Eastern Central Plateau. i = introduced												
Species	Wallaby				Wombat			Rabbit				Sheep
	Botsford grassland	Botsford heath	Double Lagoon	Liawenee	Botsford grassland	Botsford heath	Liawenee	Botsford grassland	Botsford heath	Double Lagoon	Liawenee	Liawenee
<i>Agrostis avenacea</i>		x		x			x					
<i>Aira caryophylla i</i>		x		x								
<i>Aira praecox i</i>												x
<i>Cerastium glomeratum</i>	x			x							x	x
<i>Cotula alpina</i>										x		
<i>Deyeuxia innominata</i>			x	x		x				x		
<i>Deyeuxia monticola</i>				x								
<i>Empodisma minus</i>											x	
<i>Epacris</i> sp. 1		x							x			
<i>Epacris</i> sp 2		x						x	x			
<i>Erophila verna i</i>		x									x	x
<i>Gnaphalium</i> sp.										x		
<i>Hydrocotyle pterocarpa</i>												x
<i>Hypericum japonicum</i>				x								x
<i>Isolepis montivaga</i>	x	x		x	x		x					x
<i>Leucopogon stuartii</i>											x	
<i>Luzula australasica</i>		x	x	x					x		x	x
<i>Moenchia erecta i</i>												x
<i>Oreomyrrhis ciliata</i>		x										
<i>Plantago paradoxa</i>												x
<i>Poa</i> sp.	x				x	x					x	
<i>Poa hiemata</i>	x	x										x
<i>Scleranthus biflorus</i>			x	x		x					x	x
<i>Trifolium repens i</i>												x
<i>Velleia montana</i>											x	
<i>Veronica arvensis i</i>												x
<i>Vulpia bromoides i</i>												x
<i>Australopyrum velutinum</i>	x											
<i>Veronica gracilis</i>												
<i>Pernettya tasmanica</i>										x		
<i>Gratiola nana</i>												
<i>Nertera depressa</i>	x											
<i>Holcus lanatus i</i>												x
<i>Neopaxia australasica</i>												x
<i>Sagina</i> sp.												x

Appendix 2 Mean cover (per m²) of tall herb species in March 1996 and March 1997 at Botsford grassland, Double Lagoon and Botsford heath.
 U = ungrazed; R = rabbit grazed; R/N = rabbit and native vertebrate herbivore grazed

	Botsford grassland				Double Lagoon						Botsford heath					
	U 96	U 97	R/N 96	R/N 97	U 96	U 97	R 96	R 97	R/N 96	R/N 97	U 96	U 97	R 96	R 97	R/N 96	R/N 97
<i>Brachyscome tenuiscapa</i>	0.65	0.45	0.55	0.2												
<i>Erigeron gunnii</i>				0.1												0.05
<i>Leptorhynchos squamatus</i>	11.25	9.15	9.6	8.95			2.7	2.55	0.55	0.45	2.55	2.7	0.8	1.65	2.25	1.55
<i>Microseris lanceolata</i>				0.45												
<i>Ranunculus pascuinus</i>	0.85	0.8	0.3	0.3				0.05								
<i>Craspedia coolaminica</i>	0.15	0.3	0.5	0.65												
<i>Senecio gunnii</i>							0.45	0.15	0.1	0.1						
<i>Senecio lautus</i>					0.05	0.2	0.85	0.2	0	0.15	0.4	0.35	0.9	1.2	1.15	0.9
<i>Linum marginale</i>							0.2	0.15								
<i>Bracteanthe subundulata</i>											0.1	0.15	0.65	0.45	2.25	2.45
<i>Celmisia asteliifolia</i>											0.1	0.1			0.15	



Appendix 3. NMDS of climatic variables for quadrats containing *Celmisia* from the Australian Alps and from Tasmania (see Kirkpatrick and Bridle 1998).

Appendix 4. Means and standard errors of soil attributes for five sites on the Eastern Central Plateau and nine tall alpine herbfield sites from the Australian Alps (see Kirkpatrick and Bridle 1998, 1999 for details of sites and analyses).

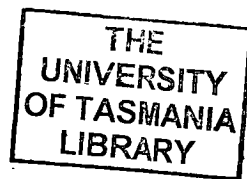
	Max Soil Depth (cm)	pH H ₂ O	Cond	Ext. P ppm	Ext K ppm	Org. C %	Total N%	Total P ppm	Total Ca ppm	Cu ppm	Fe ppm	Mn ppm	Zn ppm	NO ₃ N	NH ₄ N
ECP Mean	57.3	5.4	0.07	26.2	341	10.55	0.59	832	2091	0.72	291	22.4	3.3	0.82	11.8
SE	14.5	0.11	0.01	7.2	83	1.94	0.11	178	586	0.15	83	12.7	0.8	0.2	4.8
Aust Alps Mean	23.8	4.89	0.06	39.8	290	12.39	0.67	1005	1014	0.42	394	8.7	1.6	7.1	13.3
SE	5.9	0.12	0.01	8.3	68	1.17	0.08	107	433	0.14	38	5.5	0.8	4.8	4.6

Comparative Effects of Stock and Wild Vertebrate Herbivore Grazing on Treeless Subalpine Vegetation, Eastern Central Plateau, Tasmania

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Abstract

The existence of two 25-year-old grazing exclosures on Liawenee Moor, Eastern Central Plateau, Tasmania, created an opportunity to investigate the impacts of vertebrate herbivores on treeless subalpine vegetation. There were three treatments: sheep-, native herbivore- and rabbit-grazed; native herbivore- and rabbit-grazed; no grazing. The amount of bare ground was highest in the sheep-grazed plots, while vegetation cover was greatest in the ungrazed exclosure. The cover of all lifeform groups, except small herbs, was greater in the exclosures than in the sheep-grazed plots. The percentage frequency of tall herbs was significantly less in the sheep-grazed plots than either of the grazing exclosures.

Tall herbs were more likely to be found under the canopy of other vegetation in the sheep-grazed plots while the same species were found to be growing in locations with no other vegetation cover in the ungrazed exclosure. Revegetation of bare ground averaged 1% per year over a 20-year period in the ungrazed exclosure. While percentage bare ground has also decreased in the native- and rabbit-grazed exclosure, it has increased in the sheep-grazed plots. Domestic stock grazing appears to have a much greater impact on vegetation cover, species composition and community structure than grazing by native herbivores and rabbits. No grazing allows for the fastest rehabilitation of the area. Our results are consistent with those from alpine and treeless subalpine areas of the Australian mainland.

Introduction

Most parts of the alpine and subalpine zones of Australia that have a substantial grass or forb component in their vegetation have been grazed by domestic stock and feral rabbits during the past 200 years. This vegetation has also been grazed by wombats and wallabies, with the exception of the higher alpine areas of the Snowy Mountains and Victoria. There is a large body of evidence that exclusion of vertebrate grazers leads to dramatic changes in plant species composition and cover (Carr and Turner 1959*a*, 1959*b*; Wimbush and Costin 1979*a*, 1979*b*, 1979*c*; Leigh *et al.* 1987; Gibson and Kirkpatrick 1989; Wahren *et al.* 1994). These changes typically include an increase in forb cover, an increase in shrub cover and an increase in overall vegetation cover.

The greater proportion of changes in vegetation cover recorded in grazing exclosures on mainland mountains are generally attributed to the exclusion of domestic stock (Wimbush and Costin 1979*c*; Leigh *et al.* 1987; Wahren *et al.* 1994). However, Kirkpatrick (1989) hypothesised that the dominance of tall forbs in Australian high alpine vegetation could be a result of the lack of wallabies and wombats. These animals are abundant in equivalent vegetation in Tasmania, where tall herbs are present but not dominant. Marsupial grazers and rabbits are more commonly found in the subalpine regions of mainland Australia. Research in these regions supports the hypothesis (Leigh *et al.* 1987).

Given the relative paucity of work differentiating the effects of different mammalian herbivores on temperate grassy vegetation in Australia, (Leigh and Holgate 1979; Leigh *et al.* 1987), and the relative lack of data on total mammal grazing impacts on alpine/subalpine treeless vegetation in Tasmania (Gibson and Kirkpatrick 1989; Bridle and Kirkpatrick 1998), we undertook a study of the relative impacts of stock plus rabbits and native mammals,

rabbits and native mammals only, and no mammal grazing in Tasmania. This paper reports the impacts of stock exclosure and a total exclosure on a wide range of attributes of the treeless subalpine grassy shrubland of Liawenee Moor, Tasmania (Fig. 1). We test the hypotheses that (1) alpine vegetation is differentially affected by variability in grazing pressure and type; and (2) forb, shrub and total vegetation cover increase with increasing exclusion of mammals.

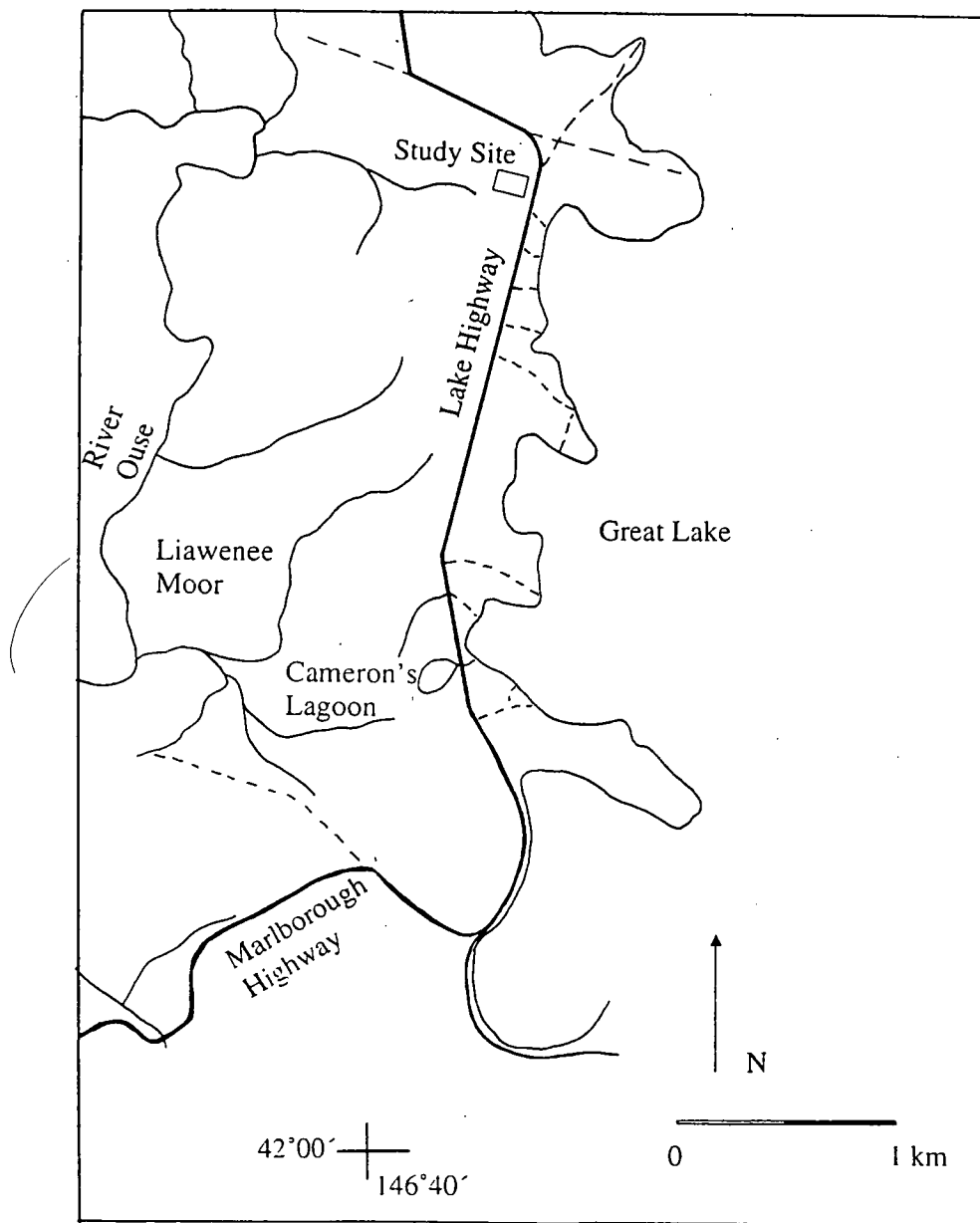


Fig. 1. Location of grazing exclosures, Liawenee Moor, Eastern Central Plateau, Tasmania. Four-wheel-drive tracks are represented by dashed lines.

Liawenee Moor on the Eastern Central Plateau is the most extensive privately owned area of alpine vegetation (*sensu* Kirkpatrick (1983)) in Tasmania. Sheep usually graze on the moor during late spring, summer and autumn (November–May). Jackson (1973) stated that, in the 19th century, the vegetation of Liawenee Moor was a tall tussock *Poa* grassland with a rich intertussock herb cover. European records from the early 1800s are sparing in their descriptions of the vegetation of Liawenee Moor, despite the area being fairly well visited from very early on. The plains were covered with ‘... high coarse grass’ (Jorgenson 1829, p. 24), ‘... intermixed with plantain and a species of heath’ (Wedge in Crawford *et al.* 1962, p. 130). Robinson (in Plomley 1966) confirms these and other reports of the region by his comments on ‘extensive plains’, with the ‘herbage as about Great Lake of a variety of herbs and wiry grass and occasionally moss [probably cushion plants]’ (p. 542). All of these 19th century observers commented on the abundance of kangaroo and sightings of wild cattle in the region.

Palaeoecological studies from Camerons Lagoon, due south of Liawenee Moor, indicate that grasses were more abundant before than after European settlement (Thomas and Hope 1994). Thomas and Hope concluded that, as exotic species appeared in the pollen record approximately 150 years ago, followed by charcoal deposits in the core, the initial impact on the vegetation of the moor was from domestic stock grazing rather than burning. Liawenee Moor was patch burned by graziers until 1978. The vegetation in an area near the exclosures was last burnt in 1974 (as observed from aerial photographs). However, there is no evidence of the exclosures being burned at this time.

Tertiary basalt is the dominant rock type on Liawenee Moor (Pemberton 1986). Average annual rainfall is 1049 mm with a mean summer rainfall of 213 mm. The summer temperature is between a mean daily minimum of 4.8°C and a mean daily maximum of 17.6°C (Bureau of Meteorology database 1997). Winter temperatures are between a mean daily minimum of –1.7°C and a mean daily maximum of 5.7°C. From January 1997 to June 1997 approximately 3000 sheep grazed on the moor. In the 1995–96 season a similar number of sheep grazed from November to May while approximately 20 sheep stayed on the moor for the winter of 1997.

Methods

The Plots

Two 100 × 30-m exclosures were set up on private land on Liawenee Moor by the Department of Agriculture in the late 1960s. The plots were set up approximately 7 m from the edge of the road and were orientated downslope from the roadside. One exclosure was built to keep out all vertebrate grazers, while the other was designed to keep out sheep and cattle only, allowing access to rabbits and native herbivores. The plots are at an altitude of 1050 m and are within vegetation in which *Grevillea australis* and *Poa* spp. form a grassy shrubland. These exclosures were not kept in good repair. Despite this lack of repair, they were the only locations on the moor where tall flowering forbs were abundant when the fences were repaired in 1995. The only baseline data available for the plots are interpretations of bare ground and vegetation cover from aerial photographs. There are no replicates of each treatment. Despite these problems, these exclosures are the oldest of their kind in the Tasmanian high country and were well placed to avoid any effects of environmental heterogeneity.

After the repairs were made in 1995 the fencelines were checked regularly for signs of visiting vertebrates. The fence was raised in autumn 1996 after wallaby scats were found in the ungrazed exclosure. No new wallaby scats were found in this plot after this time.

Aerial Photographic Analysis

Aerial photographs of the site were obtained for 1974 (January) and 1993 (December). These photographs were enlarged to a scale of 1:1500 for 1993 and 1:2500 for 1974. The location of the exclosures was marked and the distribution of bare ground patches were mapped for the whole area. Two 15-m-wide transects were located either side of the exclosures to be used as the sheep-grazed plot (Fig. 2). The covers of bare ground and vegetation were mapped onto graph paper and their areas measured.

The shrub *Grevillea australis* was also discernible from the 1993 aerial photograph. Percentage cover was determined for each treatment.

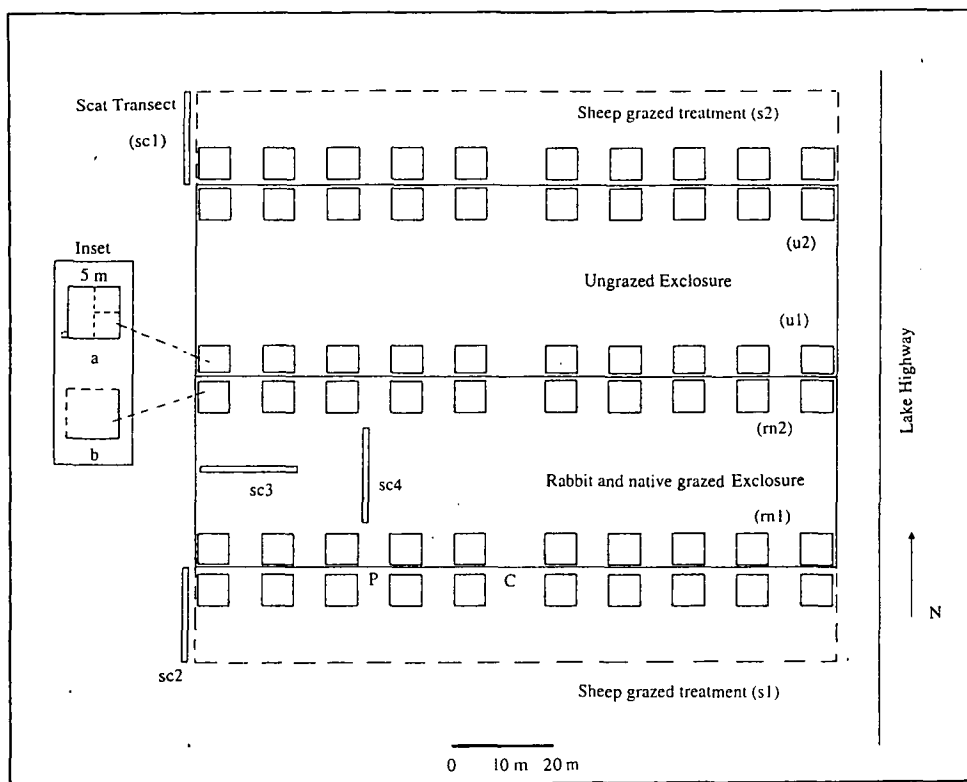


Fig. 2. Layout of transects and quadrats in and around the grazing exclosures. P and C mark the location of the *Podolepis jaceoides* and the *Craspedia coolaminica* invasion transects.

Floristic Survey

Sixty 5 × 5-m quadrats were laid out along six 100-m-long transects, two in each treatment (Fig. 2).

Each quadrat was surveyed in January 1997. The following data were collected: treatment type consisting of all herbivores (henceforth to be called sheep grazed), rabbits and natives without sheep (henceforth to be called rabbit and native grazed), and no mammalian herbivores (henceforth to be called ungrazed); presence of all observable vascular plant species; species, height and cover of the dominant species in the tallest layer; species, height and cover of the dominant species in the mid-layer; species, height and cover of the dominant species in the ground layer. The following cover code was used: 1 = < 1% cover, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–100%. Plant nomenclature follows Buchanan (1995).

Environmental Data

Distance from the road (m) and percentage bare ground were recorded for each quadrat during the floristic data collection. Slope was measured with a clinometer every 10 m along the perimeter of each of the fencelines.

Mean, maximum and minimum soil depth (in cm) was taken from five probes, from the centre and midway to each of the four corners of the 5 × 5-m quadrats.

Scat data on relative numbers of animals were calculated from four 15 × 1-m transects that were set up in the sheep-grazed (s) plots (running S–N) and in the native- and rabbit-grazed (rn) exclosure (one running

S–N, the other running E–W) (Fig. 2). Scats were removed when the transects were set up and were then cleared again after identification and counting at the end of every season (end of February, end of May, end of August, end of November) over a 2-year period.

Lifeform Surveys

In March 1995, 60 quadrats 50×50 cm adjacent to the floristic quadrats were surveyed (Fig. 2, Inset a) and percentage cover was recorded for all species present, bare ground, litter and rock cover. These quadrats were resurveyed in March 1996, in order to determine short-term fluctuations in vegetation cover.

In March 1996, data on the cover in diameter classes and average height of grasses were measured in nested quadrats (2.5×2.5 m, Fig. 2, inset a) which were located within the existing 5×5 -m quadrats. Three categories were defined: small grasses with a tussock diameter of less than 5 cm; medium grasses with a tussock diameter between 5 and 15 cm; and large grasses with a tussock diameter of greater than 15 cm.

Shrub data (percentage cover over the quadrat and average height of a representative individual of each species) were also collected in the 5×5 -m quadrats. The shrub data were also categorised into three groups: small shrubs were less than 20 cm in diameter; medium shrubs ranged from 20 to 50 cm in diameter; large shrubs were greater than 50 cm in diameter. For each class, percentage cover was estimated, the average height of the vegetation was measured and the dominant shrub species were identified.

Line Transect Survey

In February 1997, 60 transects 10 m long were surveyed (20 in each treatment) covering two sides of the 5×5 -m quadrats (Fig. 2, inset b). The structure of the vegetation (shrubby, grassy or non-existent overstoreys) was recorded every centimetre along the transects. The identity of the dominant in each layer and the average height of the dominant species were also recorded. The location of all tall herbs within the layers was noted.

Three vegetation classes were created with reference to the location of the herbs: 1, where the overstorey was greater than 10 cm tall; 2, where the overstorey was less than 10 cm tall but present; 3, where the overstorey was bare ground, litter or lichen cover to a depth of less than 1 cm. The frequency of occurrence of herb species was calculated for three classes of cover within each treatment.

Herb Invasion and Survival

In February 1997, populations of *Craspedia coolaminica* and *Podolepis jaceoides* were mapped across fencelines, from the rabbit- and native-grazed treatment to the sheep-grazed plots. At the time of the survey, damage to the vegetation by sheep grazing was limited.

Transects, 5 m in length and 50 cm apart, were located parallel to the fenceline. Any *C. coolaminica* or *P. jaceoides* rosettes located within 5 cm of the tape were noted, and the length of the longest leaf was measured. Notes were taken on the local habitat of the herb and its stage of development. Transects in the sheep-grazed area were surveyed until no more rosettes of the target species were seen in the general area. Inside the rabbit- and native-grazed treatment, three transects were surveyed to provide a comparison of the density of rosettes inside and outside the fenceline. The transects were resurveyed in September 1997 after sheep had grazed the area outside the exclosures and the number of disappearances of individuals was recorded.

Data Analysis

Global non-metric multidimensional scaling, by using the default settings offered in DECODA, was considered to be the most appropriate method by which to explore gradients in the floristic data (Minchin 1987; Faith *et al.* 1987; Clarke 1993). Ordinations were performed on the presence/absence data from the sixty 5×5 -m quadrats and on the cover data from the 50×50 -cm quadrats. Results in two and three dimensions were compared and if no major differences were found, then the two-dimensional solution was used. These data were further analysed by the fitting of sample variables as vectors to the floristic data in ordination space (Minchin 1990).

Non-parametric statistics were used to test for any differences between plant community and environmental variables by treatment (Mann–Whitney, Kruskal–Wallis, Wilcoxon signed rank test). In analyses of the structural data, the mid-points of the cover classes were used.

Results

Environmental Variation

Slope

The average slope of the transects was 1.6°. The slope of individual quadrats ranged from 0 to 3°. There was no significant relationship between treatment type and slope (Kruskal-Wallis, $H = 0.047$, $P = 0.9767$).

Scats

The number of scats varied from season to season. Sheep were absent during winter and spring of 1996. The majority of sheep scats counted for winter 1997 were deposited during June (Table 1).

Using the scat data from the 1 × 15-m transects, we found that there were significantly more rabbit scats ($U = 13845$, $P = 0.0114$) and wallaby scats ($U = 14735.5$, $P = 0.0336$) in the rabbit- and native-grazed treatment than in the sheep-grazed plots.

The number of rabbit scats decreased dramatically over the study period, while the number of wallaby scats was relatively stable (Table 1). No wombat scats were recorded in the scat transects, but scats were seen in the rabbit- and native-grazed exclosure and in the sheep-grazed area.

Floristic Variation

Ordination

An ordination of the presence data from the 5 × 5-m quadrats resulted in a two-dimensional solution being accepted, with a minimum stress of 0.2388. An ordination of the cover data for the 50 × 50-cm quadrats was also carried out. Again, the two-dimensional solution was accepted with a minimum stress of 0.1167.

The Wilcoxon signed rank test on the ordination scores of quadrats along paired transects showed that there are no significant differences in floristics of the 60 quadrats 5 × 5 m within treatments (u1 and u2, rn1 and rn2 and s1 and s2).

There was no significant difference between the ordination scores of the quadrats between the ungrazed plots (u1) and the rabbit- and native-grazed exclosure (rn2) ($z = -1.376$, $P = 0.1688$), nor was there any difference between the rabbit- and native-grazed exclosure and the sheep-grazed area ($z = -1.274$, $P = 0.2026$). However there was a significant difference between the sheep-grazed area (s2) and the ungrazed exclosure (u2) ($z = -2.803$, $P = 0.0051$).

Table 1. Seasonal variation in the occurrence of scats of vertebrate grazers

Scat concentration is shown as number of scats per m²

	Rabbit- and native-grazed exclosure		Control		
	Rabbit	Wallaby	Rabbit	Wallaby	Sheep
Summer 1995–1996	–	–	11.9	0.0	9.7
Autumn 1996	16.0	2.2	11.7	0.5	12.6
Winter 1996	4.4	0.4	10.3	0.8	–
Spring 1996	13.9	2.1	13.5	0.4	–
Summer 1996–1997	7.8	0.6	3.1	0.0	15.0
Autumn 1997	1.2	0.0	0.0	0.2	44.3
Winter 1997	4.3	0.1	0.9	0.0	7.8

Vector fitting of sample variables to the ordination axes for the presence/absence data revealed distance from the road to be the strongest differentiator of the vegetation, followed by the amount of bare ground and the height and cover of the vegetation in the tallest stratum (Fig. 3). The presence of sheep scats was also statistically significant in ordination space, but the presence of wallaby, wombat and rabbit scats was not. Other environmental variables such as slope and soil depth were also significant.

The Kruskal–Wallis H -test showed that some of the above variables were significantly different between treatments. These included the height of the dominant species in the second layer ($H = 10.431$, $P = 0.0054$); the presence of wallaby scats ($H = 36.949$, $P = 0.0001$); the presence of sheep scats ($H = 59$, $P = 0.0001$); and the presence of rabbit scats ($H = 59$, $P = 0.0001$).

Vector fitting of sample variables to the 50×50 -cm ordination supported the general results of the 5×5 -m ordination, in that distance from the road and bare ground were the two most important vectors (Fig. 4). However, none of the animal scat vectors was significant and other environmental data were not collected for these quadrats.

Species richness

There was no significant difference between treatments in the mean native species richness of the 5×5 -m plots. However, mean total species richness was greatest in the sheep grazed plots and least in the rabbit and native grazed enclosure.

There were significant differences in the number of exotic species between treatments ($s > u$, $z = -2.178$, $P = 0.0294$; $s > rn$, $z = -1.956$, $P = 0.0505$; $u > rn$, $z = -2.157$, $P = 0.031$). The rabbit- and native-grazed enclosure had the least number of exotic species per 5×5 -m quadrat. The mean values for exotic species richness were 5 per 25 m^2 in the sheep-grazed plots, 3.5 per 25 m^2 in the ungrazed plots and 3 per 25 m^2 in the rabbit- and native-grazed enclosure.

Structural Variation

While there was very little difference in species composition between treatments, structurally they were very different. There were three distinct vegetation layers in all of the 20 ungrazed quadrats. Five of the 20 rabbit- and native-grazed quadrats and 10 sheep-grazed quadrats had two layers only. Where only two layers were recorded, either the shrubby tallest stratum or the grassy middle stratum was usually missing. A grassy ground layer was present in all quadrats not dominated by bare ground.

Tall herbs

The percentage frequency of tall herbs (from presence data in the 5×5 -m quadrats) was significantly less in the sheep-grazed treatment than either the rabbit- and native-grazed enclosure ($z = -2.236$, $P = 0.0253$) or the ungrazed plot ($z = -2.088$, $P = 0.0368$). Small herbs showed the opposite effect, having greater numbers in the sheep-grazed plots than both the rabbit- and native-grazed enclosure ($z = -2.989$, $P = 0.0028$) and the ungrazed enclosure ($z = -2.006$, $P = 0.0449$). While some of the tall herbs were present in all three treatments, others showed preferences for less intensely grazed sites (e.g. *Senecio laetus*, Table 2).

Shrubs

There was no significant difference in the percentage cover of small, medium or large shrubs between treatments (large, $H = 3.711$, $P = 0.5918$; medium, $H = 4.19$, $P = 0.5224$; small, $H = 1.396$, $P = 0.9248$). The average height of large shrubs was greater where grazing pressure was reduced ($H = 17.09$, $P = 0.0043$). *Leucopogon montanus* was the dominant shrub species in the small category and *Olearia algida* was the most dominant shrub species in the medium category. Analyses of data for these species showed that there was no

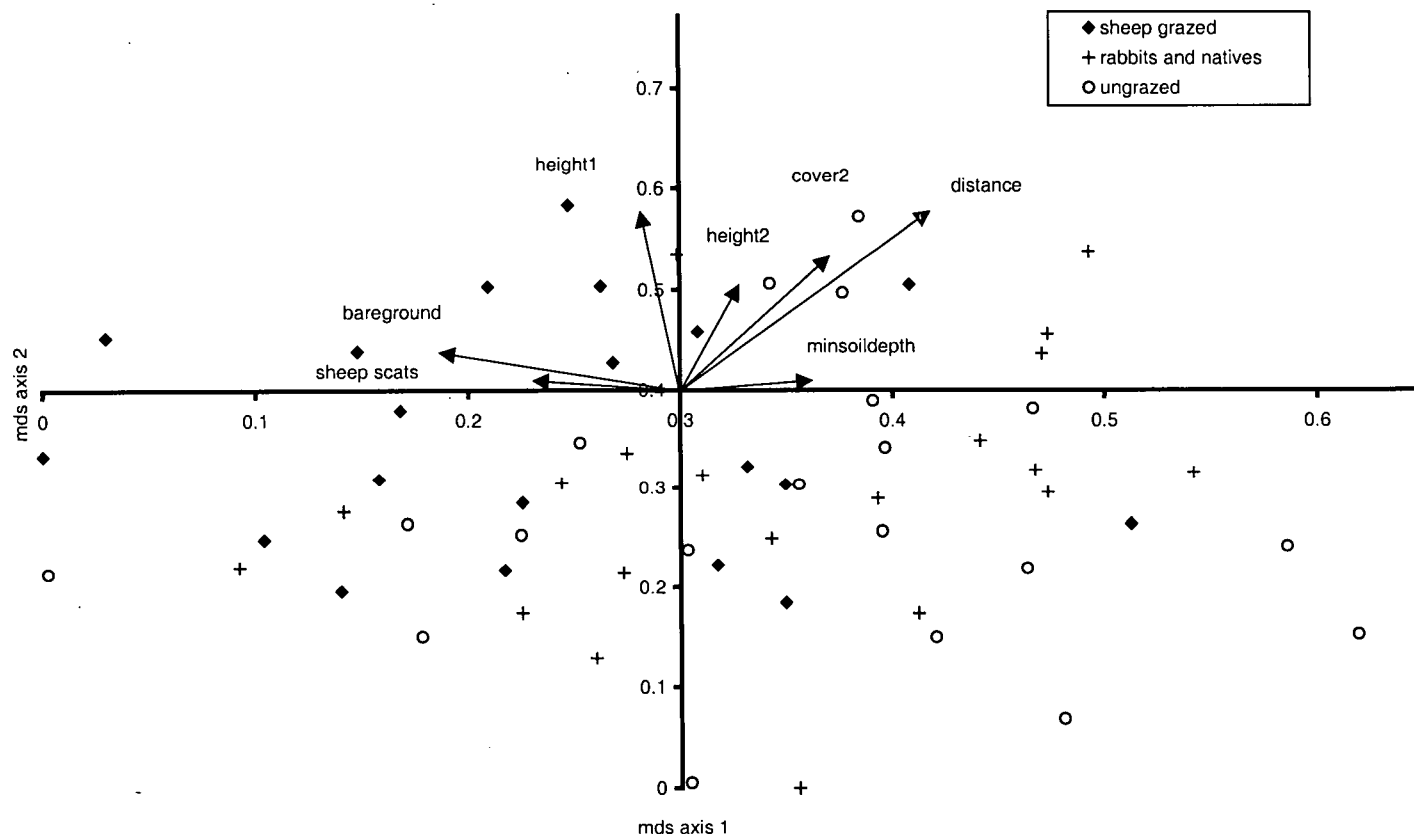


Fig. 3. Ordination (in two dimensions) and vector fitting of species presence data from the 60 5 × 5-m quadrats. Distance = distance from the road; cover2 = percentage cover of the dominant species in the middle stratum (see methods); height1/2 = average height of the dominant species in the tallest or middle stratum; minsoildepth = minimum soil depth.

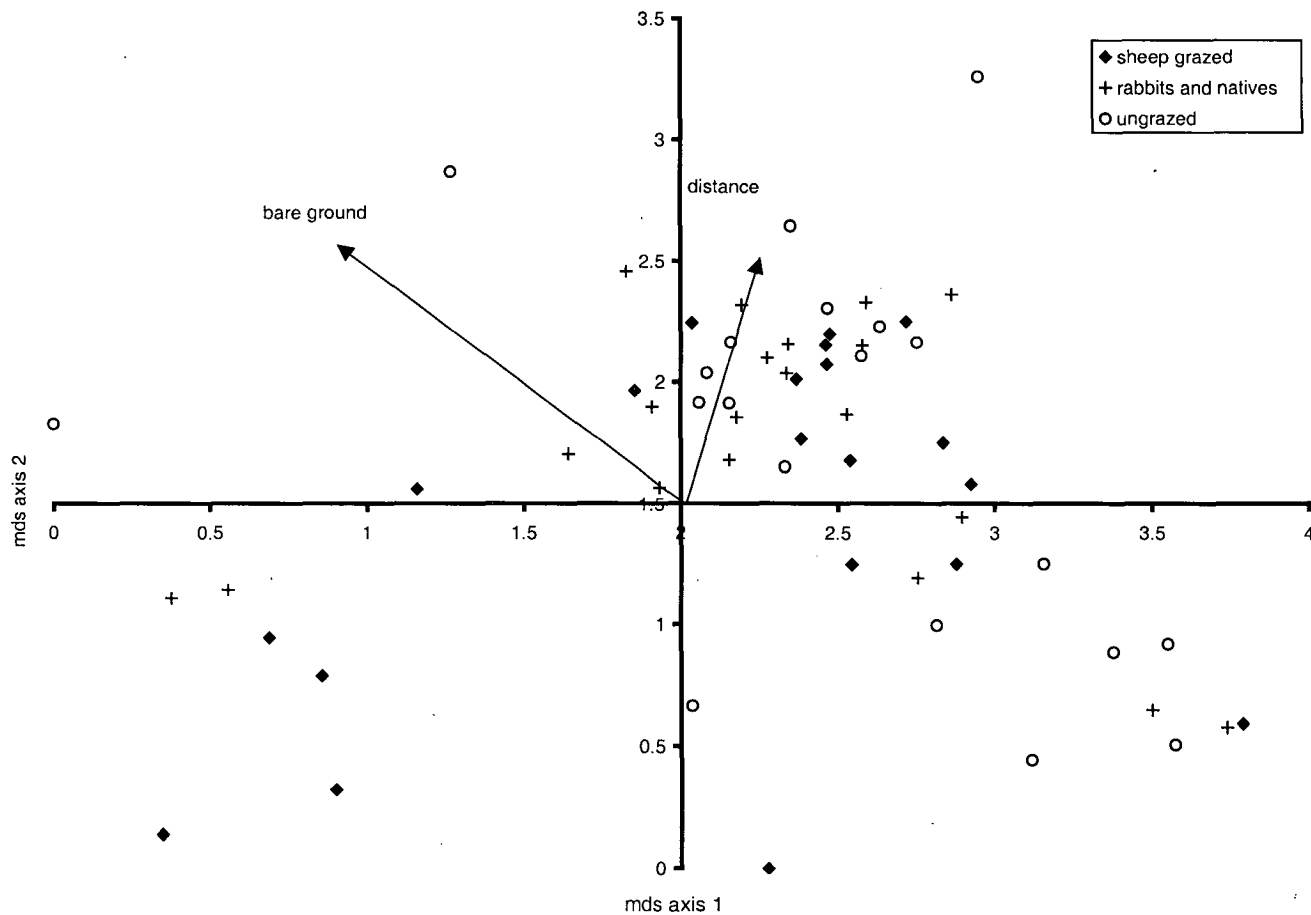


Fig. 4. Ordination (in two dimensions) and vector fitting of species cover data from the 60 50 × 50-cm quadrats.

Table 2. Percentage frequency of species in each treatment type

e = Tasmanian endemic, i = introduced. Tall herb > 10 cm, small herb < 5 cm, herb > 5 cm but < 10 cm

Lifeform	Species	Sheep-grazed	Rabbit- and native-grazed	Ungrazed enclosure
Shrub	<i>Ozothamnus hookeri</i>	—	—	5
Shrub	<i>Olearia algida</i>	100	100	100
Shrub	<i>Leucopogon montanus</i>	90	100	90
Shrub	<i>Grevillea australis</i>	80	80	90
Shrub	<i>Leucopogon stuartii</i>	50	85	35
Shrub	<i>Epacris gunnii</i>	25	35	30
Shrub	<i>Richea acerosa</i> e	15	—	15
Shrub	<i>Leucopogon hookeri</i>	10	—	10
Shrub	<i>Epacris petrophila</i>	10	10	20
Shrub	<i>Hakea microcarpa</i>	5	—	—
Mat shrub	<i>Pimelea pygmaea</i> e	100	90	80
Mat shrub	<i>Coprosma moorei</i>	90	85	95
Mat shrub	<i>Exocarpos nanus</i>	65	55	55
Mat shrub	<i>Cryptandra alpina</i> e	5	30	—
Tall herb	<i>Craspedia glauca</i>	100	100	90
Tall herb	<i>Cerastium glomeratum</i> i	100	90	100
Tall herb	<i>Craspedia coolaminica</i>	95	100	100
Tall herb	<i>Leptorhynchos squamatus</i>	95	100	100
Tall herb	<i>Microseris lanceolata</i>	70	80	90
Tall herb	<i>Ranunculus lappaceus</i>	55	70	55
Tall herb	<i>Brachyscome tenuiscapa</i>	45	50	45
Tall herb	<i>Hypochoeris radicata</i> i	25	25	65
Tall herb	<i>Podolepis jaceoides</i>	20	40	20
Tall herb	<i>Senecio lautus</i>	15	50	60
Tall herb	<i>Chionogentias</i> spp.	15	45	25
Tall herb	<i>Leptorhynchos elongatus</i>	5	—	5
Tall herb	<i>Senecio gunnii</i>	—	15	10
Tall herb	<i>Euphrasia collina</i>	—	—	5
Herb	<i>Geranium sessiliflorum</i>	100	100	95
Herb	<i>Erigeron gunnii</i> e	70	90	90
Herb	<i>Taraxacum officinale</i> i	70	50	35
Herb	<i>Ranunculus</i> spp.	65	80	65
Herb	<i>Acaena novae-zelandiae</i>	55	45	45
Herb	<i>Petrorhagia nanteuillii</i> i	30	25	20
Herb	<i>Acetosella vulgaris</i> i	30	5	15
Herb	<i>Ranunculus pascuinus</i> e	25	25	35
Herb	<i>Epilobium</i> spp.	15	25	45
Herb	<i>Cardamine</i> spp.	5	15	5
Herb	<i>Plantago glabrata</i> e	5	15	5
Herb	<i>Leontodon taraxacoides</i> i	—	5	—
Small herb	<i>Scleranthus biflorus</i>	90	90	75
Small herb	<i>Asperula gunnii</i>	90	75	90
Small herb	<i>Colobanthus apetalus</i>	90	50	55
Small herb	<i>Ajuga australis</i>	85	70	75
Small herb	<i>Oreomyrrhis argentea</i>	80	80	95
Small herb	<i>Oreomyrrhis ciliata</i>	75	55	55
Small herb	<i>Erophila verna</i> i	75	45	45
Small herb	<i>Viola betonicifolia</i>	70	60	70
Small herb	<i>Velleia montanus</i>	70	45	80
Small herb	<i>Veronica gracilis</i>	50	25	40
Small herb	<i>Trifolium repens</i> i	25	—	—

Table 2. (continued)

Lifeform	Species	Sheep-grazed	Rabbit- and native-grazed	Ungrazed enclosure
Small herb	<i>Trifolium dubium</i> i	20	—	—
Small herb	<i>Gonocarpus serpyllifolius</i>	15	5	15
Small herb	<i>Hypericum japonicum</i>	—	5	5
Small herb	<i>Stellaria</i> sp.	—	—	5
Grass	<i>Poa fawcettiae</i>	100	100	100
Grass	<i>Poa</i> spp.	100	100	100
Grass	<i>Agrostis</i> spp.	100	100	95
Grass	<i>Poa hiemata</i>	100	100	95
Grass	<i>Pentapogon quadrifidus</i>	100	100	80
Grass	<i>Agrostis venusta</i>	90	100	95
Grass	<i>Aira caryophyllea</i> i	75	40	55
Grass	<i>Danthonia</i> spp.	75	30	30
Grass	<i>Danthonia nudiflora</i>	75	30	25
Grass	<i>Agrostis billardierei</i>	65	95	85
Grass	<i>Poa costiniana</i>	45	50	65
Grass	<i>Festuca plebeia</i> e	35	20	15
Grass	<i>Vulpia myuros</i> i	25	—	5
Grass	<i>Anthoxanthum odoratum</i> i	10	—	5
Grass	<i>Holcus lanatus</i> i	10	5	—
Grass	<i>Aira praecox</i> i	5	—	—
Grass	<i>Australopyrum velutinum</i>	5	—	—
Grass	<i>Deyeuxia brachyathera</i>	5	—	—
Grass	<i>Poa pratense</i> i	—	5	—
Grass	<i>Poa labillardierei</i>	—	—	10
Grass	<i>Poa gunnii</i> e	—	—	5
Graminoid	<i>Luzula</i> spp.	100	100	100
Graminoid	<i>Luzula australasica</i> e	90	95	100
Graminoid	<i>Carex breviculmis</i>	90	90	90
Graminoid	<i>Luzula modesta</i>	90	90	90
Graminoid	<i>Pterostylis cynnocephala</i>	55	55	30
Graminoid	<i>Schoenus pygmaeus</i> e	35	10	10
Graminoid	<i>Juncus</i> spp.	—	5	—
Fern	<i>Botrychium lunaria</i>	10	5	20

significant difference in percentage cover or average height between grazing treatments (Table 3). *Grevillea australis* was the dominant species in the large category and it was significantly taller in the ungrazed treatment than in the sheep-grazed plots (Table 3). The 1993 aerial photographic analysis showed that the percentage cover of *Grevillea australis* was greater inside the enclosures, covering 17% of the rabbit- and native-grazed enclosure and 14% of the ungrazed plot. In contrast, it covered only 9.5% of the sheep-grazed area. However, there was no significant difference in cover of *Grevillea australis* between the treatments, when the plot data are used.

Grasses

The dominant grasses were in the genus *Poa*. *Poa fawcettiae* and *Poa hiemata* occurred in nearly every quadrat. *Poa costiniana*, while present in all treatments, was more frequently observed in the ungrazed plots, where *Poa labillardierei* was exclusively found (Table 2).

There was a significant difference in the percentage cover of the three grass categories (small, diameter < 5 cm; medium, diameter > 5 cm; but >15 cm, large, diameter > 15 cm)

Table 3. Mean values of shrub structural attributes for the three dominant species by treatments
s.e. = standard error

	Sheep- grazed (s2)	Ungrazed (u2)	Ungrazed (u1)	Rabbit- and native-grazed (m2)	Rabbit- and native-grazed (m1)	Sheep- grazed (s1)
<i>Leucopogon montanus</i>						
% cover	9.3	10.9	9.6	6.6	8.6	7.4
s.e.	1.36	1.34	1.11	1.42	3.22	0.51
Average height (cm)	5.2	5.2	4.5	3.7	5.4	6.4
s.e.	0.29	0.33	0.14	1.29	4.26	0.27
<i>Olearia algida</i>						
% cover	8.3	8.1	8.6	5.9	6.8	9.2
s.e.	0.47	0.60	0.76	0.35	0.41	0.29
Average height (cm)	23.3	24.9	21.9	23.6	24.1	26.3
s.e.	0.63	0.85	1.04	1.27	0.53	0.60
<i>Grevillea australis</i>						
% cover	32.5	40.1	20.4	31.6	34.2	17.8
s.e.	2.57	1.17	3.02	0.64	0.95	1.65
Average height (cm)	49.2	71.1	43.1	61.9	45.2	42.8
s.e.	1.86	2.11	2.54	0.18	0.22	1.92

between the ungrazed enclosure and the sheep-grazed treatment ($H = 21.967$, $P = 0.0001$), but not between the rabbit- and native-grazed treatment and the ungrazed enclosure ($H = 5.817$, $P = 0.0546$) nor the rabbit- and native-grazed treatment and the sheep-grazed area ($H = 3.52$, $P = 0.1721$). There were significantly more flowering heads in the ungrazed enclosure than in the rabbit- and native-grazed treatment ($H = 12.223$, $P = 0.0022$).

The percentage cover of 'small' grasses (*Poa hiemata* and *Poa fawcettiae*) was significantly greater ($z = -2.675$, $P = 0.0075$) in the sheep-grazed (s2) quadrats than in the ungrazed (u2) quadrats. *Poa costiniana* ('medium' grass) had greater cover ($z = -2.539$, $P = 0.0111$) in the ungrazed plot (u2) than in the sheep-grazed plot (s2). There were no 'large' (*Poa costiniana*/*Poa labillardierei*) grasses in the sheep-grazed plots, and there were too few cases of 'large' grass in all treatments for attributes to be tested for statistical differences between treatments.

Most of the smaller grass species (mainly exotics) were more frequent in the sheep-grazed plots, while the native *Agrostis billardierei* was most abundant in the enclosures (Table 2).

Long-term Change

Over the 20-year period, the vegetation cover of the ungrazed plot increased by 17%. Vegetation cover also increased in the native- and rabbit-grazed enclosure but more slowly (10%). In contrast the vegetation cover of the sheep-grazed plots decreased by 7%.

The ungrazed treatment had the greatest increase in vegetation cover, with the highest percentage bare ground in 1974 (39%), and the lowest value in 1993 (22%). The increase in vegetation cover in the ungrazed plot averaged 0.9% per year. The native and rabbit-grazed enclosure has a lower average change of 0.5% per year, while the sheep-grazed plots recorded a decrease in vegetation cover amounting to an average of -0.4% per year.

Climatic records from two stations at Liawenee suggest that the 3-month period before the photographs were taken was slightly wetter in 1974 than in 1993 (Bureau of Meteorology 1997). While no temperature data were available for Liawenee, in 1974 the state as a whole experienced slightly warmer maximum and minimum temperatures than normal

(Tasmanian Year Book 1975), while they were slightly cooler than normal in 1993 (Bureau of Meteorology 1997).

Short-term Change

The percentage cover of tall herbs ($z = -4.55$, $P = 0.0001$) and small herbs ($z = -2.243$, $P = 0.0249$) decreased across all treatments from March 1996 to March 1997 (Table 4). Shrub cover increased overall (tall shrubs $z = -2.232$, $P = 0.0256$; mat shrubs $z = -2.074$, $P = 0.0381$). Bare ground decreased over the 2-year period ($z = -2.965$, $P = 0.003$) and the cover of monocotyledons increased ($z = -2.363$, $P = 0.0181$).

Within treatments, there was a significant increase in the shrub *Olearia algida* ($z = -2.239$, $P = 0.0251$) and monocotyledons ($z = -2.107$, $P = 0.0351$) in the sheep-grazed plots. There was a decrease in tall herbs ($z = -3.083$, $P = 0.002$), notably *Leptorhynchos squamatus*, small herbs ($z = -2.83$, $P = 0.0047$), monocotyledons ($z = -1.99$, $P = 0.0466$) and bare ground ($z = -2.427$, $P = 0.0152$) in the rabbit- and native-grazed treatment. There was also a decrease in tall herbs ($z = -3.415$, $P = 0.0006$) (especially *Leptorhynchos squamatus*) in the ungrazed exclosure (Table 4).

Herb Occurrence by Other Vegetation and Treatment

Individuals of *Craspedia coolaminica* and *Podolepis jaceoides* were predominantly located in vegetated areas in the sheep-grazed transects, i.e. with some cover from grasses or small shrubs less than 10 cm in height. This was also the case in the rabbit- and native-grazed exclosure; however, there was a greater proportion of individuals in unprotected areas growing amongst litter, mat shrubs and herbs or in bare ground. Plants in the ungrazed transects were more abundant in the open areas and those with low cover (Table 5, *Craspedia coolaminica* $\chi^2 = 68.498$, $P = 0.001$, *Podolepis jaceoides* $\chi^2 = 32.177$, $P = 0.001$).

Individuals of *Microseris lanceolata* did not show any significant habitat differences between treatments (Table 5, $\chi^2 = 4.613$, $P = 0.329$).

Table 4. Percentage cover of lifeform groups and tall herb species in 50 × 50-cm quadrats over a 2-year period

* denotes a significant change in species or lifeforms, as a complete data set and within treatments, over the 2-year period (using the Wilcoxon signed rank test)

Species or lifeform	Ungrazed		Rabbit- and native-grazed		Sheep-grazed	
	1996	1997	1996	1997	1996	1997
Small herbs*	1.7	1.0	2.5	1.7*	1.6	1.9
<i>Leptorhynchos squamatus</i> *	9.9	7.3*	7.0	5.0*	7.1	6.8
<i>Craspedia coolaminica</i>	0.7	0.8	0.7	0.7	0.4	0.2
<i>Erigeron gunnii</i>	0.4	0.3	0.2	0.4	0.0	0.0
<i>Brachyscome tenuiscapa</i>	0.1	0.1	0.1	0.1	0.0	0.0
<i>Ranunculus</i> spp.	0.1	0.0	0.1	0.0	0.0	0.0
Tall herbs total*	12.6	9.6*	9.2	6.9*	8.2	7.3
Mat shrubs*	2.2	2.9	2.3	1.7	1.3	1.4
<i>Grevillea australis</i>	19.4	18.8	10.5	12.6	10.3	10.6
<i>Olearia algida</i> *	5.9	5.1	6.3	6.9	4.1	5.7*
<i>Leucopogon montanus</i>	5.5	6.4	6.5	7.0	6.8	7.0
Tall shrubs*	37.4	37.4	27.2	29.6	25.9	27.8
Monocotyledons*	28.1	28.4	23.8	22.1*	19.5	24.0*
Litter, moss, lichen	7.9	11.1	10.5	9.9	10.9	8.4
Rocks and bare ground*	10.5	10.0	23.8	22.1*	32.8	29.5

Table 5. The relative proportions (%) of *Craspedia coolaminica*, *Podolepis jaceoides* and *Microseris lanceolata* within different microhabitats

Low cover = overstorey < 10 cm tall, tall cover = overstorey > 20 cm tall, no cover = bare ground or < 1 cm lichen or litter

	Sheep-grazed	Rabbit- and native-grazed	Ungrazed
<i>Craspedia coolaminica</i>	<i>n</i> = 102	<i>n</i> = 481	<i>n</i> = 702
Overstorey < 1 cm tall	7	28	41
Overstorey < 10 cm tall	74	47	38
Overstorey > 10 cm tall	19	25	21
<i>Podolepis jaceoides</i>	<i>n</i> = 8	<i>n</i> = 16	<i>n</i> = 35
Overstorey < 1 cm tall	13	50	26
Overstorey < 10 cm tall	0	19	69
Overstorey > 10 cm tall	87	31	5
<i>Microseris lanceolata</i>	<i>n</i> = 33	<i>n</i> = 27	<i>n</i> = 18
Overstorey < 1 cm tall	21	37	33
Overstorey < 10 cm tall	64	52	39
Overstorey > 10 cm tall	15	11	28
Proportion (%) of transect covered by the three classes			
Proportion < 1 cm tall	24.7	30.0	32.5
Proportion < 10 cm tall	53.4	40.5	33.8
Proportion > 10 cm tall	21.9	29.5	33.7

Invasion and Survival

There were no *C. coolaminica* plants found further than 550 cm from the fence in the sheep-grazed area. Individuals of *P. jaceoides* were only found within 300 cm of the fenced population (Table 6). Both species were far greater in number and size inside the rabbit- and native-grazed exclosure than outside in the sheep-grazed area.

When the site was revisited in September 1997, one of the 20 *P. jaceoides* plants from outside the exclosure was no longer there while all of the plants inside the exclosure could still be located. Forty-three per cent (12 individuals) of the *C. coolaminica* plants found outside had disappeared, while 32% (14 plants) were missing inside the exclosure.

Discussion

The conclusions presented here rest on the assumption that the treatment plots were environmentally identical when they were created. This assumption is supported by present-day similarities in environmental conditions. Topographic variables (such as slope, aspect and soil depth) were found to be consistent for all treatments across the site, and there were no significant differences in variables related to the structure and composition of the vegetation between the sheep-grazed plots that were situated on either side of the treatments (60 m apart).

Numbers of wallaby and rabbit scats on Liawenee Moor were low compared with other high altitude environments in Tasmania (Table 7), even in other locations on Liawenee Moor (Gibson and Kirkpatrick 1989). Numbers of rabbit scats were most similar to, but slightly higher than, those noted by Leigh *et al.* (1987) for unburnt frost hollows (heathy grasslands) on the mainland. Our data were collected every 3 months, while the apparently more densely populated sites of Fensham and Kirkpatrick (1992) were collected on a monthly basis. Pilot studies on Liawenee Moor indicated that very little gain was to be made in collecting scats on a more frequent basis, and that scat decay was not a concern over a period of 3 months. The

Table 6. Distribution and average leaf length of two tall herbs in sheep-grazed and sheep-exclusion (rabbit- and native vertebrate-grazed) plots

Distance from fence (cm)	<i>Craspedia coolaminica</i>				<i>Podolepis jaceoides</i>			
	Sheep-grazed		Rabbit- and native-grazed		Sheep-grazed		Rabbit- and native-grazed	
	No.	Mean size (cm)	No.	Mean size (cm)	No.	Mean size (cm)	No.	Mean size (cm)
50	7	4.6	13	5.0	4	2.1	3	3.7
100	8	3.8	16	5.5	4	2.4	25	2.9
150	1	1.5	15	6.0	4	2.5	28	2.8
200	3	3.5			1	2.5		
250	2	3.3			3	2.2		
300	3	3.7			4	2.6		
350	1	8.0			0	—		
400	0	—			0	—		
450	1	9.5			0	—		
500	1	4.5			0	—		
550	1	3.0			0	—		

Table 7. A comparison of scat counts for Liawenee and other Australian alpine environments

Source	Altitude (m)	Location	Habitat	Rabbits (m ⁻²)	Wallabies (m ⁻²)	Total
Fensham and Kirkpatrick (1992) (12 months' data)	1000	Central Plateau	Grassland	296	360	656
Authors' data	1050	Central Plateau	Grassland (Liawenee)	42	5	47
Gibson and Kirkpatrick (1989) (one summer)	1150	Central Plateau	Grassy woodland			22 ^A
Authors data	1050	Central Plateau	Grassland (Liawenee)	8	1	9
Leigh <i>et al.</i> (1987) (1 year non-winter months)	1370–1410	Kosciusko National Park	Grassland/ frost hollow	28	0	28
Authors' data	1050	Central Plateau	Grassland (Liawenee)	38	5	43

^ANative vertebrate grazers only (species not specified).

scat transect method is inappropriate for measuring the relative populations of wombats as they have 'toilets' marking their territory.

In other studies bare ground has been found to cover a significantly larger area in grazed plots than ungrazed exclosures (Wahren *et al.* 1994), whether the grazers are predominantly

domestic stock (Wimbush and Costin 1979c; Wahren *et al.* 1994), rabbits (Leigh *et al.* 1987) or native vertebrates (Leigh *et al.* 1987; Gibson and Kirkpatrick 1989). There have been no data on the relative effects of sheep, rabbits and native vertebrates and rabbits and native vertebrates. The exclusion of sheep but not other animals results in a decrease in cover of bare ground. The increase in the percentage of bare ground in the sheep-grazed plots at Liawenee over 20 years (in the absence of periodic burning) indicates that the additional grazing pressure created by sheep has the greatest impact in degrading this environment.

A decrease in grazing pressure usually leads to an increase in vegetation cover (Carr and Turner 1959b; Wimbush and Costin 1979b; Leigh *et al.* 1987; Gibson and Kirkpatrick 1989; Wahren *et al.* 1994). The success of the recovery is largely dependent on the impact of the initial disturbances (Wimbush and Costin 1979a, 1979b, 1979c), and the scale of continuing disturbance (Wimbush and Costin 1979b; Wahren *et al.* 1994). As recovery rates in alpine environments are extremely slow, it may be many years before any differences in grazing treatments become evident (Carr and Turner 1959b; Wimbush and Costin 1979a; Leigh *et al.* 1987; Wahren *et al.* 1994). Where sites are in a disturbed state but the native vegetation is relatively intact, the recovery rate of tall herbs when protected from grazing is reported to be relatively fast (6–8 years) (Wimbush and Costin 1979a). However, it has taken nearly 50 years for 55 individuals of *Podolepis robusta* to become established on the ungrazed Pretty Valley plot on the Bogong High Plains (Wahren *et al.* 1994). The vegetation on Liawenee Moor has been severely disturbed by domestic stock grazing and burning, and has large areas of bare ground which are slowly revegetating. Differences in plant species composition were most evident between the two extreme treatments of ungrazed and sheep-grazed. The abundances of particular species or lifeforms, especially flowering tall herbs, are more distinct between all treatment types.

The cover of shrubs, grasses and tall herbs has been shown to increase with a decrease in grazing pressure (Carr and Turner 1959; Wimbush and Costin 1979a, 1979b, 1979c; Leigh *et al.* 1987). The composition of species within these lifeform groups has also been shown to change, with a greater number of palatable species establishing (Wimbush and Costin 1979b; Leigh *et al.* 1987; Gibson and Kirkpatrick 1989; Wahren *et al.* 1994). While the cover of individual shrub species was not significantly different between grazing treatments at Liawenee, many grasses and tall herbs were more frequent in the exclosures than in the sheep-grazed plots. A decrease in grazing pressure in disturbed alpine environments is known to lead to an increase in shrub cover in the short term (Williams and Ashton 1987; Wahren *et al.* 1994). Our data show that the average height of the large shrub *Grevillea australis* was significantly greater in the two exclosures than in the sheep-grazed area. The cover of the medium shrub *Olearia algida* increased significantly in the sheep-grazed plots over a 2-year period. While *Grevillea australis* is both palatable and highly susceptible to trampling, *Olearia algida* is neither. The increase in this species over this period is likely to be a result of the favourable growing season and the absence of sheep grazing at the onset of the growing season. However, large-scale establishment of shrub species in gaps was not noted, possibly because of the large sizes (greater than 1 m² in many cases) of the bare ground patches.

Tall herbs are generally eaten when they are flowering (Leigh *et al.* 1987). Herbs that are known to be palatable to domestic stock and rabbits from mainland studies (Wimbush and Costin 1979c; Leigh *et al.* 1987), are also preferentially grazed by native vertebrates at Liawenee (e.g. *Podolepis jaceoides*, *Craspedia coolaminica*, *Senecio lautus*). However, the combined effects of rabbits and native grazers at Liawenee do not appear to be as strong as those reported by Leigh *et al.* (1987) for rabbits only.

The distribution of herbs and their behaviour on Liawenee Moor is consistent with the hypothesis of Kirkpatrick (1989) in that the cover of tall herbs is less where grazing exists. Where grazing occurred, tall herbs were preferentially located within protective canopies. However, herbs that were wind dispersed were able to recolonise sites close to a seed source relatively quickly at Liawenee, as in other areas (Wimbush and Costin 1979a; Wahren *et al.* 1994).

The impacts of grazers on exotic species at Liawenee is consistent with the hypothesis of Kirkpatrick (1989), and the results of Leigh *et al.* (1987), Whinam *et al.* (1994) and Wimbush and Costin (1979b) in that palatable exotics such as *Hypochaeris radicata* (Struik 1967; Leigh *et al.* 1987) were more frequent in the ungrazed enclosure.

Short-term fluctuations in vegetation cover may mask the long-term effects of different grazing pressures. The literature suggests that these short-term fluctuations are strongly related to seasonal climatic conditions (Wimbush and Costin 1979a, 1979b, 1979c). This hypothesis is supported by the short-term data presented here, where grass growth fluctuates rapidly with the onset of good and poor growing seasons. Grass growth on Liawenee Moor during 1996–97 was greater than in 1995–96, coinciding with a more favourable growing season (Bureau of Meteorology 1997) and was also enhanced by the late arrival of sheep in January (2 months later than normal). Increases in grass and forb cover have been related to higher than average rainfall early in the season (Wimbush and Costin 1979a; Leigh *et al.* 1991). The favourable growing season, combined with the lack of sheep grazing in late spring and early summer and the relative abundance of small (< 50 cm) bare ground patches probably accounts for the 3.3% increase in vegetation cover in the sheep-grazed area. In contrast, bare ground cover only decreased by 0.5% in the ungrazed enclosure, which more closely resembles the value obtained from the aerial photographic analysis. Small bare ground patches are less common in the grazing enclosures as they are relatively easily recolonised with the removal of domestic stock (Williams 1992). The gaps that are left to be colonised are usually large (> 1 m in diameter) and tend to be recolonised from the edges of the gap, rather than establishment of individuals in the middle of the bare ground.

The major conclusions of this study are that sheep grazing is causing continued deterioration of vegetation cover and that recovery is taking place under rabbit and marsupial grazing. However, grazing pressure from rabbits and marsupials does reduce the abundance of tall herbs.

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References

- Bridle, K. L., and Kirkpatrick, J. B. (1998). Why do tall herbs rarely dominate Tasmanian alpine vegetation? Evidence from islands in the Ouse River system. *Papers and Proceedings of the Royal Society of Tasmania* **132**, 9–14.
- Buchanan, A. M. (1995). A Census of the Vascular Plants of Tasmania. Tasmanian Herbarium Occasional Publication No. 5, Hobart.
- Bureau of Meteorology (1997). Monthly data for Liawenee. Climate and Consultancy Section, Tasmania and Antarctica Regional Office, Hobart.
- Carr, S. G. M., and Turner, J. S. (1959a). The ecology of the Bogong High Plains. I. The environmental factors and the grassland communities. *Australian Journal of Botany* **7**, 12–33.
- Carr, S. G. M., and Turner, J. S. (1959b). The ecology of the Bogong High Plains. II. Fencing experiments in grassland C. *Australian Journal of Botany* **7**, 34–63.
- Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117–143.
- Crawford, G., Ellis, W. F., and Stancombe, G. H. (Eds) (1962). 'The Diaries of John Helder Wedge 1824–1835.' (The Queen Victoria Museum: Launceston.)
- Faith, D. P., Minchin, P. R., and Belbin, L. (1987). Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* **69**, 57–68.
- Fensham, R. J., and Kirkpatrick, J. B. (1992). The eucalypt forest–grassland/grassy woodland boundary in central Tasmania. *Australian Journal of Botany* **40**, 123–138.

- Gibson, N., and Kirkpatrick, J. B. (1989). Effects of the cessation of grazing on the grasslands and grassy woodlands of the Central Plateau, Tasmania. *Australian Journal of Botany* **37**, 55–63.
- Jackson, W. D. (1973). Vegetation of the Central Plateau. In 'The Lake Country of Tasmania'. (Ed. M. R. Banks.) pp. 61–85. (Royal Society of Tasmania: Hobart.)
- Jorgenson, J. (1829). 'The History of the Origin, Rise and Progress of the Van Diemen's Land Company.' London (Facsimile Ed Hobart 1979.)
- Kirkpatrick, J. B. (1983). Treeless plant communities of the Tasmanian high country. *Proceedings of the Ecological Society of Australia*, **12**, 61–77.
- Kirkpatrick J. B. (1989). The comparative ecology of mainland Australia and Tasmanian alpine vegetation. In 'The Scientific Significance of the Australian Alps'. (Ed. R. Good.) pp. 127–142. (Australian Alps Liaison Committee: Canberra.)
- Leigh, J. H., and Holgate, M. D. (1979). The responses of the understorey of forests and woodlands of the Southern Tablelands to grazing and burning. *Australian Journal of Ecology* **4**, 25–45.
- Leigh, J. H., Wimbush, D. J., Wood, D. H., Holgate, M. D., Slee, A. V., Stanger, M. G., and Forrester, R. I. (1987). Effects of rabbit grazing and fire on a subalpine environment. I. Herbaceous and shrubby vegetation. *Australian Journal of Botany* **35**, 433–464.
- Leigh, J. H., Wood, D. H., Slee, A. V., and Holgate, M. D. (1991). The effects of burning and simulated grazing on productivity, forage quality, mortality and flowering of eight subalpine herbs in Kosciusko National Park. *Australian Journal of Botany* **39**, 97–118.
- Minchin, P. (1987). An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**, 89–107.
- Minchin, P. (1990). 'DECODA—Database for Ecological Community Data, Version 2.02.' (Australian National University: Canberra.)
- Pemberton, M. (1986). 'Land Systems of Tasmania. Region 5: Central Plateau.' (Department of Agriculture: Tasmania.)
- Plomley, N. J. B. (Ed.) (1966). 'The Friendly Mission: the Tasmanian Journal and Papers of George Augustus Robinson.' (Tasmanian Historical Research Association: Hobart.)
- Struik, G. J. (1967). Growth habits of dandelion, daisy, catsear and hawkbit in some New Zealand grasslands. *New Zealand Journal of Agricultural Research* **10**, 331–344.
- Thomas, I., and Hope, G. (1994). An example of Holocene vegetation stability from Cameron's Lagoon, a near treeline site on the Central Plateau, Tasmania. *Australian Journal of Ecology* **19**, 150–158.
- Wahren, C.-H. A., Papst, W. A., and Williams, R. J. (1994). Long-term vegetation change in relation to cattle grazing in subalpine grassland and heathland on the Bogong High Plains: an analysis of vegetation records from 1945 to 1994. *Australian Journal of Botany* **42**, 607–637.
- Whinam, J., Cannell, R. J., Kirkpatrick, J. B., and Comfort, M. (1994). Studies on the potential impact of recreational horseriding on some alpine environments of the Central Plateau, Tasmania. *Journal of Environmental Management* **40**, 103–117.
- Williams, R. J. (1992). Gap dynamics in subalpine heathland and grassland vegetation in south-eastern Australia. *Journal of Ecology* **80**, 343–352.
- Williams, R. J., and Ashton, D. H. (1987). The composition, structure and distribution of heathland and grassland communities in the subalpine tract of the Bogong High Plains. *Australian Journal of Ecology* **12**, 155–163.
- Wimbush, D. J., and Costin, A. B. (1979a). Trends in vegetation at Kosciusko. I. Grazing trials in the subalpine zone, 1957–71. *Australian Journal of Botany* **27**, 741–787.
- Wimbush, D. J., and Costin, A. B. (1979b). Trends in vegetation at Kosciusko. II. Subalpine range transects, 1959–78. *Australian Journal of Botany* **27**, 789–831.
- Wimbush, D. J., and Costin, A. B. (1979c). Trends in vegetation at Kosciusko. III. Alpine range transects, 1959–78. *Australian Journal of Botany* **27**, 833–871.

WHY DO TALL HERBS RARELY DOMINATE TASMANIAN ALPINE VEGETATION? EVIDENCE FROM ISLANDS IN THE OUSE RIVER SYSTEM

by K. L. Bridle and J. B. Kirkpatrick

(with five tables, one text-figure and two plates)

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Tall alpine herbfield is largely absent from the Tasmanian alpine zone. This absence has been attributed to marsupial grazing. Small islands in the upper Ouse River valley are partly dominated by *Craspedia paludicola*, a showy tall alpine herb. The herbs dominate on the upstream ends of the islands. The surrounding vegetation on the banks is mainly grassland. The tall herbs are a very minor element of the shore vegetation, occurring on the undercut banks. Grassy islands close to the river banks are grazed and few tall herbs are found there. *Craspedia paludicola* also occurs in small numbers in damp areas on grassy heaths at other grazed locations, largely within bushes with pungent leaves. The distribution of *Craspedia paludicola* suggests that it is highly palatable and can thus only survive in larger numbers away from the influence of vertebrate grazers (rabbits and marsupials). It appears that this species requires both disturbance and a lack of grazing to dominate an area.

Key Words: tall alpine herbs, islands, grazing, Central Plateau, Tasmania, alpine vegetation.

INTRODUCTION

Tall alpine herbfield (sensu Costin *et al.* 1979) is one of the more widespread vegetation types in the Australian Alps. While many species that are found in mainland tall alpine herbfields occur in Tasmania, the community is largely absent from the Tasmanian alpine zone.

One of the main ecological differences between alpine areas in mainland Australia and those in Tasmania is the lack of grazing pressure from native herbivores on the mainland. The absence of marsupial herbivores on the mainland can be accounted for by the more continental climate of the Australian Alps, resulting in extended periods of snowlie (Carr & Turner 1959a, McVean 1969). As Tasmania has a maritime climate, persistent snowlie is restricted to the highest lee slopes, allowing vertebrate herbivores to survive and feed in the relatively unprotected vegetation of the alpine zone throughout the year (Kirkpatrick 1989).

The impacts of domestic stock and rabbit grazing on tall alpine herbs has been well documented for the Australian Alps (Carr & Turner 1959b, Wimbush & Costin 1979a,b,c, Leigh & Holgate 1979, Leigh *et al.* 1987, Williams & Ashton 1987, Wahren *et al.* 1994). However, very little information is available on the effects of native vertebrate herbivores on alpine vegetation. Leigh & Holgate (1979) found that plant survival and reproductive capacity were reduced by native vertebrate and rabbit grazing in the shrubby understorey of dry sclerophyll woodlands. Palatable forbs were considered to be the main food source of mammalian herbivores in subalpine environments (Leigh *et al.* 1991). However, the effects of native marsupial grazing have been found to be insignificant when compared to the effects of rabbits (Leigh *et al.* 1987).

In Tasmania, native herbivores (wallabies and wombats) affect the cover and heights of some shrubs and species of herbs in subalpine grassy woodlands (Gibson & Kirkpatrick 1989). Grazing by native herbivores and rabbits is considered to be the main mechanism for restricting the spread of exotic species across the Central Plateau

(Kirkpatrick 1989, Whinam *et al.* 1994, Corbett 1996). In alpine *Sphagnum* bogs, epacridaceous shrubs are subject to heavy wallaby grazing (Whinam 1990). This study also indicated that grazing pressure was greater on individual palatable species in environments with relatively few palatable plants.

Rabbit numbers widely fluctuate on the Central Plateau and are heavily reduced during times of prolonged snowlie (Cullen 1995). Historical records detail the fluctuating numbers of kangaroo around the Great Lake area during the mid 1800s, where "... vast numbers of kangaroos perished through the cold" ... and during the summer of 1845 "... one man alone killed 1100 [kangaroos] in the vicinity of Lake Arthur..." (Breton 1846: 130).

Kirkpatrick (1989) postulated that the lack of tall alpine herbfield in Tasmania was due to the palatability of the herbs and the year round presence of introduced and native herbivores. He noted that tall alpine herbs were visibly abundant in places which were isolated from grazing, such as fenced plots and islands in fast-flowing, deep streams (e.g. the Ouse River system).

This paper documents the environments, vegetation and grazing incidence on several of the islands in the Ouse River system and the adjacent banks. Our working hypothesis was that the exclusion of grazing by a fast-flowing deep stream would result in a greater degree of tall herb cover than in adjacent, environmentally similar areas.

METHODS

In January 1997, five islands in the upper Ouse River valley, on the eastern Central Plateau, Tasmania, were surveyed (fig. 1). These islands were the first five seen on a traverse of the region. The closest adjacent area of the same size on the banks of the rivers was also surveyed.

The following data were recorded:

- dimensions of the island;
- minimum distance from the island to the shore;
- presence and cover of vascular plant taxa using the following

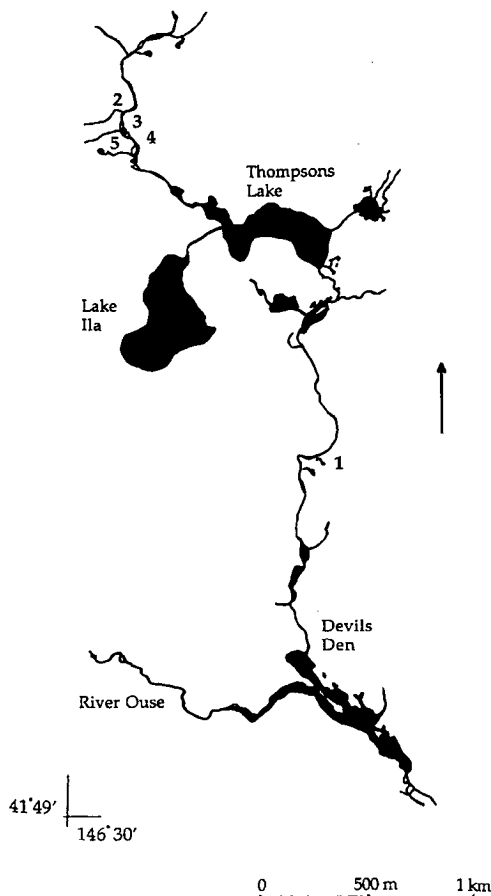


FIG. 1 — The upper Ouse River system showing the location of the island and shore sites (1–5) surveyed.

scale — 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–100%;

• presence, identity and number of scats present.

Plant nomenclature follows Buchanan (1995) except for *Chionogentias* spp. (L.G. Adams 1995).

Three bulked samples of surface soil (< 5 cm deep) were taken from each island and adjacent shore. These were analysed for copper, iron, manganese, zinc, ammonium N, nitrate N, total nitrogen, total phosphorus, total calcium, extractable phosphorus, extractable potassium, organic carbon, conductivity and pH, using the following methods — DTPA for Cu, Fe, Mn, Zn; KCl extraction for NH_4/N , NO_3/N ; semimicro Kjeldahl, steam distillation for total N; ICP analysis for total P & Ca; bicarbonate-extractable P; bicarbonate-extractable K; organic C (Walkley & Black); pH(CaCl_2) 1:5 soil/0.01M calcium chloride extract; conductivity 1:5 soil/water extract (Rayment & Higginson 1992).

Plant species were grouped according to lifeform: shrub, grass, herb (dicotyledons), graminoids (herbaceous monocotyledons other than members of the Poaceae). Herbs were further divided into three groups on the basis of stature; tall alpine herbs (*sensu* Costin *et al.* 1979), medium stature herbs (between 5 and 10 cm tall) and small herbs (less than 5 cm tall). All “small herb” *Ranunculus* species were grouped under the genus.

The numbers of Bennett’s wallaby (*Macropus rufogriseus*) and wombat (*Vombatus ursinus*) scats and plant species richness were calculated for each pair of island/shore plots.

The Mann-Whitney U test was used to determine whether there were any significant differences in soil characteristics or numbers of scats between the islands and the shores, while the Wilcoxon signed-rank test was used to test for significant differences in species richness between the paired plots. The Fisher’s Exact Probability test was used to determine the significance of differences between the distribution of individual taxa on islands and shores.

The midpoints of the cover classes were used to estimate the total cover of lifeforms for each of the island/shore plots. The Fisher’s Exact Probability test was used to determine the significance of different lifeform groups on islands and shores.

RESULTS

The islands varied in size from 2.25 to 24 m² and were from 1.5 to 12 m away from the shores (table 1).

The number of scats recorded for the islands and the shore was significantly different ($z = -2.643$, $p = 0.0082$). Not surprisingly, the only scats recorded on the islands were wallaby scats, whilst both wallaby and wombat scats were recorded on the shore. Scats were only found on islands four and five which lay less than 2 m away from the river bank (tables 1, 2).

There were no significant differences between the soils of the island and the shore sites (table 3).

In all, 40 plant species were identified on the islands and adjacent shores. Most of the species recorded were herbs (23/40) followed by graminoids and shrubs (table 4).

Only one species, *Plantago daltonii*, occurred in all ten plots, while 13 species occurred in one plot only (table 4). Species richness was consistently higher in the shore plots than on the islands ($z = -2.812$, $p = 0.0049$) (table 4).

The grass *Hierochloa redolens*, the graminoid *Carpha alpina* and the tall alpine herb *Craspedia paludicola* were the only species to have significantly different frequency distributions on the islands and the shores ($p = 0.004$ for all three species).

There was no significant difference in the presence or cover of shrubs, grasses, graminoids or small herbs between the islands and the shore sites. Medium stature herbs (h) and tall herbs (tah) were significantly more abundant on the islands ($p = 0.024$, $p = 0.004$ respectively).

Seven species occurred on the islands only, while 11 species were recorded for the shore sites only (table 5). Of these, small herbs made up the greater proportion of plants recorded for the shore sites only. Tall herbs and grass species were faithful only to the islands.

DISCUSSION

Visually, the tall herb *Craspedia paludicola* identifies the main difference in species composition and stature between the island and the shore sites (pl. 1). This difference in the vegetation cannot be attributed to differences in soil fertility (table 3). These islands do differ from the shores in the number of scats per unit area with several having none (table 2). We were unable to measure flood disturbance impacts but deduce that these would be greatest on the upstream ends of islands and least on the downstream ends. There seems little doubt that flood activity favours the establishment of tall herbs as these were concentrated on the

TABLE 1
Physical characteristics of the five paired sites

Island	Dimensions (m)	Distance to banks	
		West	East
1	4 x 6	2 m	4 m
2	2 x 2	3 m	6 m
3	1.5 x 1.5	6 m	6 m
4	3 x 2	8 m	1.5 m
5	4 x 2	12 m	2 m

TABLE 2
Number of scats/m²

Site	Number of scats		Identity of scats	
	Islands	Shores	Islands	Shores
1	0	0.9		Wallaby
2	0	9.5		Wallaby/wombat
3	0	14.2		Wallaby
4	2.3	5.8	Wallaby	Wallaby
5	1	6.4	Wallaby	Wallaby/wombat

TABLE 3
Soils analyses for the island and the shore sites

	Cu ppm	Fe ppm	Mn ppm	Zn ppm	NH ₄ ppm	NO ₃ ppm	N %	P ppm	Ca ppm	ExtP ppm	ExtK ppm	C %	Cond. dS/M	pH CaCl ₂
Shore														
1	0	0	0	0	39	0.05	0.81	643	2945	3	265	17.8	0.08	5.6
2	2.34	241.2	753	6.4	37	0.05	0.87	771	1485	1	530	14.8	0.07	6.1
3	3	293	432	12	149	0.05	0.88	794	954	1	340	15.5	0.06	4.9
4	4.95	495	513	13.5	22	0.05	0.83	865	537	1	260	13.5	0.05	4.7
5	3.15	614	507	15.3	37	0.05	0.8	790	801	2	410	15.4	0.06	4.9
mean	2.69	328.6	441	9.44	56.8	0.05	0.84	772.6	1344.4	1.6	361	15.4	0.06	5.2
sd	1.79	237.7	274.5	6.23	52		0.04	80.8	959.3	0.9	112.7	1.56	0.01	0.6
Island														
1	0	0	0	0	116	0.05	0.97	690	3355	2	350	16.5	0.08	5.3
2	2.88	386.4	285.6	5.57	23	0.05	0.94	710	1154	2	430	14.6	0.09	6
3	3.6	348	597	11.7	31	0.05	0.86	835	1548	2	590	12.9	0.11	5.1
4	3.12	383.4	678.6	12.7	42	0.05	0.78	840	737	3	275	14.9	0.06	4.8
5	2.76	279	282	7.83	35	0.05	0.74	766	824	2	190	11.5	0.07	5.8
mean	2.47	279.4	368.6	7.56	49.4	0.05	0.86	768.2	1523.6	2.2	367	14.1	0.08	5.4
sd	1.42	162	273.1	5.12	37.9		0.1	69.2	1072.3	0.5	153.1	1.93	0.02	0.5

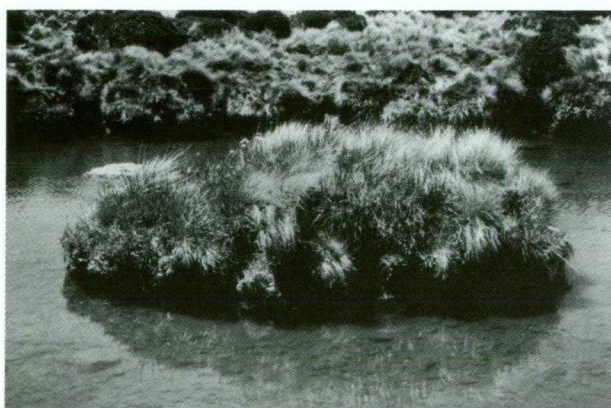


PLATE 1

An ungrazed island in the upper Ouse River system, dominated by *Craspedia paludicola* on the upstream end. Vegetation on the opposite shore shows *C. paludicola* on the undercut banks only.

upstream ends of islands and on the vertical banks of both the islands and the shore. However, on the shores the tall herbs are only found where the steepness of banks prevented grazing while on the islands they occurred throughout.

The dominant grass species *Hierochloa redolens*, which occurred on the downstream ends of the islands, was rare on the shore. Small herbs that were absent on the highly grazed shore were rare in the taller vegetation of the islands. Many of the species more common on the islands are reported to be palatable and/or not grazing resistant. The tall herb species on the islands are considered to be very palatable and relatively intolerant to grazing (Carr & Turner 1959a,b, Wimbush & Costin 1979a,b, Leigh *et al.* 1987, Wharen *et al.* 1994). The shrub *Bellendena montana* is also palatable to native herbivores. Of those species faithful to the shore (table 5), the following are grazing resistant; *Cotula alpina* (Gibson & Kirkpatrick 1989, Leigh *et al.* 1987), *Hydrocotyle sibthorpioides* (Gibson & Kirkpatrick 1989), *Hypericum japonicum* and *Viola betonicifolia* (Gibson & Kirkpatrick 1989, Leigh *et al.* 1987). *Astelia alpina* is palatable to native vertebrates when choice of food is limited (Whinam 1990). *Asperula gunnii* (Gibson & Kirkpatrick 1989, Leigh *et al.* 1987), *Epacris gunnii* (Gibson & Kirkpatrick 1989, Whinam 1990) and *Epacris serpyllifolia*

TABLE 4
Cover of species and lifeforms in the island/shore paired plots

	life	island 1	shore 1	island 2	shore 2	island 3	shore 3	island 4	shore 4	island 5	shore 5
<i>Astelia alpina</i>	gm				0.5		0.5				
<i>Carex gaudichaudiana</i>	gm			2.5	37.5	15	2.5	62.5	2.5	0.5	2.5
<i>Carpha alpina</i>	gm		0.5		0.5		37.5		15	2.5	15
<i>Empodisma minus</i>	gm	37.5	62.5								15
<i>Oreobolus distichus</i>	gm		0.5								
<i>Restio australis</i>	gm	2.5	15								
<i>Deschampsia caespitosa</i>	gr					2.5					
<i>Hierochloa redolens</i>	gr	2.5	0.5	37.5	0.5	0.5		0.5		62.5	2.5
<i>Poa costiniana</i>	gr	37.5	37.5	2.5	15	0.5	2.5		2.5	37.5	37.5
<i>Acaena montana</i>	hs		0.5								
<i>A. novae-zelandiae</i>	hs	0.5	0.5								
<i>Asperula gunnii</i>	hs		0.5				2.5				0.5
<i>Cotula alpina</i>	hs				0.5						
<i>Dichosciadium ranunculaceum</i>	hs	0.5	0.5		0.5						
<i>Diplaspis hydrocotyle</i>	hs	0.5	0.5		0.5	0.5	0.5	0.5	0.5		
<i>Hydrocotyle sibthorpioides</i>	hs		0.5								2.5
<i>Hypericum japonicum</i>	hs		0.5				0.5				
<i>Oreomyrrhis ciliata</i>	hs			2.5	0.5		0.5	2.5	0.5	2.5	2.5
<i>Ourisia integrifolia</i>	hs		0.5	0.5	0.5	0.5	0.5	0.5	2.5		
<i>Ranunculus</i> sp.	hs	0.5	0.5	38.5	3	65	62.5	15.5	63.5	3	3
<i>Viola betonicifolia</i>	hs										0.5
<i>V. cunninghamii</i>	hs			0.5	0.5	0.5	0.5	2.5	0.5	0.5	0.5
<i>Epilobium</i> sp.	h		0.5								
<i>Geranium potentilloides</i>	h	2.5	0.5								
<i>Plantago daltonii</i>	h	0.5	0.5	15	0.5	15	0.5	2.5	2.5	2.5	0.5
<i>Ranunculus lappaceus</i>	h					0.5	0.5				
<i>Chinogentias</i> sp.	tah			0.5							
<i>Craspedia coolaminica</i>	tah	0.5									
<i>C. paludicola</i>	tah	2.5	0.5	62.5	0.5	37.5		0.5		2.5	0.5
<i>Baeckea gunniana</i>	sh	2.5	2.5								
<i>Bellendenia montana</i>	sh	0.5									
<i>Coprosma</i> sp.	sh	0.5									
<i>Epacris gunnii</i>	sh		0.5								
<i>E. serpyllifolia</i>	sh		0.5								
<i>Olearia obcordata</i>	sh	2.5	0.5								
<i>Orites acicularis</i>	sh	15	15								
<i>Richea acerosa</i>	sh	2.5	15								
total graminoids	gm	40	78.5	2.5	38.5	15	40.5	62.5	17.5	3	32.5
total grasses	gr	40	38	40	15.5	3.5	2.5	0.5	2.5	100	40
total small herbs	hs	2	4.5	42	6	66.5	67.5	21.5	67.5	6	9.5
total medium herbs	h	3	1.5	15	0.5	15.5	1	2.5	2.5	2.5	0.5
total tall herbs	tah	3	0.5	63	0.5	37.5	0	0.5	0	2.5	0.5
total all herbs	h	8	6.5	120	7	119.5	68.5	24.5	70	11	10.5
total shrubs	sh	23.5	34	0	0	0	0	0	0	0	0
species richness/m ²		18/24	25/24	12/4	15/4	12/2.3	13/2.3	10/6	11/6	10/8	14/8

Life = lifeform group; gm = graminoid, gr = grass, hs = small herbs, h = medium stature herbs, tah = tall herbs, sh = shrubs.

Species names and lifeform groups in bold type have significantly different frequency distributions on the islands and the shores.

TABLE 5
Lifeforms of species occurring only on either the islands
or the adjacent shores

Species	Island	Shore
<i>Astelia alpina</i>		graminoid
<i>Oreobolus distichus</i>		graminoid
<i>Deschampsia caespitosa</i>	grass	
<i>Acaena montana</i>		small herb
<i>Asperula gunnii</i>		small herb
<i>Cotula alpina</i>		small herb
<i>Epilobium</i> sp.		small herb
<i>Hydrocotyle sibthorpioides</i>		small herb
<i>Hypericum japonicum</i>		small herb
<i>Viola betonicifolia</i>		small herb
<i>Ranunculus glabrifolius</i>	small herb	
<i>R. rivularis</i>	small herb	
<i>Chinogentias</i> sp.	tall herb	
<i>Craspedia coolaminica</i>	tall herb	
<i>Bellenden montana</i>	shrub	
<i>Coprosma</i> sp.	shrub (mat)	
<i>Epacris gunnii</i>		shrub
<i>E. serpyllifolia</i>		shrub

(Whinam 1990) are palatable species, though they can tolerate some grazing.

Grazing can affect the overall stature of communities and individual taxa. The difference in stature of herbs that we found between the islands and shores is likely to be related to grazing pressure. Wimbush & Costin (1979a, c) found densities of minor herbs to be less in grazing exclosures over time while tall herbs increased. The dominance of small herbs on the shore sites suggests that grazing is important in creating and maintaining habitat requirements (and higher species richness) where small herbs are not outcompeted by taller species (Wimbush & Costin 1979a). Small herbs existing on the islands had suitable habitat provided for them by disturbance from the river itself, such as bank erosion and occasional flood events. Where grazing is present on the islands, the cover of *Craspedia paludicola* is less than where grazing is absent (table 4, see data for islands 4 and 5).

Similar reports on community composition on ungrazed islands have been noted elsewhere on the Central Plateau. Colonel Legge, on visiting the now drowned Pine Island in Great Lake, recorded a plant community dominated by "... the tall Alpine Holy grass *Hierochloa redolens*, the *Craspedia richiei* whose tall stalk and downy, button-shaped flower towered above the dwarf *Poa* grass ..." (Legge 1902: 141). Other tall herbs such as "*Brachycome* sp.", "*Helichrysum bracteatum*" and "*Celmisia longifolia*" were also noted. Legge did not see any sign of vertebrate herbivores whilst he was on the island, and his companions only reported sightings of whip-snakes, echidnas and pipits.

Islands in the Ouse River system were grazed if they were in close proximity to the shore or to other islands. Where there were a series of islands linked together, scats were found on them all. While *Hierochloa redolens* was present on these grazed islands, *Craspedia paludicola* was noticeably absent or present only on the steep undercut banks (pl. 2).



PLATE 2

A lightly grazed island in the upper Ouse River system, showing *Craspedia paludicola* only on the undercut banks of the island and the shore.

These islands were generally larger or more protected than the islands with tall herbs, due to their proximity to other islands, and they appear to be physically more stable. The dominance of *C. paludicola* on the upstream ends of the surveyed islands and along the undercut banks suggests that it is able to withstand physical disturbance and may indeed require it, in order to gain dominance in a strongly competitive environment.

The dominance of tall alpine herbs in herb-rich grasslands on the mainland may be partly a result of some disturbance event(s) (Carr & Turner 1959a, McVean 1969, Costin *et al.* 1979). Tall herbs such as *Craspedia* spp. are capable of colonising bare ground (Wahren *et al.* 1994), and they are also opportunistic when gaps appear in the vegetation, such as during the senescence of *Poa* tussocks or shrubs (Carr & Turner 1959b, McVean 1969, Costin *et al.* 1979). Where exogenous disturbances (such as domestic stock grazing) have been removed, the most commonly recorded effect in the plant community is an increase in species richness and cover of tall alpine herbs (Carr & Turner 1959b, Wimbush & Costin 1979a,b,c, Wahren *et al.* 1994). Whether tall alpine herbfields persist in the long term appears to rely on occasional extreme climatic events, such as drought or extended snowlie, or exogenous disturbance, such as fire. In Tasmania, climatic events may not be so extreme, but endogenous disturbance in the form of grazing exists. While disturbance itself may be a necessary requirement for tall alpine herbs to dominate in grasslands, they need to be able to reproduce to do so!

Given the above reasoning, we accept our working hypothesis by concluding that an absence of marsupial grazing is necessary for tall herbs to have the opportunity to obtain dominance in Tasmanian alpine vegetation on fertile soils. However, we also conclude that this has to be combined with physical disturbance to ensure tall herb dominance.

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REFERENCES

- ADAMS, L.G., 1995: *Chionogentias* (Gentianaceae), a new generic name for the Australian "snow-gentians", and a revision of the Australian species. *Aust. Syst. Bot.* 8: 935–1011.
- BRETON, W.H., 1846: Excursion to the Western Range, Tasmania. *Tasm. J. Nat. Sci.* II: 121–141.
- BUCHANAN, A.M. (Ed.), 1995: *A CENSUS OF THE VASCULAR PLANTS OF TASMANIA*. *Tasm. Herb. Occ. Publ.* 5. Tasmanian Herbarium, Hobart.
- CARR, S.G.M. & TURNER, J.S., 1959a: The ecology of the Bogong High Plains. I. The environmental factors and the grassland communities. *Aust. J. Bot.* 7: 12–33.
- CARR, S.G.M. & TURNER, J.S., 1959b: The ecology of the Bogong High Plains. II. Fencing experiments in grassland C. *Aust. J. Bot.* 7: 34–63.
- CORBETT, E.B., 1996: *VEGETATION OF THE CENTRAL PLATEAU TASMANIAN WILDERNESS WORLD HERITAGE AREA*. *Wildl. Rep.* 95/3. Parks & Wildlife Service, Tasmania, Hobart.
- COSTIN, A.B., GRAY, M., TOTTERDELL, C.J. & WIMBUSH, D.J., 1979: *KOSCIUSKO ALPINE FLORA*. CSIRO/Collins, Sydney.
- CULLEN, P., 1995: *LAND DEGRADATION ON THE CENTRAL PLATEAU, TASMANIA: THE LEGACY OF 170 YEARS OF EXPLOITATION*. *Occ. Pap.* 34. Parks & Wildlife Service, Tasmania, Hobart.
- GIBSON, N. & KIRKPATRICK, J.B., 1989: Effects of the cessation of grazing on the grasslands and grassy woodlands of the Central Plateau, Tasmania. *Aust. J. Bot.* 37: 55–63.
- KIRKPATRICK, J.B., 1989: The comparative ecology of mainland Australian and Tasmanian alpine vegetation. In Good, R. (Ed.): *THE SCIENTIFIC SIGNIFICANCE OF THE AUSTRALIAN ALPS*. Australian Alps National Parks Liaison Committee. CPN Publications: Ch. 8.
- LEGGE, W.V., 1902: Contribution to the physiography of Tasmania. *Pap. Proc. R. Soc. Tasm.* 1902: 137–142.
- LEIGH, J.H. & HOLGATE, M.D., 1979: The responses of the understorey of forests and woodlands of the Southern Tablelands to grazing and burning. *Aust. J. Bot.* 4: 25–45.
- LEIGH, J.H., WIMBUSH, D.J., WOOD, D.H., HOLGATE, M.D., SLEE, A.V., STANGER, M.G. & FORRESTER, R.I., 1987: Effects of rabbit grazing and fire on a subalpine environment. I. Herbaceous and shrubby vegetation. *Aust. J. Bot.* 35: 433–464.
- LEIGH, J.H., WOOD, D.H., SLEE, A.V. & HOLGATE, M.D., 1991: The effects of burning and simulated grazing on productivity, forage quality, mortality and flowering of eight subalpine herbs in Kosciusko National Park. *Aust. J. Bot.* 39: 97–118.
- MCVEAN, D.N., 1969: Alpine vegetation of the central Snowy Mountains of New South Wales. *J. Ecol.* 57: 67–86.
- RAYMENT, G.E. & HIGGINSON, F.R., 1992: *AUSTRALIAN LABORATORY HANDBOOK OF SOIL AND WATER CHEMICAL METHODS*. Inkata Press, Melbourne.
- WAHREN, C.-H.A., PAPST, W.A. & WILLIAMS, R.J., 1994: Long term vegetation change in relation to cattle grazing in subalpine grassland and heathland on the Bogong High Plains: an analysis of vegetation records from 1945 to 1994. *Aust. J. Bot.* 42: 607–639.
- WHINAM, J., 1990: A study of the ecology of Tasmanian *Sphagnum* peatlands. Unpubl. PhD Thesis, Univ. Tasm., Hobart.
- WHINAM, J., CANNELL, E.J., KIRKPATRICK, J.B. & COMFORT, M., 1994: Studies on the potential impact of recreational horseriding on some alpine environments of the Central Plateau, Tasmania. *J. Environ. Man.* 40: 103–117.
- WILLIAMS, R.J. & ASHTON, D.H., 1987: The composition, structure and distribution of heathland and grassland communities in the subalpine tract of the Bogong High Plains, Victoria. *Aust. J. Ecol.* 12: 155–163.
- WIMBUSH, D.J. & COSTIN, A.B., 1979a: Trends in vegetation at Kosciusko. I. Grazing trials in the subalpine zone, 1957–1971. *Aust. J. Bot.* 27: 741–787.
- WIMBUSH, D.J. & COSTIN, A.B., 1979b: Trends in vegetation at Kosciusko. II. Subalpine range transects, 1959–1978. *Aust. J. Bot.* 27: 789–831.
- WIMBUSH, D.J. & COSTIN, A.B., 1979c: Trends in vegetation at Kosciusko. III. Alpine range transects, 1959–1978. *Aust. J. Bot.* 27: 833–871.

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