PATTERNS OF PLANT DIVERSITY AND THEIR MANAGEMENT ACROSS SOUTH AFRICAN RANGELANDS

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ABSTRACT

Forbs dominate southern Africa's rangeland plant diversity, but have been ignored in favour of grasses that are important for livestock production. To facilitate better conservation management I examined the interaction between patterns of diversity, forb recruitment and disturbance effects across the mesic to semi-arid rangelands east of the escarpment in southern Africa. Results were compared to a well studied North American tallgrass prairie, Konza.

Sampled between 1 m^2 and 1000 m^2 across 25 sites, species and family richness increased with mean annual precipitation up to —2000 m a.s.l., above which cooler temperatures accounted for a decline. Forb functional types ranged from persistent (long-lived, resprouters) in the fire-prone mesic rangelands to more recruiting (short-lived, reseeders) taxa in the drought-prone semi-arid areas. Mesic rangelands should therefore tolerate frequent, low intensity defoliation, and semi-arid floras be better suited to infrequent intense disturbances.

Seedling recruitment matched richness patterns, primarily increasing with precipitation. Recruitment was highest in the fire treatment at the three mesic sites, but proportionately higher in the animal digging and drought treatments at the three semi-arid sites. Seedling composition differed from the adult sward, suggesting that some species may not recolonise transformed lands.

Despite predictions of the Milchunas *et al.* (1988) and Olff and Ritchie (1998) grazing models, exclusion of large mammalian grazers from 40 m x 40 m plots did not appear to impact forb diversity. Instead, grazing effects sampled in 100 x 1m' quadrats per treatment, across ten sites, were overridden by the mesic to semi-arid gradient along which the sites were orientated. Species richness declined under heavy communal cattle grazing along fence-line contrasts at two mesic sites, with soft-leaved monocot forbs being replaced by short-lived divot weeds not found inside the adjacent lightly grazed nature reserves.

Marked differences in the diversity and disturbance responses of tallgrass prairie and southern African rangelands suggest that management strategies cannot be extrapolated from similar ecosystems around the world.

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1 Background

Southern Africa's rangelands represent a wealth of floral diversity, but the biology of most of their plant taxa remains poorly understood (Cowling at *at,* 1989). This is because rangeland research in the region has largely been driven by agriculture rather than conservation (Tainton, 1999). Consequently, most of the research has focussed on the few dominant grasses that are important for livestock production. This, at the expense of the wild flower or forb (petaloid herbaceous) taxa that (due to their generally low grazing potential and difficulty to identify when not flowering) have largely been ignored by agricultural research. Despite grasses usually dominating the biomass of rangelands, the floral richness of these ecosystems does not lie in this single family, but in the diversity of forb taxa (e.g. Freeman, 1998 [North America]; Bullock *et at.,* 2001 [United Kingdom]; Lunt and Morgan, 2002 [Australia]; Chapter 3). As the biology of these forbs remains largely unexplored, there is lithe information on the effectiveness of current management strategies applied to conserve the floral diversity of rangelands in southern Africa. This work seeks to help address this void and in so doing improve our ability to conserve these ecosystems.

1.1 Importance of the forb flora

Forbs constitute most of the floral richness of southern Africa's rangelands (Chapter 3) and support a range of ecosystem processes such as highly specialised faunal pollinator systems (Curry, 1994). In addition to their biological significance, southern Africa's rangeland forbs also have great cultural significance to the peoples of the region and potential benefits for all of humankind. A wide range of these forbs have long formed part of the diet and traditional medicines of peoples in the region (Fox and Norwood Young, 1982; Hutchings *et al.,* 1996; Arnold *et al.,* 2002). The importance of this plant use is attested to by the wealth of common names that exists for this flora (e.g. Pooley, 1998, 2003). Around 80 % of the population of South Africa still consult traditional healers and the demand for ethnopharmaceuticals is resulting in some taxa being collected so intensively that they have become locally extinct in the wild (Mander, 1998; Cunningham, 1990). Nevertheless, despite the incredible pharmaceutical potential of this flora, its medicinal value has only begun to be explored by science. Similarly, the African flora presents a lucrative market, the Cape Fynbos being worth R27 ($4.50) he year' on average to the horticultural trade (Turpie *et al,* 2003). The horticultural potential of the rangeland forbs is, however, only beginning to be explored. There is a wealth of rangeland taxa in families such as the Hyacinthaceae, Iridaceae and Scrophulariaceae with immense horticultural potential that has yet to be realised. Amongst the ecosystem services provided by rangeland floras, pollination services from rangelands (which are supported by their native floras) are estimated to come to R150 ($25) he year' (Costanza *et at,* 1997). Thus, this flora needs to be conserved, not only for its ecological significance, but also to maintain the cultural heritage of the region and potential benefits it holds for humankind.

1.2 Threats to biodiversity

The biodiversity of all of southern Africa's biomes is threatened by habitat loss, but the rangelands are of particular conservation concern (Driver *et at,* 2005). Southern Africa's rangelands are home to most of the region's agricultural, industrial and mineral resources, and consequently also its people (Rutherford and Westfall, 1994). Meeting the demands of this ever growing population is placing the biodiversity of these ecosystems under increasing threat of land transformation (predominantly by plantation forestry, maize farming and sugar cane farming) and ecosystem degradation (predominantly by medicinal plant collecting, alien plant invasions, overgrazing and altered fire regimes) [Scott-Shaw, 1999]. Around two-thirds of southern Africa's rangelands are already thought to be degraded (Scheepers and Kellner, 1995). However, less than three percent of the grassland biome is represented in conservation lands and some vegetation types, such as the Mistbelt Grasslands, are hardly represented at all (Rutherford and Westfall, 1994; Low and Rebelo, 1996). Worse still, we often do not know what species (besides the dominants) occur in many of our conservation areas, let alone how they respond to key disturbances (namely fire and grazing) and should therefore be managed. Consequently, biodiversity may not even be adequately protected in conservation lands.

1.3 Developing management strategies for conservation

Understanding forb dynamics is essential to conserving the floral diversity of rangelands. Rangeland biomass is generally dominated by several grass taxa, while the richness of these ecosystems is spread across a range of forbs. Consequently, disturbances that reduce the dominance of the grass sward are believed to favour the forbs and thus promote species richness. Frequent fires in the North American tallgrass prairies were found to encourage grass production and result in a decline in the richness of forbs (Hartnett *et at,* 1996). If the increased grass production in annually burnt prairies was controlled by the selective grazing of bison *(Bison bison),* forb species richness was found to increase (Hartnett *et at,* 1996). Thus, disturbances that reduced the dominance of the grass sward were seen to encourage greater floral diversity.

Disturbance effects recorded in the prairie do not, however, extrapolate to all rangelands around the world. For example, forb species richness does not appear to respond as strongly to fire regimes in Australian and southern African C_4 rangelands as in the North American tallgrass prairie (Hartnett *et al ,* 1996; Lunt and Morgan, 2002; Uys *et at,* 2004). Instead, the majority of southern Africa's rangeland forbs appear to tolerate a range of frequent fire regimes five year fire intervals) and their composition is determined more strongly by environmental gradients than fire treatments (Uys at *at.,* 2004). These forts probably do not respond to the fire regime as they have the ability to resprout from underground organs that do not get damaged by fire. These underground organs also appear to allow forbs to survive several years of shading under a moribund grass sward (Uys *et* at, 2004). Resprouting is a commonly observed trait in fire-prone floras around the world, including forbs in the Australian rangelands (Pate and Dixon, 1981). Yet, despite the apparent importance of this trait to rangeland forb dynamics in southern Africa, until recently, the only suggestion that these forbs may be able to resprout came from the casual observations of some of the region's early botanists (Bews, 1925; West, 1951; Bayer, 1955; Hilliard and Burt, 1987). Although fire effects and their relation to plant functional traits have received some attention in southern African rangelands, the effects of other forms of disturbance remain to be explored and may not relate to the same traits. Developing an understanding of the effects of disturbance regimes to meet conservation needs is thus going to require considerable further study of the plant traits of the region.

To further complicate matters, disturbance effects may not only differ between rangelands on different continents, but also within continents. Pastoralists in southern Africa have long distinguished between the grazing potential and ecological responses of mesic and semi-arid rangelands in the region *(i.e.* sourveld and sweetveld) [Ellery et *al.,* 1995; Tainton, 19991 Similar studies, however, have yet to be conducted for the disturbance responses of the forbs. It is therefore important that we not only understand the effects that various disturbances have on forb diversity, but also how these effects differ across regions. Relating plant traits to disturbance tolerance and noting how these traits change across environmental gradients will indicate the extent to which disturbance effects may be extrapolated across a region. We nevertheless also need to examine how disturbance responses differ between continents and why this might be so. This is necessary, not only to satisfy our curiosity, but also for us to understand whether and why our own ecosystems should be managed differently.

1.4 Counting the cost of mismanagement

In addition to understanding how rangelands should be managed, we need to understand the consequences of mismanaging these ecosystems. Rangeland forbs evolved under a particular suite of disturbance regimes, but these have changed dramatically with the rapid human population expansion in southern Africa's rangelands, particularly over the last 150 years. While there is lithe record of the natural disturbance regimes, fire and grazing are believed to have been radically intensified and altered through peoples' actions. Fire is thought to have become more frequent and is applied across all seasons, while grazing has intensified and has shifted from native herbivores to occur mostly by domesticated livestock (Bond, 1997).

In addition to altering natural disturbance regimes, people have introduced new forms of disturbance to which forbs are most likely unaccustomed. Many of the mesic rangeland forbs resprout from underground organs, suggesting that this flora has adapted to aboveground disturbances (Chapter 4). Southern Africa's rangelands are, however, being increasingly cultivated, exposing forbs to levels of soil disturbance not previously experienced. Similarly, underground organs appear to allow these forbs to tolerate short periods of shading by grass swards. Plantation forestry is, however, resulting in these forbs being shaded for much longer periods than they appear to be able to tolerate. The cultivation of these rangelands therefore poses potential unexplored threats to their diversity that need to be understood.

1.5 Way forward

To address the conservation concerns facing southern Africa's rangelands, the biodiversity of these ecosystems needs to be adequately represented and managed. Various efforts are currently underway to map the vegetation units, and extent of land transformation and ecosystem degradation of the rangelands (e.g. Mucina and Rutherford, In Press; National Landcover Database of the Department of Agriculture). This will allow GAP analyses to set conservation targets for each vegetation unit and to identify priority areas that need to be included in the conservation network. A better understanding of the dynamics of these ecosystems is nevertheless required in conjunction with meeting conservation targets to ensure that conservation areas do not exist only in name.

Fire and grazing are the two most important disturbances that managers are able to influence to maintain rangeland biodiversity. As these disturbances present few opportunities to be examined through natural experiments, much of our understanding of their effects has come from plot trials (Collins, 1987; Lunt and Morgan, 1990; Ash and McIvor, 1998; Bullock *et at,* 2001; Fynn *et al.,* 2004; Uys *et al,* 2004). Plot trials, however, are costly to establish and maintain and are therefore seldom replicated across environmental gradients. Consequently, there is little evidence to suggest how widely results from such isolated studies may be extrapolated. Environmental gradients are widely seen to influence patterns of diversity at both micro and macro scales (Cowling *et at,* 1997). Thus, for the results of disturbance trials to be placed into context, we need to understand how environmental gradients are influencing patterns of species richness. Likewise, if plant functional traits can be linked to disturbance responses, the distribution of these traits across environmental gradients may suggest how widely results from disturbance studies may be extrapolated. Forb recruitment also needs to be examined across environmental gradients to understand how disturbance regimes mediate forb coexistence with the dominant grass sward under different environmental conditions. This is not only important for the maintenance of these ecosystems, but also so that we can begin to develop a better understanding of how to revegetate disturbed areas.

As most of southern Africa's rangelands exist outside of conservation areas, it is important that we understand the impact that alternative types of land-use to formal conservation are having on biodiversity. While the impact of increased burning regimes on rangeland fort diversity has received some attention (Fynn *et al.,* 2004; Uys et *at,* 2004), the effects of increased grazing pressure remain largely unexplored. Considerable areas are being grazed with domesticated livestock under communal tenure at stocking rates approaching double those of commercial farms (Vetter, 2005). The palatable grass species composition is often observed to be negatively impacted in these communal lands, but the effect of this intense stocking on biodiversity remains to be examined. Similarly, southern Africa's rangelands are increasingly falling under plantation forestry, but its effects on plant diversity remain to be quantified. While ploughed lands are easily recognised as being transformed, the impact of forestry can be more subtle. In some instances, virgin land is "ripped" for planting, but in others trees are planted directly into holes without further disturbance to the surrounding rangeland giving the impression of minimal impact, especially if the trees are removed after a single rotation. The impact that shading by the closed tree canopy has on this forb flora, along with the changes in soil chemistry mediated by some of the species being planted (du Toit, 1993; Nowicki, 1997) and disturbance involved in extracting the timber need to be understood for this potential threat to be placed into context.

1.6 Scope of this study

Given how little work has been done beyond developing the taxonomy of the plant diversity of southern Africa's rangelands, I chose to work at the regional scale in an attempt to uncover broad patterns across these ecosystems. However, given the extent of these ecosystems across the region I limited my studies to the rangelands east of the escarpment (see Chapter 2 for rationale). I examined alpha diversity at the plant species, family (Chapter 3) and functional type levels (Chapter 4) across broad attitudinal and mean annual precipitation (MAP) gradients. Based on the patterns observed, I attempted a cross-continental comparison, predicting the richness and composition for a North American tallgrass prairie, Konza (Chapter 8). Across these environmental gradients I also initiated six recruitment trials to examine the effects of animal diggings, drought and fire (grazing being impractical to replicate) on the richness and composition of forb seedling emergence (Chapter 5).

Having previously examined the effects of different fire regimes across these rangelands (Uys, 2000; Uys *et al.,* 2004), I expanded my studies to examine grazing effects. I tested the predictions of the Milchunas et al. (1988) and Olff and Ritchie (1998) grazing models using a native herbivore exclusion trial (Chapter 6). This trial, consisting of ten sites across mesic to semi-arid savannas in Hluhluwe-Imfolozi Park, was designed to compare the impacts of moderate grazing by an intact native herbivore assemblage to the exclusion of large mammals. To examine the impacts of intense grazing in mesic rangelands, I examined two fence-line contrasts between lightly grazed conservation areas and adjacent communal lands intensively stocked with cattle (Chapter 7).

2 Study area

The work reported on was conducted across a range of sites, with some sites used for various studies. To avoid repetition, I describe the environmental context of my study area and the characteristics of each study site here and refer back to these descriptions in subsequent chapters.

2.1 Extent of study area

Southern Africa's rangelands are mostly represented by treeless grasslands, but include open-canopy treed savannas, where the tree canopy forms less than 25 % of the aerial cover (White, 1983; Rutherford and Westfall, 1986; Acocks, 1988; Tainton, and Walker, 1993; Low and Rebelo, 1996; O'Connor and Bredenkamp, 1997; Mucina and Rutherford, In Press). In southern Africa, grasslands and their adjacent savannas often appear to have very similar herbaceous layers dominated by the same grass taxa (Tainton, 1999). Furthermore, the floral composition of these two biomes is the most similar of the seven biomes in the region (Rutherford and Westfall, 1986; Gibbs Russell, 1987). The evolution of these grass-dominated ecosystems and the determinants of their current distribution is not dealt with here, but may be explored in reviews by Rutherford and Westfall (1986), O'Connor and Bredenkamp (1997), Scott (2002) and Bond *et al.* (2003). To investigate the rangeland dynamics in the region, I therefore included the herbaceous understoreys of open canopy savannas in my studies.

Unable to survey all the rangelands of southern Africa, I focussed my research on the grasslands and savannas of the distinct biological region east of the escarpment in South Africa. Southern Africa's rangelands are broadly divided into eastern and western biological regions around 27° longitude, based on their dominant grass subfamilies (Vogel *et at,* 1978; Gibbs Russell et *at,* 1990). The aspartate forming (NAD-ME and PCK photosynthetic types) Chloridoid grasses are concentrated in the relatively arid west, while the malate forming (NADP-ME photosynthetic type? Panicoid grasses predominate in the more mesic east (Vogel et *at,* 1978; Gibbs Russell *et at,* 1990). The dominant grasses of these biological regions not only represent different taxonomic groups and photosynthetic pathways, but also different disturbance responses. "Sweetveld" rangelands in the more arid west remain palatable year round, but cannot tolerate intense fire or grazing regimes, while the "sourveld" rangelands of the more mesic east lose their palatability over winter, but can tolerate and are most productive under more intensive fire and grazing regimes (Tainton, 1999). My choice to focus on the rangelands east of the escarpment was prompted by the extent to which these rangelands are threatened. This region also provided suitable conditions for me to test my hypotheses, as it covered strong rainfall and attitudinal gradients over a short distance. I located most of my study sites in conservation areas as these usually had documented land-use histories and generally had not been transformed or degraded (Chapter 2.5).

I focussed my sampling on KwaZulu-Natal (South Africa), as the province provided an ideal combination of broad environmental gradients, a range of vegetation types, and was well represented by easily accessible conservation areas (Chapter 2.5.7 - 2.5.20 and 2.5.22). The flora of KwaZulu-Natal has also been well explored by taxonomists and consequently has a wealth of herbaria collections and field guides to assist with species identification (e.g. Trauseld, 1969; Ross, 1972; Gibson, 1975 and 1978; Gurm and Codd, 1981; Hilliard and Burt 1987; Killick, 1990; Walker, 1996; Pooley, 1998, 2003). What KwaZulu-Natal lacked, however, was particularly dry rangelands, the driest I sampled being in the far north at Ndumo Game Reserve that received - 520 mm mean annual precipitation (MAP) [Figure 2.1; Table 2.1; Chapter 2.5.7].

I sampled in the Kruger National Park to include rangelands east of the escarpment that received < 500 mm MAP (Figure 2.1; Table 2.1). This extensive tract of conservation land (1948 km') extends between the Mpumalanga and Limpopo Provinces in South Africa along the country's border with Mozambique (Grant and Hendry, 2000). Prior to the anti-nagana or tse-tse fly insecticide spraying campaign, begun in the 1940's, the region was largely uninhabitable by people due to the prevalence of trypanosomiasis (sleeping sickness). Excessive game hunting, however, prompted the proclamation of two reserves, the Sabi Game Reserve (1898) and Shingwedzi Game Reserve (1903), that were later combined (1926) to form the park. Due to the size of the park, it not only covered a broad rainfall gradient, but also provided several distinct vegetation types on different substrates (Grant and Hendry, 2000) [Chapters 2.5.1 - 2.5.6).

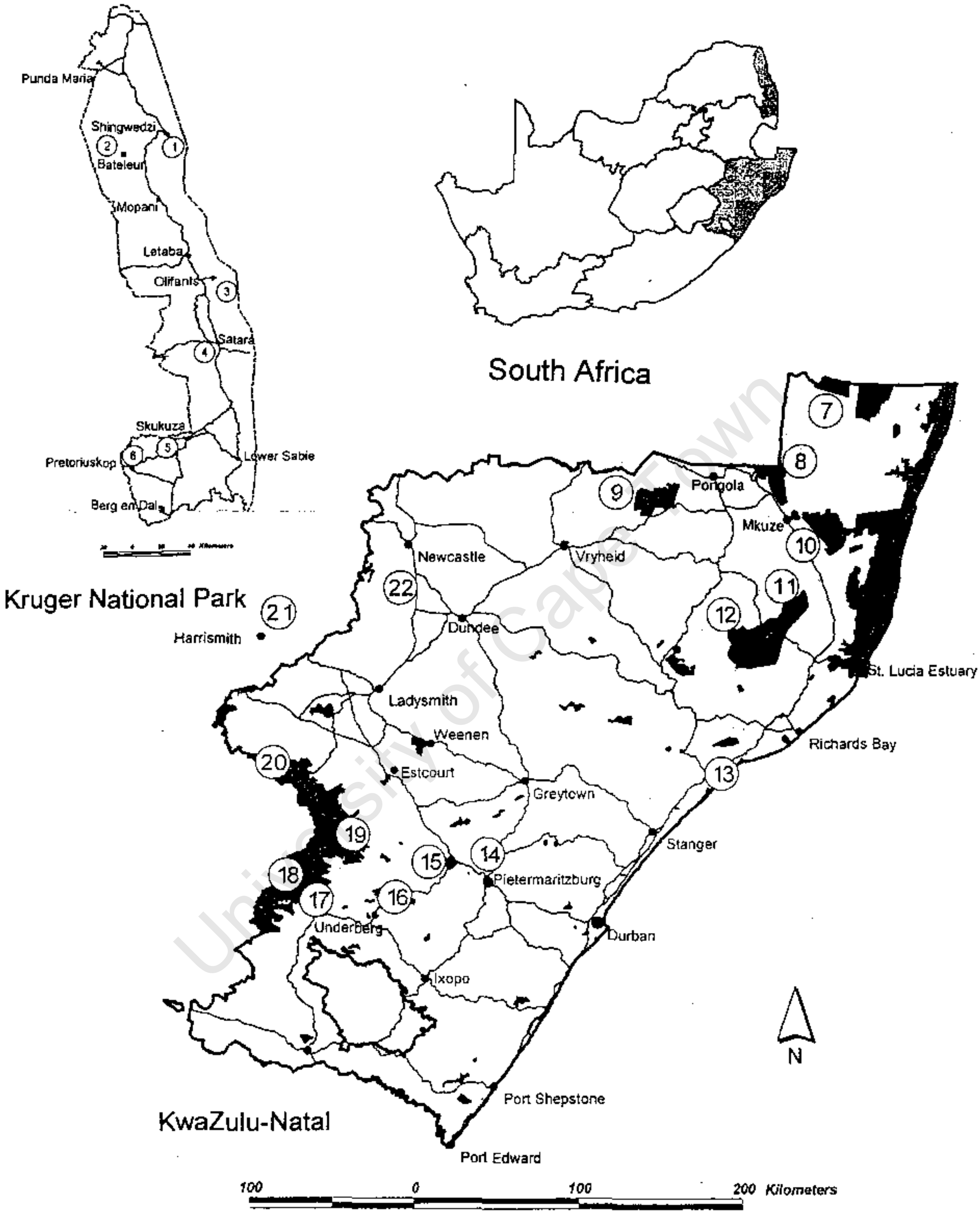


Figure 2.1 Distribution of study sites across the Kruger National Park and KwaZulu-Natal Province, with a map showing their location in South Africa. See Table 2.1 on the next page for a key to study sites.

Table 2.1 Key to the map of the study sites (Figure 2.1), including the local vegetation type, mean annual precipitation (MAP) [mm yr^{1}], and altitude (Alt.) [m a.s.l.] of each site.

#	Site	Acock's (1988) Veld Type		Low and Rebelo (1996) Vegetation Type		MAP	Alt.
1	Shingwedzi	15	Mopani Veld	9	Mopane Shrubveld	460	280
2	Bateleur	15	Mopani Veld	10	Mopane Bushveld	440	340
3	Olifants	11	Arid Lowveld	20	Sweet Lowveld Bushveld	465	250
4	Satara	11	Arid Lowveld	20	Sweet Lowveld Bushveld	490	290
5	Skukuza	10	Lowveld	19	Mixed Lowveld Bushveld	550	460
6	Pretoriuskop	10	Lowveld	21	Sour Lowveld Bushveld	690	570
7	Ndumo	10	Lowveld	26	Natal Lowveld Bushveld	520	90
8	Pongolapoort	10	Lowveld	20	Sweet Lowveld Bushveld	650	150
9	Ithala (savanna)	10	Lowveld	26	Natal Lowveld Bushveld	790	720
9	Ithala (tall grass)	64	Northern Tall Grassveld	26	Natal Lowveld Bushveld	790	850
9	Ithala (short grass)	8	North-Eastern Mountain Sourveld	43	North-Eastern Mountain Grassland	820	1400
10	Mkuze (clay)	10	Lowveld	26	Natal Lowveld Bushveld	665	120
10	Mkuze (sand)	10	Lowveld	26	Natal Lowveld Bushveld	670	120
11	Hluhluwe	10	Lowveld	26	Natal Lowveld Bushveld /	770	245
12	Imfolozi	10	Lowveld	25	/ Natal Central Bushveld	680	230
13	Amatigulu	1a	Typical Coast-belt Forest	23	Coastal Bushveld-Grassland	1170	20
14	QE Park	45	Natal Mist Belt 'Ngongoni Veld	47	Short Mistbelt Grassland	1070	950
15	Midmar Dam	65	Southern Tall Grassveld	25	Natal Central Bushveld	875	1100
16	Impendle	44	Highland Sourveld	42	Moist Upland Grassland	1100	1400
17	Cobham	44	Highland Sourveld	42	Moist Upland Grassland	1000	1780
18	Sani Pass	58	*Themeda-Festuca* Alpine Veld	46	Alti Mountain Grassland	1600	2500
19	Highmoor	44	Highland Sourveld	42	Moist Upland Grassland	1150	1960
20	Cathedral Peak	44	Highland Sourveld	42	Moist Upland Grassland	1380	1830
21	Moolhoek	56	Highland Sourveld to *Cymbopogon* -*Themeda* Veld Transition	40	Moist Cold Highveld Grassland	700	1780
22	Chelmsford Dam	66	Natal Sour Sandveld	25	Natal Central Bushveld	1000	1270

2.2 Climate

The study area receives most of its rainfall in summer (October to April), and is characterised by regularly recurring drought (Tyson and Dyer, 1978). Mean annual precipitation (MAP) is generally low in the north (400 - 600 mm yr-1), increasing southwards, exceeding 1000 mm yr' along the north coast, the escarpment and on isolated patches of high lying ground in the KwaZulu-Natal midlands (Schulze, 1997). The converse is true for the coefficient of variation in annual rainfall which is highest in the north (25 - 35 %), decreasing into KwaZulu-Natal, with the lowest variation (< 20 %) recorded along the north coast, the escarpment and on high lying ground in the midlands of KwaZulu-Natal (Schulze, 1997). Rainfall variability therefore increases as *mean* annual precipitation decreased across the region, reflecting a worldwide trend (Trewartha, 1968).

Temperatures east of the escarpment generally decreases from north to south and decrease with increasing altitude from east to west. Mean annual temperature is highest in the north (> 22 °C) and along the coast (20 - 22 °C), decreasing towards the escarpment (8 - 10 °C) [Schulze, 1997]. Summer (December to February) mean daily maximum temperatures range from - 30 °C in the north to 24 °C in the KwaZulu-Natal midlands and the minima from > 20 °C to - 10 °C, respectively. In winter (June to August) the mean daily maximum temperatures range from > 24 °C in the north to - 16 °C in the south and the minima from > 10 °C on the coast to - 0 °C towards the escarpment (Schulze, 1997). The warmer temperatures along the coast are ascribed to the warm Mozambique Current which is also responsible for the high rainfall and frost free conditions along the eastern seaboard (Schulze, 1997). The incidence of frost generally increases with altitude, but most of area east of the escarpment receives on average < 30 days of heavy frost per year. Snow was rare and largely confined to the highest peaks along the escarpment mostly in mid winter (Schulze, 1997).

2.3 Physical features

East to west, across the centre of southern Africa (South Africa, Lesotho and Swaziland), the land rises abruptly from the coast to the eastern escarpment (- 3000 m a.s.l.) and declines gradually to the west coast. Relief east of the escarpment ranges from undulating plains in the Kruger National Park in the north, to hilly and mountainous terrain in the province of KwaZulu-Natal in the south (Figure 2.1). The Kruger National Park is broadly divided into nutrient rich basalt derived substrates in the east and nutrient poor granite derived substrates in the west (Grant and Hendry, 2000). The geology of KwaZulu-Natal is broadly represented by a monocline of igneous basalt forming the high mountains (above - 1800 m a.s.l.) down through increasingly finer grained bands of sand- to mudstone deposits of the Karoo System (including, in descending order, the Stormberg, Beaufort, Ecca and Dwyka Series). Below these lie the sandstones of the Table Mountain Series that overly the Basement layer of granites, gneisses and quartzites. Dolerite dykes are heavily interspersed across the Beaufort and Ecca Series, and are also found in the Table Mountain Sandstones and even in the Basement granite-gneiss. In northeastern KwaZulu-Natal this sequence is interrupted by the presence of volcanic extrusions that produce the Rhyolite-based Lebombo Mountain range (King, 1982; McCarthy and Rubidge, 2005). Soils across the study area represent this diversity of underlying substrata, mediated strongly by the distinct rainfall gradient across the region. Soils range from igneous based, nutrient rich, clayey soils (derived mostly from the basalts and dolerites), through soils derived from the finer grained sedimentary layers, to coarse grained sands with low nutrient contents and water retention ability (O'Connor and Bredenkamp, 1997; Tainton, 1999). The geology and soils represented at each of the study sites are highlighted below.

2.4 Vegetation

Vegetation types across my study area ranged from broad-leaved savannas in the north, through fine-leaved savannas, to treeless grasslands in the south (Figure 2.1; Table 2.1; Chapter 2.5) [Mucina and Rutherford, In Press]. Structurally, the herbaceous layer of these rangelands is similar to the C_4 grasslands of Australia, the prairies of North America, pampas of South America, and steppe grasslands of south-east Asia (Archibold, 1995). Like all of these regions, the biomass of southern Africa's rangelands is dominated by tufted C_4 grass taxa, while the floral richness of these ecosystems lies in their forbs *(e.g.* Freeman, 1998 [North America]; Bullock et *al,* 2001 [United Kingdom]; Lunt and Morgan, 2002 [Australia]; Chapter 3). Southern Africa's rangelands, however, differ from those in other temperate areas in that C_3 grasses (represented by the subfamily Pooideae in southern Africa) are particularly rare in the grassland biome and only come to dominate at high attitudes (> 1800 m a.s.l.) in the Maloti-Drakensberg Mountains that form the eastern escarpment between Lesotho and South Africa (Vogel et *at,* 1978; Hilliard and Burt, 1987; Killick, 1990; Gibbs Russell *et al.,* 1990).

To the north of my study area the savanna was characterised by Mopane trees *(Colophospermum* mopane), shifting to fine-leaved Acacia savanna from south of the Olifants River through into northern KwaZulu-Natal. Sward height and basal cover of these savannas generally increased with rainfall from medium height (- 0.5 m) swards with poor basal cover in the north to tall (> 1 m) swards further south into northern KwaZulu-Natal. Medium (- 0.5 m) to tall (> 1 m) rangelands dominated along the coast into the KwaZulu-Natal midlands. West towards the escarpment, sward height decreased, while basal cover increased with increasing altitude and rainfall. Forest patches (many only - 1 ha in extent) are interspersed with the rangelands across KwaZulu-Natal from the coast up to - 2000 m a.s.l., predominating in the areas of highest rainfall (Mucina and Rutherford, In Press).

The accumulation of herbaceous biomass across these rangelands is predominantly determined by rainfall, but is also influenced by the sward species composition, length of the growing season, site conditions and previous management (Tainton and Walker, 1993; O'Connor and Bredenkamp, 1997). Production ranges from - 500 Kg ha' per year in the drier parts to > 4000 Kg ha' per year in the mesic rangelands of KwaZulu-Natal (Rutherford, 1978; Tainton and Walker, 1993; O'Connor and Bredenkamp, 1997). Consequently, moribund swards develop within three years of fire protection in the coastal belt, midlands and northern KwaZulu-Natal. In the cooler KwaZulu-Natal uplands and drier northern savannas, however, it takes up to five years for the sward to become moribund. The accumulation of moribund, or dead, leaf litter is responsible for shading the basal meristems of the bunch-grasses. Such shading prevents new leaf growth through basal tillering in bunch-grasses (Everson *et al.,* 1988). As bunch-grasses dominate the biomass and represent most of the species palatable to livestock in these rangelands, the presence of moribund material is actively reduced to maintain grass production. This is achieved through frequent burning (with biennial spring burning widely recommended) or intense livestock utilization to prevent the accumulation of moribund material and so maintain grass production (Tainton, 1999).

2.5 Site descriptions

Numbering of the site descriptions in this chapter is consistent with the numbering in the site distribution map (Figure 2.1; Table 2.1). The taxonomic and forb functional type richness of each of the sites described was sampled using two Whittaker Plots (20 m x 50 m quadrats) [Chapters 3 and 4]. As a result of these two plots being located as widely apart as possible (while remaining within the same environmental context), grid references, mean annual precipitation (MAP), and altitude readings reflect the average values for each site. Forb recruitment trials were conducted at Pongolapoort (Chapter 2.5.8), Mkuze (Chapter 2.5.10), Hluhluwe (Chapter 2.5.11), Imfolozi (Chapter 2.5.12), Midmar Dam (Chapter 2.5.15) and Highmoor (Chapter 2.5.19) [Chapter 5]. The effects of excluding various natural grazers on forb taxonomic and functional type richness were examined at Hluhluwe (Chapter 2.5.11) and Imfolozi (Chapter 2.5.12) [Chapter 6]. The effects of cattle overgrazing in mesic rangelands was explored using fence-line contrasts at Ithala (Chapter 2.5.9) and Impendle (Chapter 2.5.16) [Chapter 7].

2.5.1 Shingwedzi

The two Shingwedzi quadrats (460 mm MAP; 280 m a.s.l.) were located south of Shingwedzi Camp in the north of the Kruger National Park (KNP) [23° 07'S, 31° 27'E]. One quadrat was sampled along the S134 road and the other along the extension to Mashagadzi watering point off the S134. The vegetation in this region is locally described as Mopane Shrubveld, dominated by stunted, multi-stemmed, shrubby Mopane (*Colophospermum* mopane) trees on a nutrient rich basalt derived substrate (Grant and Hendry, 2000). The grass layer was dominated by *Eragrostis* spp. and annual grasses such as *Aristide congesta* subsp. *barbicollis* and *Eneapogon cenchroides,* with few abundant forbs.

2.5.2 Bateleur

The two Bateleur quadrats (440 mm MAP; 340 m a.s.l.) were sampled along the road to Rooibosrant Dam which is located south of Bateleur Camp in the north of the KNP (23° 14'S, 31° 13'E). At approximately the same latitude and MAP as my Shingwedzi sites (460 mm MAP; 280 m a.s.l.), these sites differed by being located on a nutrient poor granite derived substrate. Here the vegetation is locally described as Mopane / Bushwillow (*Combretum* spp.) woodlands, dominated by taller, yet sparser Mopane trees than on the basalts, with a less dense sward (Grant and Hendry, 2000). Shingwedzi and Bateleur represented my northernmost and lowest MAP sites, as well as being the only sites I sampled in broad-leaved savanna.

2.5.3 Olifants

The Olifants quadrats (465 mm MAP; 250 m a.s.l.) were located south of the Olifants River - 5 km apart along the S90 (Old Main Road) southeast of its junction with the S89, roughly in the centre of the KNP (24° 05'S, 31° 46'E). These two quadrats represented my northernmost and driest samples in fine-leaved savanna, the Mopane having its southernmost distribution ending north of the Olifants River. Located on the nutrient rich basalts, the vegetation in this region is locally classified as Stunted Knob-thorn *(Acacia nigrescens)* Savanna (Grant and Hendry, 2000). The two quadrats I sampled in this vegetation type were sparsely wooded, with an open sward dominated by *Eragrostis* spp. and *Aristide congesta* subsp. *barbicollis.* Although I sampled all my KNP sites in January, which should have been the peak of the rainy season (Schulze, 1997), the spring rains at the end of 2002 appeared to have been unseasonally late. As a result, some species may not have emerged from their winter dormancy and my sampling may have under estimated the richness of these sites.

2.5.4 Satan

The two Satara quadrats (490 mm MAP; 290 m a.s.I.) were sampled on the basalt derived soils in the Satara string of the Satara experimental burn plots. The experimental burn trial in KNP was initiated in 1954 to provide information on the effects that fire has on the flora and fauna in the park. The trial was initiated at four sites, each with four strings (rows of plots) of 12 or 14 fire treatments (Biggs *et al.,* 2003). The Satara string of plots was located immediately west of Satara Camp along the H7 Road, approximately a third of the way up the KNP (24° 24'S, 31° 46'E). One quadrat was located in an annual winter (August) burn (plot # 7) and the other in a triennial spring (October) burn (plot # 10). Although this site did not have the lowest MAP, it appeared to have received the least amount of rain at the time of sampling. This may, in part, account for the incredibly low species richness (— 16.5 taxa per 1000 m^2). Locally classified as Knob-thom / Marula Savanna (Grant and Hendry, 2000), the plots themselves were almost treeless, dominated by large, sparse tufts of *Themeda triandra,* with large (up to 0.5 m) inter-tuft distances.

2.5.5 Skukuza

The two Skukuza quadrats (550 mm MAP; 460 m a.s.I.) were sampled in the Napi string of the Skukuza experimental burn plots. These are located on the granite derived soils, southwest of Skukuza Camp along the Napi Road (HI-1), in the south of the KNP (25° 05'S, 31° 26'E). One quadrat was located in an annual winter (August) burn (plot # 3) and the other in a triennial spring (October) burn (plot # 11). Locally classified as Sabie / Crocodile Thorn Tickets (Grant and Hendry, 2000), the woody vegetation was dominated by a mix of: *Acacia* spp., *Combretum apiculatum,* *Dichrostachys cinema, Lannea discolor,* Pterocarpus *rotundifolius, Sclerocarya birrea* and *Terminalia sericea.* The woody canopy was very open in the plots sampled, with a good covering of grasses in the triennial burn, characterised by *Themeda biandra* and *Panicum maximum,* and a less dense sward including *Aristida congesta* subsp. *barbicollis, Eragrostis superba, Perotis patens* and *Pogonarthria* in the annual burn.

2.5.6 Pretoriuskop

The two Pretoriuskop quadrats (690 mm MAP; 570 m a.s.l.) were sampled in the Shambeni string of the Pretoriuskop experimental burn plots located north of Pretoriuskop Camp on the east side of the S7 Road where it joins the Albasini Road (S1), in the south of the KNP (25°06'S, 31°14'E). One quadrat was located in an annual winter (August) burn (plot # 3) and the other in a triennial autumn (April) bum (plot # 9). Locally classified as Pretoriuskop Sourveld (Grant and Hendry, 2000), this area of granite derived soils is dominated by Silver Cluster-leaf *(Terminalia sericea)* with a tall (- 1 m) *Themeda triandra Panicum maximum* dominated grass layer. This site had the highest MAP (690 mm yr) of the areas I sampled in the KNP and also the richest herbaceous flora (- 60 taxa per 1000 m^2).

2.5.7 Ndumo

Ndumo Game Reserve (101 km^2; 520mm MAP; 90m a.s.l.) is situated between the town of Ndumo and the Mozambican Boarder (Usuthu River / Rio Maputo) in northeastern KwaZulu-Natal (KZN) [26°53'S, 32°15'E]. Proclaimed in 1924 as a refuge for Hippo *(Hippopotamus amphibius),* the reserve continued to be utilized for subsistence goat and cattle grazing until 1959 (De Moor *et al.,* 1977; Pooley, 1978). The reserve is located on the Cretaceous sediments of the broad Zululand coastal plain, the undulating terrain encompassing both wet and dryland communities. Vegetation ranges from reed beds and forests on the flood plains and perennial pans to dense thorny scrub, broad-leaved woodland and fine-leaved *Acacia* savanna on the higher ground (De Moor et at, 1977; Pooley, 1978). I sampled two quadrats, - 2 km apart, in the southwest of the reserve along the

Phaphukulu Road, east of the Mapondo viewing site. Here the woody canopy opens into a - 6 m tall *Acacia nigrescens* savanna on deep red sandy clay soils (Hutton form, Makatini soil series). The sward is dominated by a closed grass canopy of tall (- 1 m) *Themeda triandra* and *Panicum maximum,* characterised by large inter-tuft distances (De Moor *et al.,* 1977: Vegetation type 9 B). Most notable amongst the forbs were the bright red flowers of *Crossandra zuluensis.*

2.5.8 Pongolapoort

Pongolapoort Nature Reserve (117 km^2; 650 mm MAP; 150 m a.s.l.) is located in northeastern KZN, east and south of the town of Golela, with the Swaziland border as its northern boundary and the Pongolapoort Dam as its eastern boundary (27° 19'S, 31^{2}25E). The reserve is situated on the undulating flats immediately west of the Lebombo Mt. Range on rhyolite derived red clayey soils. Here the vegetation forms a tall (- 6 m) *Acacia nigrescens* savanna with a tall (- 1 m) sward dominated by *Themeda triandra* and *Panicum maximum.* Like at Ndumo, the sward had a closed canopy, but with large basal inter-tuft distances. I sampled one plot along the Swaziland Boarder fence road - 300 m from the north-western corner of the reserve and a second roughly half way along the road below the railway line. I also located my forb recruitment trial at this second site, - 30 m in from the road (Chapter 5).

2.5.9 Ithala (savanna, tall grass and short grass)

Ithala Game Reserve (297 km^2) is located north of the town of Louwsburg in the hilly terrain of central-northern KZN (27° 25'-27° 36'S, 31° 10'-31° 25'E). Initially farmed communally, and later commercially, the area now comprising the reserve was acquired between 1972 and 1982 (Bond and Loffell, 2001). Prior to conservation, the area was intensively grazed by cattle, goats and sheep, and much of the arable bottom lands were turned for cultivation. Due to this, I restricted my sampling to the shallow black clayey soils on the shale ridges in the west of the reserve that appear to have escaped transformation. Within the reserve the vegetation is composed of a matrix of tall (- 1 m) *Themeda triandra / Tristachya* *leucothrix* grassland (790 mm MAP; 850 m a.s.l.) and fine-leaved *Acacia* savanna (790 mm MAP; 720 m a.s.l.). On the Louwsburg plateau (on the southwestern boundary) [820 mm MAP; 1400 m a.s.l.] the vegetation changes to short grassland dominated by medium to short grasses (< 0.5 m) typical of the montane grasslands of the main eastern escarpment, namely: *Alloteropsis semialata, Diheteropogon fillifolius, Loudetia simplex, Microchloa caffra* and *Trachypogon spicatus.*

2.5.10 Mkuze (clay and sand)

Mkuze Game Reserve (346 km^2) in northern KZN is located southeast of the town of Mkuze, with the Lebombo Mt. Range as its western boarder (27°38'S, 32°10'E). Proclaimed in 1912, people continued to live in the reserve until 1956, exposing the land to subsistence cultivation and grazing (Goodman, 1990). Geologically, the reserve is a mix of Quaternary sediments and Rhyolite, producing a range of soil types across the undulating landscape. I sampled two quadrats on sandy (670 mm MAP; 120 m as!) and a further two quadrats on clayey (665 mm MAP; 120 m as].) soils in the west of the reserve where the Acacia savanna is very open. The sands had a medium sward (0.5 m -1 m) dominated by grasses commonly observed in dryer areas, namely: *Aristida congesta, Digitaria* spp., *Eragrostis* spp. and *Perotis patens.* On the clays, the sward was tall (- 1 m), changing to a denser canopy of *Heteropogon contortus, Panicum* spp. and *Themeda triandra.* I also located one of my forb recruitment trial sites on these clay soils, - 2.5 km from the entrance to the reserve - 100 m north of road (27°37'46"S, 32°10'30"E) [Chapter 5].

2.5.11 Hluhluwe

Hluhluwe Game Reserve, is located in the hilly northern part of the Hluhluwe-Imfolozi Park (HIP) [28°00'-28°26'S, 31°43'-32°09'E; 900 km^2], west of the town of Hluhluwe in northeastern KZN. The park consists of two reserves, Hluhluwe (225 km^2) and Imfolozi (447 km^2), proclaimed in 1897 to control hunting. Subsequently the intervening corridor of state land (227 km^2) was included to create the park. Prior to conservation, cultivation and livestock grazing was conducted on a subsistence basis (Vincent, 1970). Across Hluhluwe Game Reserve the vegetation ranges from tall grasslands (> 1 m) with patches of short grass lawns (- 0.3 m), to *Acacia burkei, A. karroo* and *A. nilotica* savanna, and *Euclea divinorum* and *Spirostachys africana* woodland, with patches of forest in the wetter, northwestern regions of the reserve (Whateley and Porter, 1983). I sampled the tall grass (LeDube) and short grass (Seme) swards on black clayey soils in the control (unmanipulated) treatments of the Zululand Grass Project grazing exclosure trials (770 mm MAP; 245 m as].) [see also Chapter 6]. The tall grass (- 1 m) site (LeDube) was dominated by a *Themeda triandra* sward, with a local abundance of the forb *Otthosiphon serratus* at the time of sampling. The short grass (- 0.2 m) site (Seme) was dominated by creeping grass tam: *Dactyloctenium australe, Digitaria longillora, Panicum* spp. and *Urochloa mosambicensis.* I also located one of my forb recruitment trial sites on the open hills opposite the last house before the nursery (used by the game drive operators at the time of sampling) on the eastern side of the road that runs from Hill Top Camp through the staff village to the skinning shed (28^{2}0702"S, 32°03'39"E) [Chapter 5].

2.5.12 Imfolozi

Imfolozi Game Reserve, the southern part of the Hluhluwe-Imfolozi Park (900 km^{2}), is located west of the town of Matubatuba in northeastern KZN. Imfolozi is less hilly than Hluhluwe and receives considerably less MAP (from - 990 mm to < 635 mm MAP). Correspondingly there is an absence of forests and a shift in vegetation to *Acacia gerrardii, A. nigrescens* and *A. tortilis* savannas interspersed with *Combretum apiculatum* and C. *molle* woodlands (Whateley and Porter, 1983). Lawn grass areas were more abundant in Imfolozi (Archibald, 2003) and both short and tall grass sward were less dense than Hluhluwe (see also Chapter 6). I sampled a tallgrass (Sokwezela) and shortgrass (Thobothi) sward on red clayey soils in the control treatments of the Zululand Grass Project (680 mm MAP; 230m a.s.l.). I also located a forb recruitment trial site in the valley below Mpila Camp, - 500 m beyond the old game boma on the road to the trails camp (28^{2}32'01"S, 31°56'45"E) [Chapter 5].

2.5.13 Amatigulu

Amatigulu Nature Reserve (15 km^2; 1170 mm MAP; 20 m a.s.l.) is located at the mouth of the Matigulu River, north of the Tugela River and southeast of the town of Gingindlovu on the KZN north coast (29°06'S, 31°35'E). Established in 1987, this small reserve includes a mosaic of coastal forest and medium height (- 0.5 m), closed canopy grassland on coastal dunes. Although *Acacia karroo* occurred in some of the grassland areas, I sampled in the treeless grasslands on top of the tertiary dunes close to the gate. Here the grasslands were dominated by: *Digitaria eriantha, Hyparrhenia filipendula, Imperata cylindrica* and *Paspalum dilatatum* with a noteworthy richness of Fabaceous forbs.

2.5.14 QE Park

The mistbelt grasslands in the midlands of the KZN represent one of the most poorly conserved (< 3 %) grassland types in southern Africa (Low and Rebelo, 1996). Unlike other grassland types, however, lithe of the unconserved area of this vegetation type remains untransformed. Consequently, endemic species such as the Hilton Daisy *(Gerbera aurantiaca)* are facing extinction due to extreme habitat loss (Scott-Shaw, 1999). I sampled two small (< 0.01 km^2; 1070 mm MAP; 950 m a.s.l.) remnant patches close to the EKZNW headquarters, Queen Elizabeth Park, on the northwestern outskirts of the city of Pietermaritzburg (29°34'S, 30°19'E). One plot was located on the Victoria Country Club golf course just below Queen Elizabeth Park and the other on the road bank along Old Howick Road. Although patches of mistbelt forest occur within this vegetation type, they are largely confined to the valleys and the grasslands are treeless. The two sites sampled were dominated by a dense sward of *Alloteropsis semialata, Setaria sphacelata, Themeda triandra, Trachypogon spicatus,* and *Tristachya leucothrix,* with *Cymbopogon excavatus* abundant at the site along Old Howick Road.

2.5.16 Midmar Dam

Midmar Nature Reserve (10 km^2; 875 mm MAP; 1100 m a.s.l.) is located on the southern banks of Midmar Dam northwest of the city of Pietermaritzburg and west of the town of Howick in central KZN (29°31S, 30°09'E). Established in 1968, this small reserve is currently being used for the breeding of less common antelope such as: Black Wildebeest *(Connochaetes gnu),* Blesbok *(Damaliscus dorcas phillipsi),* Common duiker *(Sylvicapra grimmia),* Reedbuck *(Redunca arundinum),* Oribi *(Ourebia ourebi),* Red Hartebeest *(Alcelaphus busclaphus)* and Zebra *(Equus burchelh).* Although many of the tall grasslands (> 1 m) found in KZN midlands represent *Acacia sieberiana* savanna, the area around Midmar Dam is largely treeless. The undulating grasslands in the reserve were dominated by the tall grasses, *Hyparrhenia hirta* and *Themeda triandra* on black clayey soils overlying shales. I sampled around the oval loop road at the furthest end of the game park, placing one plot at the start of the loop and the other just below the road along the top end of the loop approximately three quarters of the way between the start of the loop and the boundary fence. I also located a forb recruitment trial downslope from this latter plot, - 200 m into the loop from the road (Chapter 5).

2.5.16 Impendle

Impendle Nature Reserve (80 km^2; 1100 mm **MAP; 1400** m a.s.l.) [formally Seven Mile Bush] is located south of the village of Impendle, roughly half way between Pietermaritzburg and Underberg in central KZN (29°41'S, 29°48'E). The reserve was established in 1985 from 11 farms and today represents an important habitat for southern populations of the endangered bird, the Blue Swallow *(Hirundo atrocaerulea).* Although large parts of the reserve were cultivated, I sampled in the untransformed grasslands between the main gate and staff accommodation. Impendle is located on a dolerite plateau in the foot hills of the Drakensberg escarpment, which supports a productive medium grass (- 0.5 m) sward. Dominated by *Themeda triandra,* along with *Heteropogon contortus* and *Tristachya leucothrix,* this sward forms a dense basal cover and rapidly accumulates moribund material (< 3 yrs) [Tainton, 1999].

2.5.17 Cobham

Cobham is located in the Mzimkulu Wilderness Area (283 km^2; 1000 mm MAP; 1780 m a.s.l.) northwest of the village of Himeville in the foothills of the central KZN Drakensberg Mts (29°44'S, 29°18'E). Following the earlier establishment of the Cobham State Forest (1927), the Mzimkulu Wilderness Area was proclaimed in 1979. Between the main escarpment and the foot hills on the eastern side of the Drakensberg Mts is the Little Berg. This is a region of broad plateaus with deep valleys forming fire refugia for patches of Afromontane Forest. The grassland contains a similar *Themeda triandra, Heteropogon contortus* and *Tristachya leucothrix* dominated sward to that found in the eastem foot hills of the Drakensberg, but there is an additional component of medium to short grasses such as: *Alloteropsis semialata, Diheteropogon fillifolius, Loudetia simplex, Microchloa caffra, Monocymbium ceresiiforme, Panicum &Monk P. natalense* and *Rendlia alters.* Characteristic forts include: *Acalypha schinzii Helichrysum nudifolium, H. pilosellum, Hermannia woodii, Pentanisia prunelloides* and *Senecio bupleuroides,* with an increasing abundance of *Helichrysum* spp. in the montane regions. Even in *Themeda triandra* dominated areas sward canopies remain open, but there is a good basal cover of grass tufts and accumulated moribund material. At Cobham I sampled two quadrats along the sandstone ridge above the entrance to the reserve that had been burnt that winter.

2.5.18 Sani Pass

The Sani Pass road runs up the Umkomozana River valley, through the Mzimkulu Wildemess Area (283 km^2), breaching the Drakensberg eastern escarpment at 2875 m a.s.l. to form the main access route to the Maloti Mountains (the highest point of which is - 12.5 km northwest of Sani top at Thabana Ntlenyana at 3482 m a.s.l.) on the eastern side of the Kingdom of Lesotho (29°35'S, 29°32'E). Originally a foot path, the opening of the pass to motorised transport in 1945 dramatically improved access to eastern Lesotho and (for botanists) the central region of the High Berg (Pearse, 1973). Around 1800 m a.s.l. (the start of the basalt escarpment) the *Themeda triandra* sward begins to include a C3 component, *(e.g.*

Festuca caprina and *Koeleria capensis),* a wealth of *Helichrysum* spp. and, at higher altitudes, dwarf heaths characterised by *Erica* spp.. I sampled in deep black turfy soils on the southern side of the pass below the Sani Staggers (the steep switch-back section before the top of the pass) [1600 mm MAP; 2500 m a.s.l.]. Here the vegetation was dominated by large tufts (- 0.3 m) of the forb *Helichrysum drakensbergense* and the grass, *Harpochloa fa&* which is known to increase in the absence of burning. Although parts of the pass have suffered under heavy grazing and subsequently colonized by the native shrub, *Leucosidea sericea,* the pass having *been* a major livestock herding route in the past, I purposefully sampled in a steep section that was representative of these montane grasslands.

2.5.19 Highmoor

Highmoor is located in the Mkhomazi Wilderness Area (562 km^2; 1150 mm MAP; 1960 m a.s.l.) in the central KZN Drakensberg Mts (29°15'S, 29°32'E). Originally proclaimed as the Highmoor State Forest (1951) the forest station was later included into the Mkhomazi Wilderness Area in 1973. Although termed a forest station, Highmoor, like all the other stations along the escarpment, was managed for water production, with negligible timber planting limited to the immediate vicinity of the nature conservator's house. Essentially, the vegetation is the same as that at Cobham, except that whereas the Cobham sites were located on sandstones, Highmoor sits on basalt. One plot was located in the fire-break on the plateau just before the first trout dam and the other - 0.5 km beyond the campsite on the on the ridge above the old dirt road which was also the site for the forb recruitment trial (Chapter 5).

2.5.20 Cathedral Peak

Cathedral Peak is located in the Mlambonja Wilderness Area (63 km^2; 1380 mm MAP; 1830 m ask) in the northern KZN Drakensberg Mts (28°28'S, 29°14'E). Mlambonja Wilderness Area was proclaimed in 1989 from part of what was previously the Cathedral Peak State Forest (proclaimed in 1927). The vegetation is similar to that found at Cobham and Highmoor, except that the northern part of the

KZN Drakensberg is generally warmer and has a higher MAP than the southern portion. The sites at Cathedral Peak, like those at Highmoor, were sampled on basalt derived soils. One plot was sampled below Arendsig I-1111 (close to the vulture restaurant) and the other just beyond the weather station, between the fork in the road on the way to the Brotherton burning trial.

2.5.21 Mooihoek

Mooihoek Farm (plot number 130; 700 mm MAP; 1780 m a.s.l.) is located just on top of the eastern escarpment, off the DeBeers Pass Road, north of the town of Harrismith in the Orange Free State (28°12'S, 29°09'E). At the time of sampling, the farmer, Mr Phillip Patterson, was using the farm to fatten weaners for the market. Although atop the escarpment, the farm lies in the rain shadow of the DeBeers Pass mountains and is therefore drier than one might expect. Here the hilly sandstone landscape supports a short (< 0.5 m) dense *Themeda triandra Tristachya leucothrix* sward. The region experiences severe frost and is largely treeless. Both plots were located in the paddock east of the road, with one plot on the flattish land towards the main gate and the other half way up the slope.

2.5.22 Chelmsford Dam

Chelmsford Nature Reserve (60 km^2; 1000 mm MAP; 1270m a.s.l.) is located on banks of Chelmsford Dam, south of the town of Newcastle in northwestern KZN (28°00'S, 29°50'E). Established in 1975, the reserve was previously a farm and large parts had been turned by the plough. To avoid these, I limited my sampling to the shallow soils overlying the shales in the undulating landscape at the northwest end of the dam. Here the vegetation formed an open *Acacia sieberiana* savanna, with a medium to tall (0.5 m - 1 m), open canopy sward of small tufted grasses producing a poor ground cover. Dominants in the sward included: *Bothriochloa insculpta, Eragrostis* sop., *Heteropogon contortus, Hyparrhenia hirta, Trachypogon spicatus* and *Tristachya leucothrix.*

3 Patterns of taxonomic richness

Abstract

I surveyed altitudinal and mean annual precipitation gradients across the South African rangelands east of the escarpment to explore patterns of species richness and their determinants. Species and family richness were recorded at 25 sites, each sampled using 2 x 1000 m^2 modified Whittaker plots with nested sub-quadrats. Species (at both 1 m2 and 1000 m^2) and family (at 1000 m^2) richness displayed strong unimodal responses across my study area increasing with increasing precipitation up to - 2000 m a.s.l., above which richness declined with altitude irrespective of increasing precipitation. This regional pattern held irrespective of local environmental differences, with sites of similar rainfall, but distinctly different soil types having similar levels of taxonomic richness.

3.1 Introduction

Identifying patterns of species richness and understanding their determinants has been one of the longest rurming concerns of ecology and biogeography (Gaston, 2000). Over the years, these efforts have grown from mere curiosity to form the core of biodiversity conservation science, governing everything from where reserves are needed to their management (Cowling *et at.,* 1997). They have guided the development of the concepts of biodiversity in space and time, and provide a basis upon which to predict the effects of changing climates (e.g. Rosenzweig, 1995; Woodward and Wolfgang, 1996). Accordingly, it is important that we understand how biodiversity is distributed across southern Africa's rangelands to guide conservation strategies in these ecosystems (Cowling *et at,* 1997).

Patterns of species richness have been explored at a range of scales, but I was particularly interested in how species richness varied at the regional scale. A number of hypotheses have been advanced to predict patterns of plant species richness at the regional scale. These include the relationships between species richness and: sample area, environmental heterogeneity, environmental energy, environmental favourableness, resource abundance (seasonality and irregularity), the dispersal range of species, speciation history, and the manner in which local and regional richness converges (for review see Cowling *et al,* 1997). Next to species-area relations, the most generally applicable of these hypotheses appear to be the ones that relate species richness to patterns of primary resource quantity and quality (resource-richness hypotheses) [Cowling *et al.,* 1997].

Across my study area, primary environmental resources appeared to correlate to altitude. Different hypotheses, however, provide conflicting predictions as to the expected pattern of species richness. Two broad sets of resource-richness hypotheses emerge, those suggesting that richness should increase with increasing altitude (increasing resource-richness), and those that suggest that richness should decrease with increasing altitude (decreasing resource-richness). Topographic diversity increased with altitude, meaning an increase in habitat heterogeneity that should promote greater species richness in the mountains than in the lowlands. Mean annual precipitation also generally increases with altitude, suggesting an increase in environmental favourableness and theoretically species richness (Cowling *et* al., 1997; Schulze, 1997). As biomass accumulation is linearly related to mean annual precipitation across the southern African grasslands (O'Connor and Bredenkamp, 1997; Rutherford, 1980), primary production (a measure of environmental energy) should also increase, promoting greater species richness in the mountains (Cowling et *al.,* 1997). Increased mean annual precipitation also results in a lower coefficient of rainfall variation, meaning less irregularity which should correspond to an increase in species richness (Cowling *et al.,* 1997; Schulze, 1997). In contrast, however, temperature (a measure of favourableness) and the duration of the growing season (a measure of energy) decline with increasing altitude, suggesting that richness should decline into the mountains (Cowling *et al,* 1997; Schulze, 1997). The two conflicting sets of hypotheses thus suggest that species richness may either increase or decrease with altitude.

To test these competing hypotheses I surveyed the species richness along altitudinal and mean annual precipitation gradients across my study area. Mean annual precipitation was chosen to contrast against the other environmental correlates of altitude as it has been shown to be a determinant of floral patterns across southern Africa (Linder, 1991; O'Brien, 1993; O'Cormor and Bredenkamp, 1997; O'Brien *et al.,* 1998; Caylor *et al.,* 2004).

3.2 Methods

3.2.1 Sampling design

Twenty-five study sites were sampled across the rangelands east of the escarpment in South Africa (Chapter 2). Sites were selected to represent the broad altitudinal and mean annual precipitation gradients across this region. In addition, site selection was structured to encompass a range of vegetation types occurring under different local conditions. Thus, sites with similar altitudes and mean annual precipitation were selected on different substrates or in different vegetation types such as adjacent grasslands and savannas (See: Shinwedzi 2.5.1; Bateleur 2.5.2; 'theta 2.5.9; Mkuze 2.5.10).

All sampling was conducted at the height of the local flowering season (November - February), by surveying two modified Whittaker plots (20 m x 50 m) at each site to represent the vegetation in the area. While a greater number of small plots *(e.g.* 10 m x 10 m) might have provided better coverage of the sites, a modification of Whittaker's 0.1 ha plot design was selected as it allows comparison with the large body of studies conducted with similar sampling designs around the world (Rice and Westoby, 1983; Keeley and Fotheringham, 2005). Only two modified Whittaker plots were sampled at each site, as a number of vegetation types, particularly the coastal and mistbelt grasslands, had been reduced to mere remnants not allowing for more extensive surveys.

Each modified Whittaker plot was sampled as a series of nested sub-quadrats, increasing in size from 1 m^2, to 10 m^2, 50 m^2, 100 m^2, 250 m^2, 500 m^2 and 1000 m^2 (Figure 3.1). Each 20m x 50m quadrat was divided into quarters (25 m x 10 m). A row of five adjacent 1 m^2 quadrats was sampled across the width of one of these quarters, across the middle of the main quadrat. This 5 m x 1 m strip was extended across the width of the quarter (10 m x 1 m) to form a 10 m^2 sub-quadrat.

The 10 m x 1 m strip was then extended by 4 m down the length of the quarter to form a 10 m x 5 m sub-quadrat (50 m^2) and then extended by a further 5 m down the length of the quarter to form a 10 m x 10 m sub-quadrat (100 m^2). The remaining 10 m x 15 m area of the quarter was then sampled to bring the total area sampled to 250 m^2. Next, the adjacent 25 m x 10 m quarter along the long axis of the plot was sampled to bring the total area sampled to 500 m^2. Finally, the remaining two quarters were sampled to complete the 1000 m^2 quadrat. Species and family presence / absence was recorded individually in each of the five 1 m^2 sub-quadrats and then cumulatively in successive sub-quadrats to give a total species count for the quadrat.

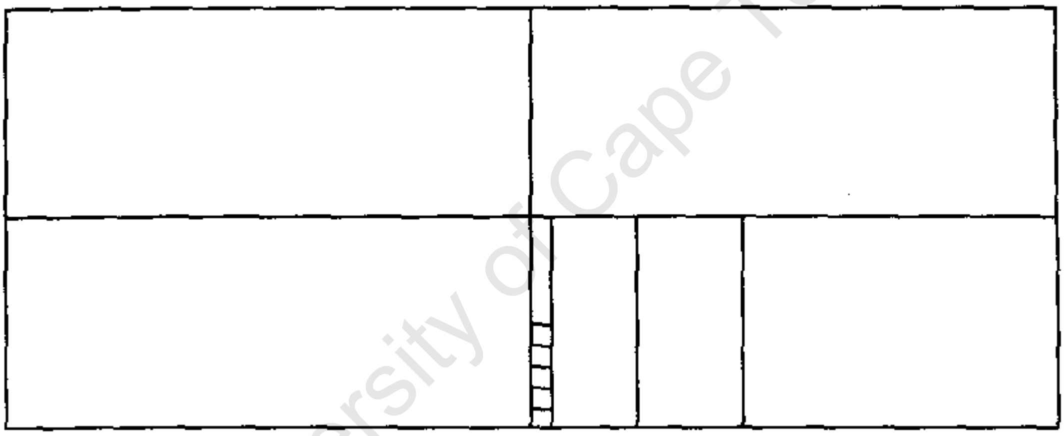


Figure 3.1 Scale illustration of the layout of the modified Whittaker quadrat (20 m x 50m) showing the layout of the 5 x 1 m^2, 10 m^2 (10 m x 1 m), 50 m^2 (10 m x 5 m), 100 m^2 (10 m x 10m), and 4 x 250 m^2 (10 m x 25 m) nested sub-quadrats used in sampling.

3.2.2 Data analysis

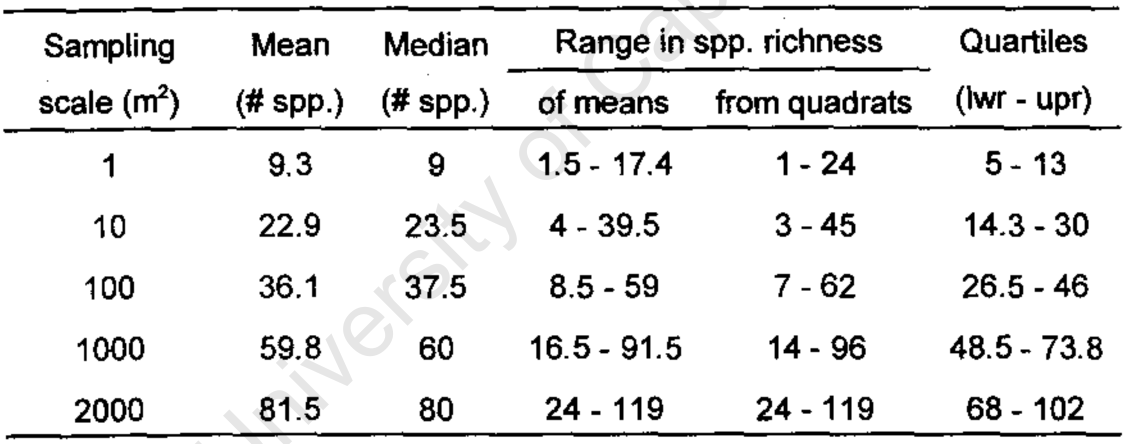
Species richness was calculated at 1 m^2, 10 m^2, 100 m^2, 1000 m^2 and 2000 m^2 for each site, and the mean, median, range and quartile species richness calculated at these scales from the 25 sites sampled. Total species richness for each family was calculated from the two 1000 m^2 quadrats sampled at each site. This allowed the 12 richest families to be identified and contrasted with their specific and generic richness in southern Africa and around the world. Site species richness of the eight richest families was displayed with the sites ranked according to mean annual precipitation. Mean species and family richness at 1 m^2 (n = 2 sets of 5) and 1000 m^2 (n = 2) were both examined according to the distribution of the sites across the altitudinal and mean annual precipitation gradients along which they were sampled. I applied the best subset regression approach and used the Akaike information criterion (AlC) to determine the best model for describing the distribution of taxonomic richness across the altitude and MAP gradients surveyed. Based on the AlC values for the fit of species richness at 1 m^2 and 1000 m^2 and family richness at 1000 m^2 against altitude and MAP, I made no attempt to regress a relationship with altitude ($p > 0.05$ for all three levels of taxonomic richness). The distribution of species according to MAP was, however, found to be significant ($p <$ 0.001) and best fitted by a quadratic equation for both levels of species richness and family richness, as judged by delta AlC and AlC weights. Regression lines were subsequently fitted to display the relationship between MAP and taxonomic richness.

3.3 Results

3.3.1 Species richness

Total herbaceous species richness (forbs, grasses and sedges) varied considerably, but predictably across my study sites (Appendix 3.1). At the smallest scale sampled (1 m^2), richness ranged from only a single species of grass occurring in seven of the two sets of 5 x 1 m^2 quadrats sampled at Satara to 24 species of forbs, grasses and sedges recorded in one of the quadrats at Amatigulu (Table 3.1). The range in the mean species richness at 1 m^2 (n = 10 for each site) was more conservative (1.5 - 17.4 spp.), particularly for the richer sites. The best demonstration of the variation in species richness across the sites was that the richest site had a greater mean species richness at 1 m^2 (17.4 spp. at Impendle) than the poorest site had in 1000 m^2 (16.5 spp. at Satara). It is worth noting that despite the difference in their nutrient status, Shingwedzi (on nutrient rich soils) and Bateleur (on nutrient poor soils) with similar levels of MAP (460 mm and 440 mm respectively) had similar levels of mean species richness at 1000 m^2 scale (34.5 spp. and 36 spp. respectively). The Mkuze day (665 mm MAP) and sand (670 mm MAP) sites also had similar levels of mean species richness at 1000 m^2 scale (51.5 and 56 spp. respectively). At lthala the savanna and tall grass sites were at similar altitudes (720 m a.s.l. and 850 m a.s.l. respectively) and MAP (both -790 mm MAP), and also had similar levels of mean species richness at 1000 m^2 scale (64.5 app. and 68.5 spp. respectively) [Appendix 3.1].

Table 3.1 Distribution of species richness across the 25 study sites, at different sampling scales. Range values are provided for the mean species richness calculated for each site (range of means) and for all the quadrats sampled across the sites (range from quadrats). All quadrat sizes were sampled twice at each of the 25 sites, except for the 1 m^2 quadrats, where 10 quadrats were sampled per site.



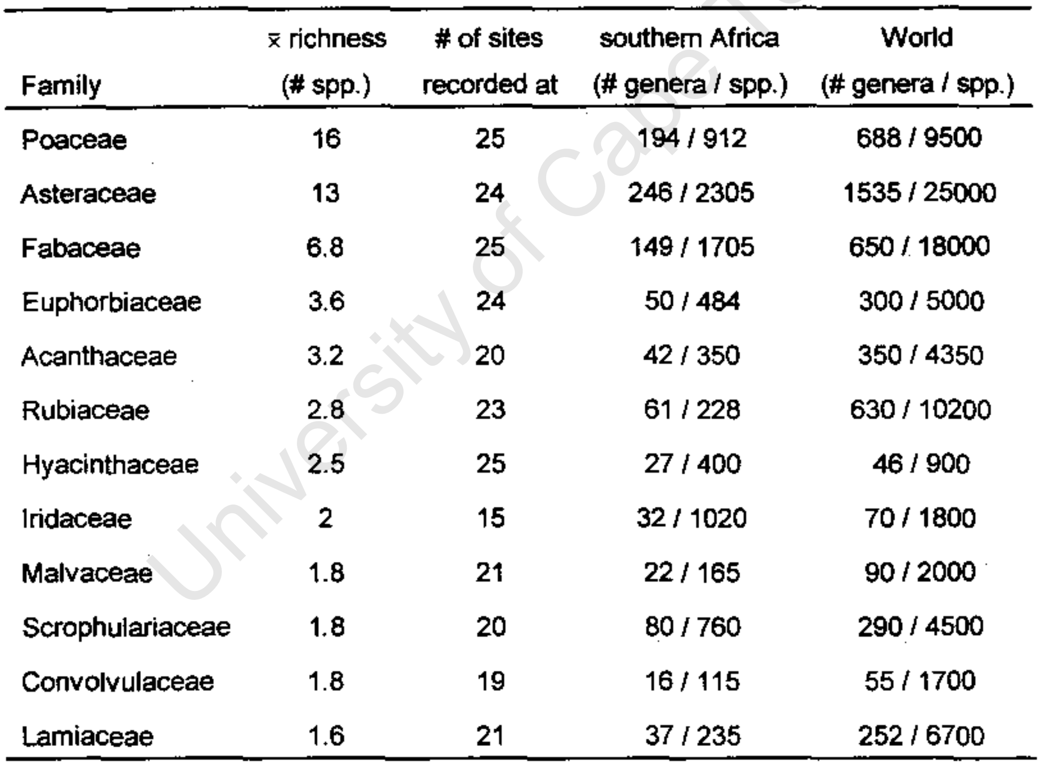
Sampling scale (m^2)	Mean (# spp.)	Median (# spp.)	Range in spp. richness of means	Range in spp. richness from quadrats	Quartiles (lwr - upr)
1	9.3	9	1.5 - 17.4	1 - 24	5 - 13
10	22.9	23.5	4 - 39.5	3 - 45	14.3 - 30
100	36.1	37.5	8.5 - 59	7 - 62	26.5 - 46
1000	59.8	60	16.5 - 91.5	14 - 96	48.5 - 73.8
2000	81.5	80	24 - 119	24 - 119	68 - 102

Total herbaceous (forbs, grasses and sedges), forb and non-petaloid monocot (grasses and sedges) species richness all displayed a humpbacked relationships to MAP at all scales sampled between 1 m^2 and 1000 m^2. Richness increased with MAP from - 400 mm yr' to — 1200 mm yr^{-1} above which it declined (Figures 3.2 and 3.3; Appendix 3.1 and 4.1). Species richness also showed a similar, yet less distinct, hump-backed relationship to altitude at both 1 m^2 and 1000 m^2 scales(Figures 3.4 and 3.5). However, at both scales (1 m^2 and 1000 m^2) lower altitude sites (< 250 m a.s.l.) displayed greater levels of richness than would be predicted by the general decrease in richness between - 1200 m a.s.l. and - 500 m a.s.l. (Notably: Amatigulu, 20 m a.s.l.; Huhluwe, 245 m a.s.l.; Imfolozi, 230 m a.s.l.; Mkuze [clay], 120 m a.s.l.; Mkuze [sand], 120 m a.s.l.; Ndumo, 90 m a.s.l.; Pongolapoort, 180 m a.s.l.). Amatigulu in particular, strongly contradicted the expected pattern by being on the coast (20 m a.s.l.), but having one of the richest grasslands sampled (5c of 15.6 spp. in 1 m^2 and 91.5 spp. in 1000 m^2) [Appendix 3.1].

3.3.2 Family richness

Family richness at the 1000 m^2 scale showed a similar, although less pronounced, hump-backed pattern across both the MAP and altitudinal gradients to that displayed by species richness (Figures 3.6 and 3.7). Most of the plots sampled contained between 16 and 28 herbaceous plant families (per 1000 m^2), with an average of 23 families recorded per plot (1000 m^2). Mean family richness amongst the drier sites (< 800 mm MAP) fell below the average family richness (- 20.5 families per 1000 m^2), while the intermediate MAP sites (800 -1200 mm MAP) were richer than average (- 26 families per 1000 m^2). Family richness, like the species richness, declined at the two highest sites, which also had the highest MAP. Of the 67 families recorded across the sites, only eight (12 %) were represented by an average of z two species per site and 20 families (30 %) by zone species per site (Table 3.2; Figure 3.8; Appendix 3.2). The distribution of families across sites was also limited, with only 12 families (18 %) occurring in z 20 out of the 25 sites. Two-thirds of the families (44/67) were recorded in s 12 (1/2) of the sites (Appendix 3.2).

Table 3.2 Twelve richest plant families encountered in the 2 x 1000 m^2 quadrats sampled at each site. Families were ordered according to the mean number of species across the sites and then by the number of sites, out of the total of 25, in which they occurred (Appendix 2.2). Data are presented with the numbers of genera and species represented by each family in southern Africa and in the world (Leistner, 2000).



Family	$\bar{x}$ richness (# spp.)	# of sites recorded at	southern Africa (# genera / spp.)	World (# genera / spp.)
Poaceae	16	25	194 / 912	688 / 9500
Asteraceae	13	24	246 / 2305	1535 / 25000
Fabaceae	6.8	25	149 / 1705	650 / 18000
Euphorbiaceae	3.6	24	50 / 484	300 / 5000
Acanthaceae	3.2	20	42 / 350	350 / 4350
Rubiaceae	2.8	23	61 / 228	630 / 10200
Hyacinthaceae	2.5	25	27 / 400	46 / 900
Iridaceae	2	15	32 / 1020	70 / 1800
Malvaceae	1.8	21	22 / 165	90 / 2000
Scrophulariaceae	1.8	20	80 / 760	290 / 4500
Convolvulaceae	1.8	19	16 / 115	55 / 1700
Lamiaceae	1.6	21	37 / 235	252 / 6700

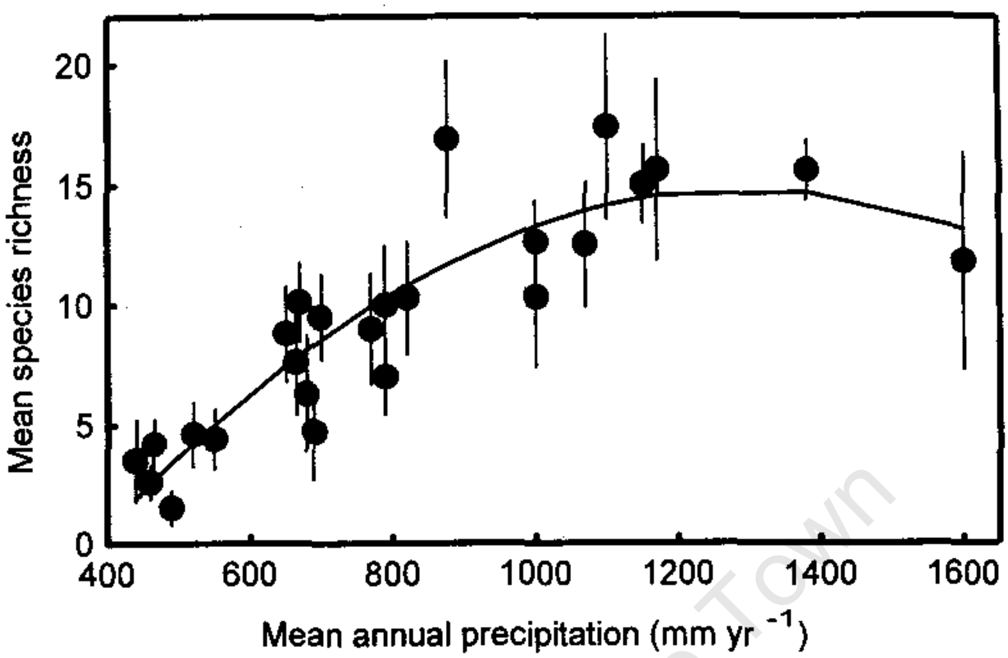
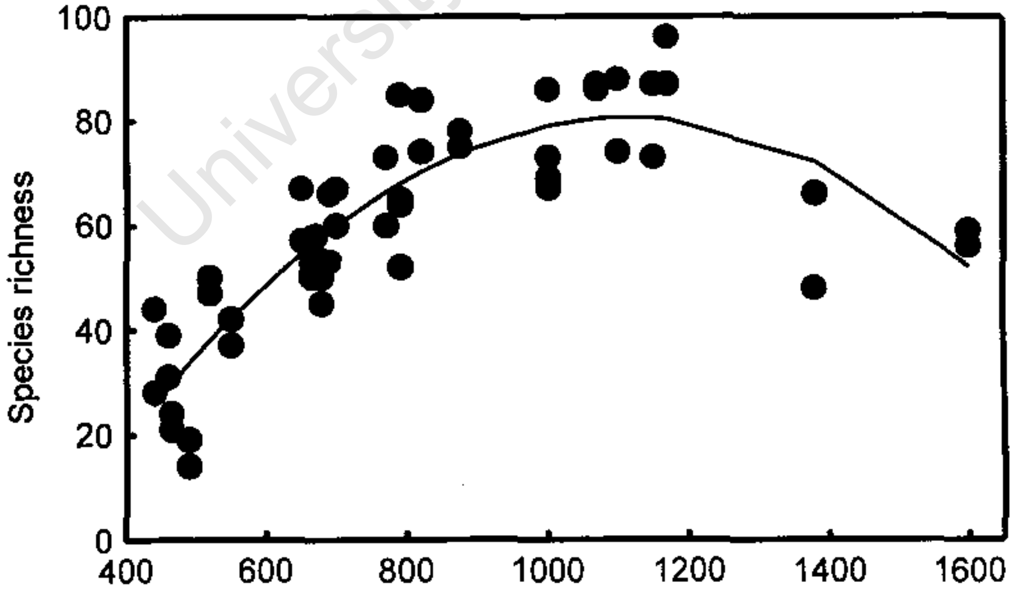


Figure 3.2 Relationship between mean annual precipitation and the mean species richness sampled in two sets of 5 x 1 m^2 quadrats at each site. Best fit by quadratic regression ($R^2 = 0.81$; F [2.22] = 46.61; $p < 0.001$).



Mean armual precipitation (mm yr^{-1})

Figure 3.3 Relationship between mean annual precipitation and total species richness sampled across 2 x 1000 m^2 quadrats at each site. Best fit by quadratic regression ($R^2 = 0.77$; F [2.47] = 80.62; $p < 0.001$).

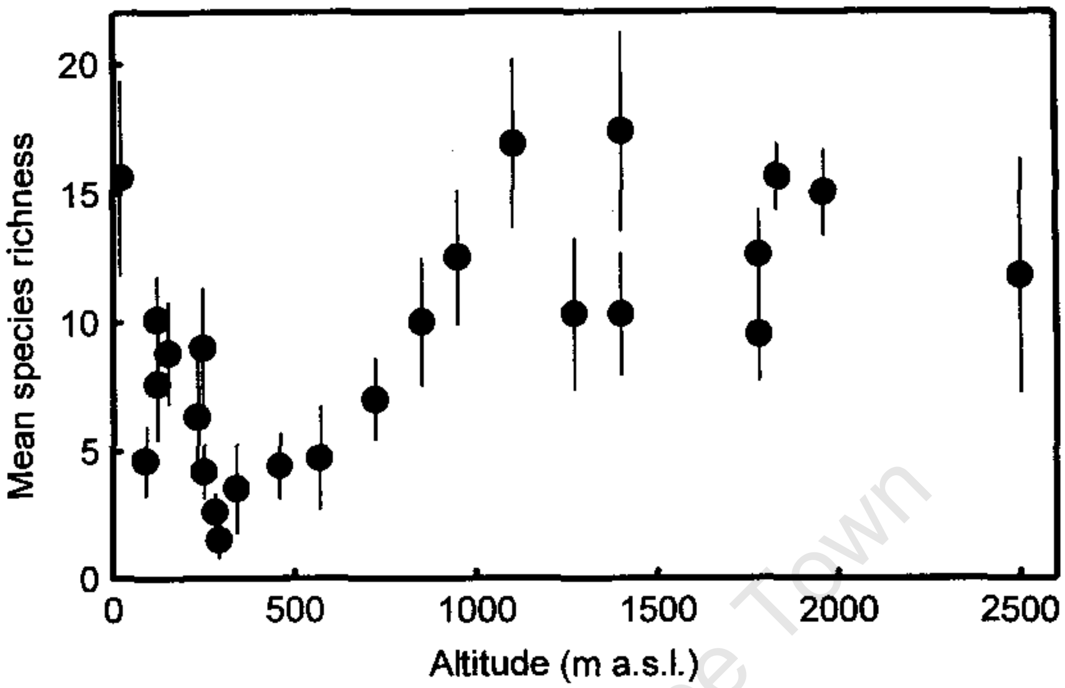


Figure 3.4 Relationship between altitude and mean species richness sampled in two sets of 5 x 1 m^2 quadrats at each site.

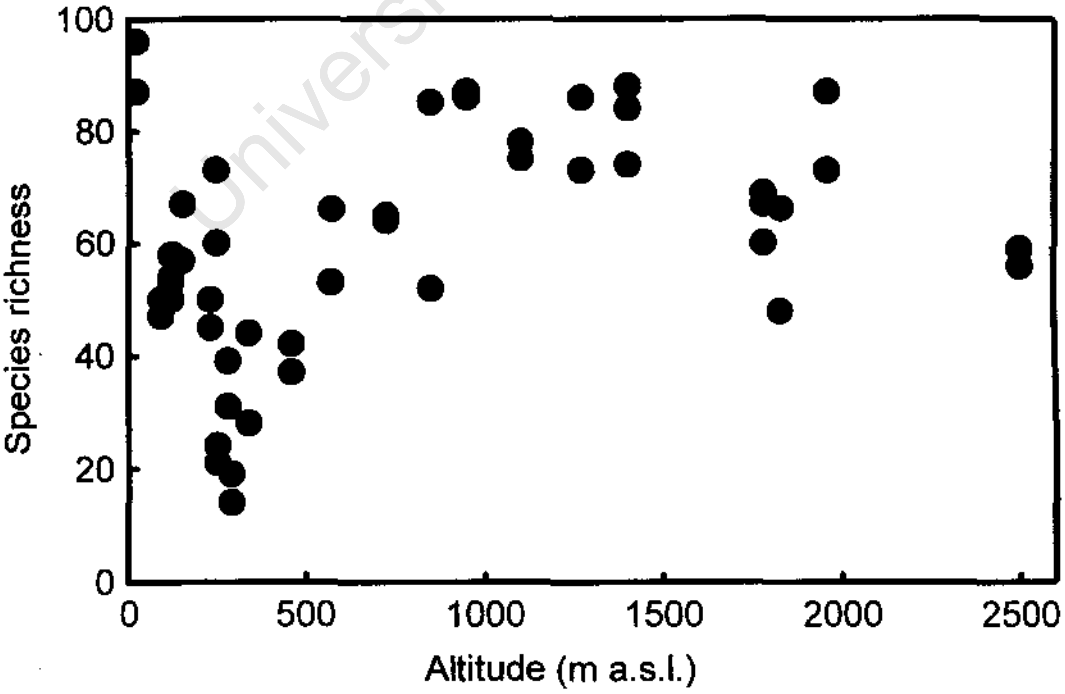


Figure 3.5 Relationship between altitude and total species richness sampled across 2 x 1000 m^2 quadrats at each site.

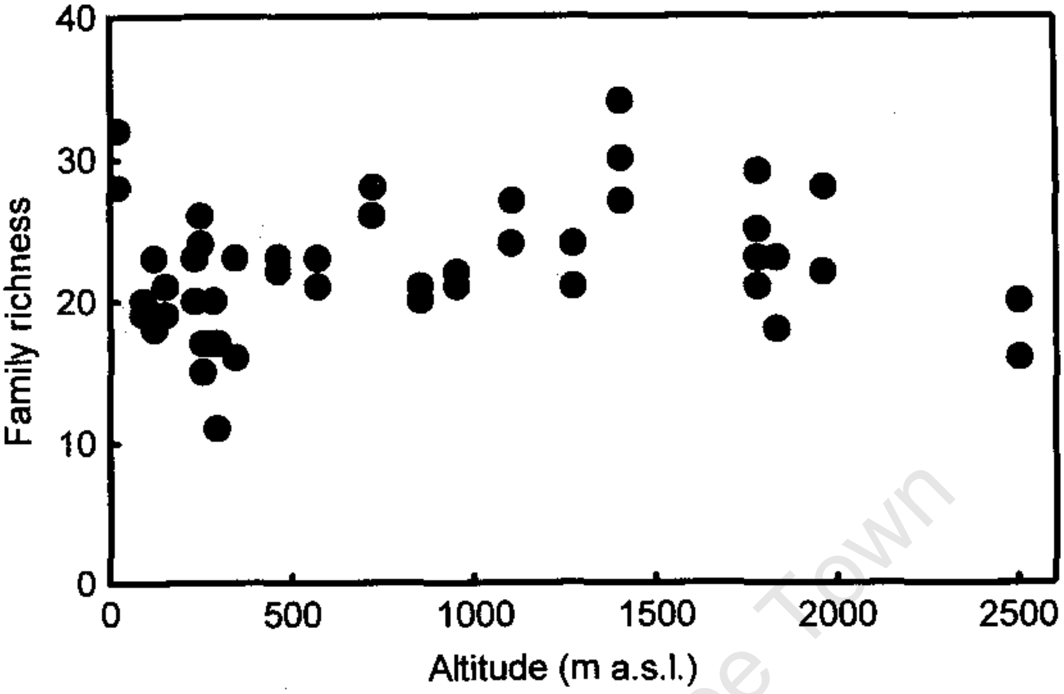


Figure 3.6 Relationship between altitude and total family richness sampled across 2 x 1000 m^2 quadrats at each site.

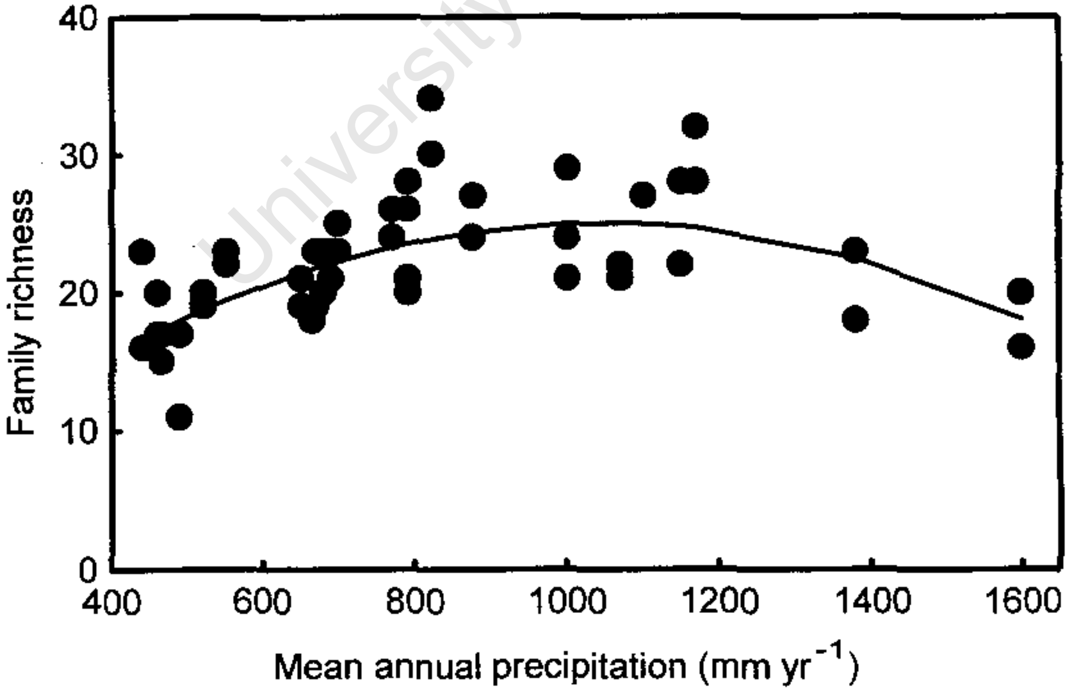


Figure 3.7 Relationship between mean annual precipitation and total family richness sampled across 2 x 1000 m^2 quadrats at each site. Best fit by quadratic regression ($R^2 = 0.59$; F [2.22] = 15.88; $p < 0.001$)

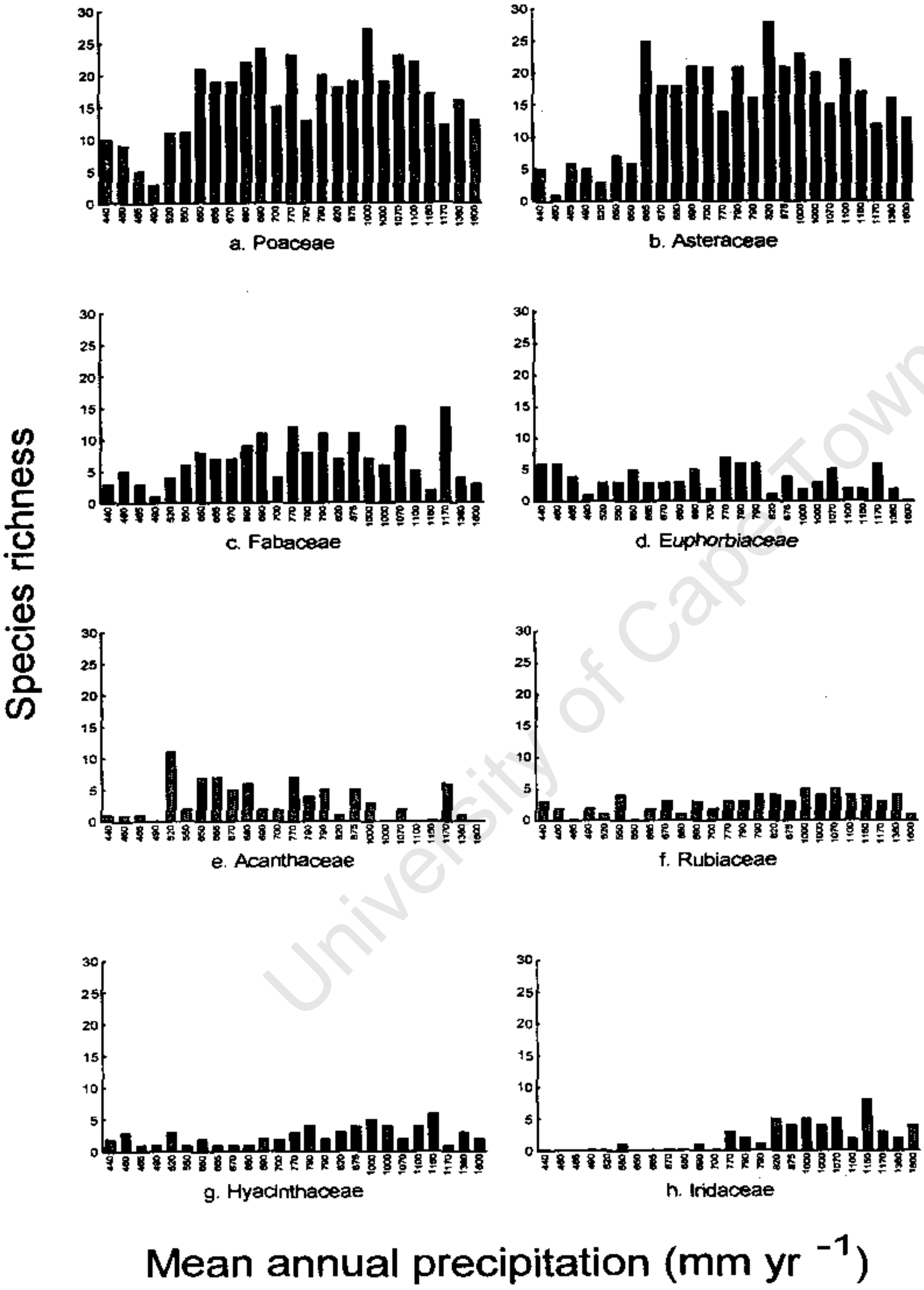


Figure 3.8 Species richness of the eight richest families, recorded across the 2×1000 m^2 quadrats sampled at each site, ranked according to mean annual precipitation across the sites (Table 3.2; Appendix 3.2).

3.4 Discussion

3.4.1 Importance of rangeland forbs

Rangeland research in southern Africa has focussed on the grass component of these systems (Tainton, 1999), but the results presented here clearly show that it is the forbs that constitute most of the floral richness of these systems. Forbs represented - % of the alpha-diversity that I encountered per 1000 m ^{2} across the southern African rangelands, which equated to between 3 - 5 forb taxa for every non-petaloid monocot (grasses and sedges). On average, I encountered 22 families per 1000 m^2, with over 30 fort families recorded in 1000 m^2 quadrats at some of the mesic sites. To place this in perspective, consider that a 1000 m ^{2} quadrat sampled in the South African fynbos (the floral kingdom with the highest species density in the world) would probably only contain between 10 - 15 families (Cowling, 1992). ln a rangeland flora prized for its value as traditional medicines, where major phytochemical differences occur between families rather than taxa, the impressive levels of alpha family diversity must hold immense pharmaceutical potential (Arnold *et al.,* 2002). Yet, despite this obvious value, southem Africa's rangeland flora is not being managed towards conservation goals. lnstead, the fire and grazing management of these ecosystems is still all too often based on agricultural ideals of grass and animal production. Forbs obviously constitute most of the richness of these ecosystems and therefore need to feature more prominently in conservation management. However, before this can happen, we need to develop a better understanding of grassland forb biology.

3.4.2 Hump-backed patterns of taxonomic richness

Both species and family richness displayed unimodal responses to mean annual precipitation (MAP) across my study area, peaking around 1100 mm MAP. Taxonomic richness peaked at 2000 m a.s.l., however, altitude effects were less clear than those of mean annual precipitation, especially at lower altitudes between 0 - 250 m a.s.l.. lnterestingly, this strong unimodal response to rainfall across the southern African rangelands, mirrored results of a similar study from east Africa (Anderson *et at,* 2004).

Neither of the two sets of resource-richness hypotheses were exclusively supported along the entire altitudinal or mean annual precipitation gradients sampled across my study area. Species richness has often been found to decrease monotonically along altitudinal gradients, resulting in altitudinal effects being compared to similar patterns recorded along latitudinal gradients (Whittaker, 1960; Kruger and Taylor, 1979; Shmida and Wilson, 1985; Linder, 1991; Stevens, 1992; Rahbek, 1995; Odland and Birks, 1999; Ohlemuller and Wilson, 2000; Grytnes and Vetaas, 2002; Wang *et al,* 2002; Grytnes, 2003; Jacquemyn *et al,* 2005). However, in reviewing 90 examples of elevational gradients sampled from below 500 m a.s.l. to above 1500 m a.s.l., Rahbek (1995) found that although there was general support for a decline in species richness with altitude, this decline was not necessarily monotonic. Instead, the relationship often appeared to be unimodal, with an initial increase in richness with altitude, before the widely observed decline. This unimodal response may account for the conflicting hypotheses, being explained by richness increasing with topographic diversity (heterogeneity) or mean annual precipitation (representing energy, favourableness and resource abundance) to a point, beyond which insufficient heat resources (temperature and duration) may account for its decline (Körner, 2000). Interestingly, the 1800 m to 2000m a.s.l. attitudinal band of the Drakensberg escarpment, above which taxonomic richness was found to decline, is also the point at which the grasslands shift from C4 to C3 grass dominance and represents the treeline, above which forests rapidly thin out (Hilliard and Burt, 1987; Vogel *et al.,* 1987; Gibbs Russell *et al,* 1990; Killick, 1990). As both the shift from C4 to C3 grass dominance and treelines have been ascribed to temperature (Ehleringer *et al.,* 1991; Collatz *et al.,* 1998; Körner, 1998, 2003; Keeley and Rundel, 2003, 2005) I suggest that decreasing temperature was also responsible for the decrease in taxonomic richness above - 2000 m a.s.l.. Taxonomic richness therefore appears to have been initially determined by the set of increasing resource-richness hypotheses *(i.e.* mean annual precipitation) up to 2000m a.s.l.. Above - 2000 m a.s.l., heat resources were probably insufficient to support the effects of increasing MAP, resulting in the set of decreasing resource-richness hypotheses coming into effect.

3.5 Conclusions

As in other C, grass dominated rangelands around the world, most of the herbaceous plant richness across my study area was represented by a diversity of forb taxa spread across a range of families. For the diversity of southern Africa's rangelands to be adequately conserved, we therefore need to investigate management strategies beyond the current agriculturally based practices aimed at promoting grass production.

Taxonomic richness was also found to vary considerably, yet in a predictable unimodal fashion across my study area. The increase in taxonomic richness with altitude up to — 2000 m a.s.l. was explained by resources that also increased with attitude, particularly mean annual precipitation. Above — 2000 m a.s.l., the decline in taxonomic richness was probably due to reduced energy availability. Thus, different sets of resource-richness hypotheses appeared to account for the unimodal pattern of taxonomic richness across my study area.

It will be interesting to see how well these patterns hold up as more people become interested in, and extend the survey of the plant diversity across southern Africa's rangelands. As a cautionary note to future research, I must stress that these patterns are based on rangelands considered to be in good condition and lower than expected levels of species richness are not unusual in degraded lands. My survey was confounded by altitude and its related temperature effects. However, I predict that if appropriate sites receiving more than 1200 mm MAP can be surveyed below 1800 m a.s.l., species richness will be found to continue to increase with mean annual precipitation beyond the limit of this survey. If these patterns of rainfall and temperature effects do hold, we will be able to use them to rethink the effects that global climate change might have on the plant diversity of these rangelands.

4 Patterns of forb functional type richness

Abstract

I examined patterns of forb functional type richness to test whether drought and fire, that predominate in the semi-arid and mesic areas respectively, were influencing the life-form and life-history strategies of rangeland forbs. The forb flora across the rangelands east of the escarpment in southern Africa was dominated by long-lived, resprouting, dicots, displaying cauline erect growth forms, traits that appear to characterise C_t, rangeland floras around the world. Re-seeding species proportionately increased into the semi-arid regions and re-sprouting species into the mesic regions, providing support for separate drought and fire adapted floras at either end of the mean annual precipitation gradient. Monocot forbs proportionately decreased into the semi-arid areas, with a corresponding decrease in radical growth forms. Cauline-prostrate (creeping) species, however, showed a slight increase into the drier areas, possibly capitalizing on the increased inter-tuft space.

4.1 Introduction

Disturbances play an important role **in** maintaining rangeland plant diversity, yet their effects are often only examined at one site and then extrapolated into management regimes for entire regions (Stuwe and Parsons, 1977; McNaughton, 1983, 1985; Collins and Barber, 1985; Belsky, 1992; Collins, 1992; Montalvo *et al.,* 1993; Tremont and McIntyre, 1994; Noy-Meir, 1995; Hartnett *et al.,* 1996; Damhoureyeh and Hartnett, 1997; Collins et a1.,1998; Freeman, 1998; Zhang, 1998; Knapp *et al.,* 1999; Uys, 2000; Lunt and Morgan, 1999, 2002; Bullock *et al.,* 2001; Fynn *et al.,* 2004; Uys *et al.,* 2004). This has potentially damaging consequences for rangeland conservation, as studies have predicted, and shown, that disturbance responses may vary across environmental gradients (e.g. Milchunas *et al.,* 1988; 0lff and Ritchie, 1998). To avoid extrapolating the results of disturbance studies to ecosystems where they do not apply, we need to identify specific response groups **and determine how these groups are distributed across the region and between** areas influenced by different types of disturbance (Lavorel *et al,* 1997).

Drought, fire and grazing, the major forms of 'natural' disturbance influencing rangeland plant diversity, are closely associated with mean annual precipitation (MAP) across southern Africa (Tainton and Walker, 1993; O'Connor and Bredenkamp, 1997; Tainton, 1999; Uys, 2000; Fynn et *al.,* 2004; Uys *et al.,* 2004). Pastoralists have long recognised differences in the grazing potential of grasses in mesic and semi-arid rangelands (sweetveld *versus* sourveld), yet similar patterns remain to be explored for species diversity (Ellery *et at,* 1995; Hardy *et al,* 1999). Of these disturbances, drought and fire have markedly different regimes across this same mesic to semi-arid rangeland gradient. As MAP decreases across the region it also becomes increasingly erratic, resulting in drought conditions being more regularly experienced in the semi-arid than mesic grasslands (Le Houerou, 1984; Tyson, 1986; Schulze, 1997). Droughts occur fairly regularly across the region, with intense droughts (< 60 % MAP) being experienced at intervals of a decade or more. Less intense droughts (< 75 % MAP) occur more frequently at intervals inversely related to the mean annual precipitation (Tyson, 1986; Tyson and Dyer, 1978; Vogel, 1994). Fire frequency is closely linked to the rate of biomass accumulation (Bond and Van Wilgen, 1996), which increases linearly with MAP across the southern African rangelands (O'Connor and Bredenkamp, 1997; Rutherford, 1980). The incidence of lightning strikes also increases with rainfall, presenting a more ready natural (non-anthropogenic) source of ignition in the mesic than semi-arid grasslands (Edwards, 1984). Fires thus occur more frequently in the mesic than semi-arid grasslands (O'Connor and Everson, 1998; Balfour and Howison, 2001). If the floras have adapted to tolerate these disturbances, we would expect fire-tolerance traits to dominate in the mesic areas and drought-tolerance traits to dominate in the semi-arid areas.

Specific disturbance response groups are identified on the basis of shared life-form and / or life-history traits that influence their response (Lavorel *et al,* 1997; Mclntyre *et al,* 1999; Weiher *et at,* 1999; Cornelissen et *al,* 2003). The choice of which traits to examine has often been made on an *ad* hoc basis. However, a number of attempts have been made to identify 'core lists' of traits to guide this process (Grime, 1977; Noble and Slatyer, 1980; Lavorel *et al.,* 1997; Westoby, 1998; Mclntyre et *at,* 1999; Weiher et *al.,* 1999; Lavorel and Gamier, 2002; Comelissen *et at,* 2003). An alternative view is that generic functional types neither exist nor are desirable, and that the selection of traits needs to be refined on a study-by-study basis (Skarpe, 1996). I selected plant traits that would allow me to describe the flora and attempt to identify patterns of forb functional type response across my study area. Subsequently, I used a mixture of core list traits and those commonly observed in drought and fire prone herbaceous floras around the world (Lavorel *et al.,* 1997; Mclntyre *et at,* 1999; Weiher *et at,* 1999; Lavorel and Gamier, 2002; Cornelissen *et al.,* 2003).

Adult plants are only able to survive droughts if they have enough storage reserves (Weaver and Albertson, 1943). However, in highly variable environments, there may not be enough time between droughts for plants to recover these reserves. Under such circumstances it would pay for plants to rapidly complete their life-cycles in favourable periods and persist as dormant seed over extended drought (Weaver and Mueller, 1942; Margalef, 1969; Ehrendorfer, 1970). Short-lived taxa (annuals and biennials) are, by their nature, obligate re-seeders and thus appear ideally suited to tolerate frequent drought.

The effects of fire are more immediate but limited to removing most or all of the above ground parts. Plants that are able to resprout from underground organs therefore have an advantage in fire-prone regions. It is not surprising therefore that resprouting is a commonly observed trait in rangeland floras around the world (Weaver and Albertson, 1943; Weaver, 1958; Gill, 1981; Pate and Dixon, 1981; Huston, 2003).

I selected a suite of life-form and life-history traits that described the basic biology of the flora and inferred the presence of seeding and sprouting habits, namely: whether plants were dicots or monocots; short-lived (armual or biennial obligate re-seeders) or long-lived (perennials); and above ground morphology and below ground structures, especially as related to re-sprouting.

4.2 Methods

4.2.1 Sampling design

I used the same twenty-five study sites that I sampled to examine patterns of plant species richness to examine patterns of forb functional type richness (Chapters 2 and 3). Forb species recorded in each of the two modified Whittaker plots (20 m x 50 m) were then categorised according to their various life-form and life-history characteristics. Plants were easily separated into divots and monocots based on their floral and leaf morphology, but separating re-seeding from re-sprouting species proved more difficult.

Most perennial forbs in Australian grasslands appear to be able to resprout (Lunt and Morgan, 2002), but perennial species may also display re-seeder life-history strategies *(e.g.* Bond and Van Wilgen, 1996). While most perennial rangeland forbs in southern Africa appear to be re-sprouters, I was unable to determine the extent to which non-sprouting perennial forbs rely on re-seeding. Subsequently, the only species that I could definitely assign to the re-seeder life-history strategy were the obligate re-seeding short-lived annuals and biennials. Taxa displaying these short-lived life-history traits were identified through a combination of the scant functional type information on southern Africa's rangeland forbs and their root and stem morphology.

Re-sprouting taxa were identified as those perennial forbs that possessed underground storage organs or thickened root stocks. These structures included, and were classified as, bulbs, corms, rhizomes, root tubers, stem tubers, woody tap roots (tap roots with secondary thickening), woody caudexes (enlarged, woody, subterranean stem mass) and woody caudexes with root tubers. Excluded from my re-sprouter classification were fibrous roots, species whose roots were parasitic on other plants (including several Scrophulariaceae), and tap roots lacking signs of secondary thickening. As the literature on the underground parts of southern Africa's forbs is limited to their traditional use potential, and because these parts are often not included in herbarium specimens, I was forced to rely solely on my collecting to describe this aspect of the flora. To ensure that I encompassed local variations, I cross referenced my collections of species underground organs between sites.

I classified the above-ground forb growth forms into four categories according to the point of leaf emergence and the orientation of the plant Leaf emergence was divided into radical (at or below the ground) or cauline (from the stem). Plant orientation referred to whether the plant grew erect or prostrate with its leaves on the ground. Thus, the four categories were: cauline prostrate (creeping taxa e.g. *Commelina* spp.), cauline erect (most divots), radical prostrate (typified by the Hyacinthaceae), and radical erect (typified by the Iridaceae) [Figure 4.1]. These growth forms were identified according to their ability to compete with the grass sward. Erect forms are forced to grow directly up through the sward and can only successfully compete for light by growing taller than the grasses or into broad bushes. Radical prostrate growth forms, however, appear to displace the grasses by their lateral growth, creating a gap in the sward. Cauline prostrate growth forms have the real advantage of being able to either creep up over the sward or grow away from other plants to utilize unoccupied space.

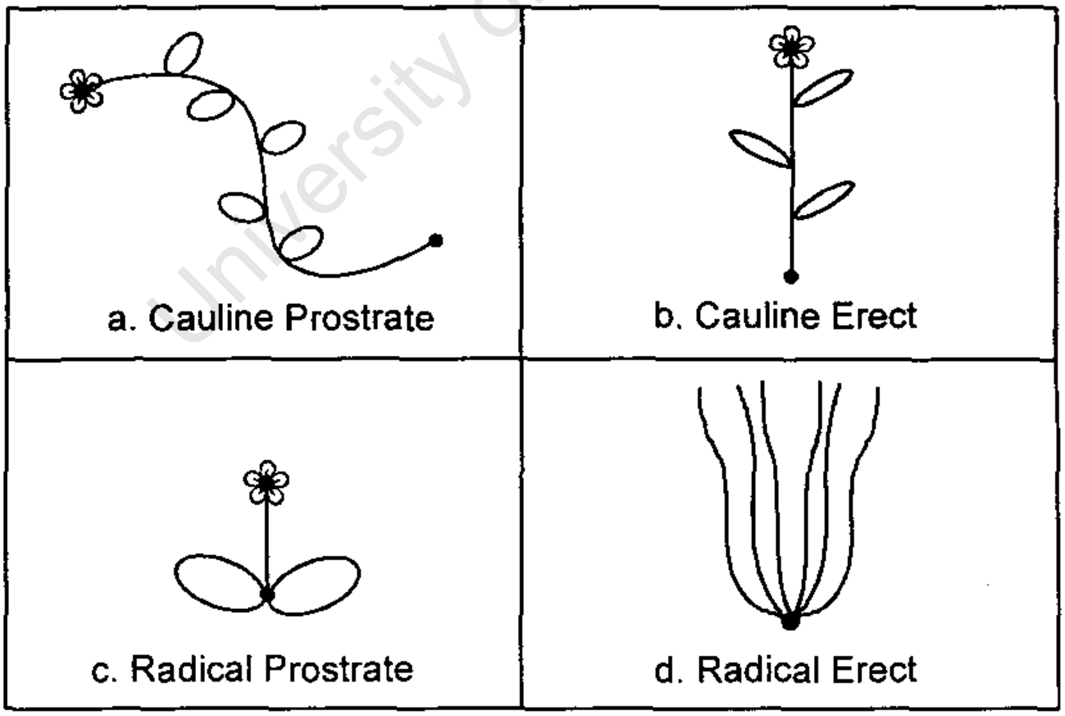


Figure 4.1 Stylised illustration of the four forb above-ground growth forms examined in this study.

4.2.2 Data analysis

The number of forb species displaying the various life-form and life-history strategies across the 2 x 1000 m^2 plots sampled at each site was displayed, along with the total forb richness, according to the mean annual precipitation of each site. I then calculated the mean proportion of forb species displaying a trait across all the sites and used this to calculate, for each site, the number of species that would be expected to display the trait based on the trait's average occurrence. I subtracted the observed numbers of forbs displaying the trait from the expected numbers, and ranked the differences according to mean annual precipitation. Correlation between these differences and the mean annual precipitation gradient were then tested for using a Spearman's ranked correlation. A similar test was conducted against altitude for each trait sampled. The altitude results are, however, not displayed as stronger correlations were found to occur against mean annual precipitation (Tables 4.1 and 4.2).

4.3 Results

The forb flora of the rangelands east of the escarpment was dominated by long-lived, sprouting, dicots with cauline erect growth forms (Figures 4.2, 4.4, 4.6 and 4.8; Appendix **4.1).** These traits were so dominant amongst the forbs that the numbers of species displaying them closely matched the total forb species richness and its trends across the sites. For all the forb functional types examined across the sites, patterns of species richness significantly ($p < 0.01$) correlated to both altitude and mean annual precipitation (MAP). Mean annual precipitation, however, accounted for a greater proportion of the observed variation for all traits except the species richness of cauline erect growth forms (Tables 4.1 and 4.2).

The richness of both the divot and monocot forbs declined sharply below 800 mm MAP, but the monocots showed a proportionately greater loss of species. Monocots never represented more than $^{1}/3$ of the forb species recorded at a site, but dropped to - 13 % of the forb species recorded at sites receiving < 800 mm MAP (Table 4.2; Figures 4.2 and 4.3; Appendix 4.1).

Short-lived forbs were also poorly represented, never constituting more than %of the species at any of the sites. In contrast to the monocots though, their numbers increased in the drier areas. Short-lived forbs represented < 2 % of the species at the wetter sites (> 800 mm MAP), but averaged 13 % of the forb flora in the drier sites (< 800 mm MAP) [Table 4.2; Figures 4.4 and 4.5; Appendix 4.1].

The number of non-sprouting forbs remained fairly constant across the sites irrespective of MAP. Thus, because the total forb and sprouter species richness declined dramatically below 800 mm MAP, this translated into a proportionate increase in non-sprouting forbs with aridity (Table 4.2; Figure 4.6 and 4.7; Appendix 4.1).

The radical forb growth forms were largely represented by monocot species, while the cauline growth forms were mostly represented by dicot forts. It was not surprising then that the representation of both radical growth forms declined significantly in the drier grasslands (< 800 mm MAP). Cauline erect forbs represented around 60 % of forb flora, their richness roughly matching the total forb species richness across the sites. Cauline prostrate forts displayed a broad hump-backed relationship across the rainfall gradient which translated into a proportional increase in richness with aridity (Table 4.2; Figures 4.8 and 4.9; Appendix 4.1).

Table 4.1 Spearman's correlation values for the various fort life-forms and life-history strategies, correlated with altitude. (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$)

Trait	Spearman's R	t(n-2)	*p* - Level
Dicots	-0.50	-2.77	*
Monocots	0.49	2.70	*
Perennials	0.67	4.37	***
Annuals	-0.73	-5.05	***
Sprouters	0.54	3.05	**
Non-sprouters	-0.53	-3.03	**
Cauline Prostrate	-0.64	-3.95	***
Cauline Erect	-0.62	-3.82	***
Radical Prostrate	0.78	6.03	***
Radical Erect	0.67	4.36	***

Table 4.2 Spearman's correlation values for the various forb life-forms and life-history strategies, correlated with mean annual precipitation. (* = $p < 0.05$; ** = $p < 0.01$: *** = $p < 0.001$)

Trait	Spearman's R	t(n-2)	*p* - Level
Dicots	-0.58	-3.40	**
Monocots	0.59	3.48	**
Perennials	0.79	6.15	***
Annuals	-0.78	-5.88	***
Sprouters	0.71	4.79	***
Non-sprouters	-0.70	-4.73	***
Cauline Prostrate	-0.80	-6.29	***
Cauline Erect	-0.54	-3.04	**
Radical Prostrate	0.74	5.34	***
Radical Erect	0.76	5.59	***

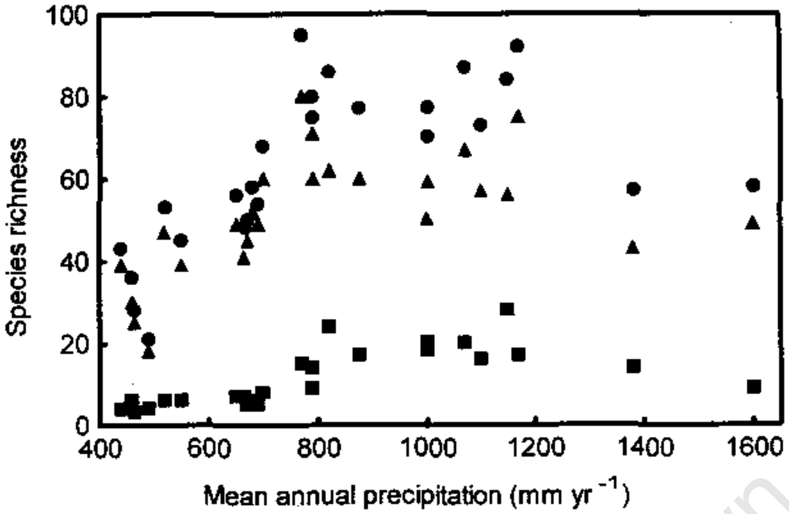


Figure 4.2 Relationship between mean annual precipitation and the total number of forts (s), number of divot forts (A), and number of monocot forbs (11) sampled in 2 x 1000 m^2 quadrats at each site.

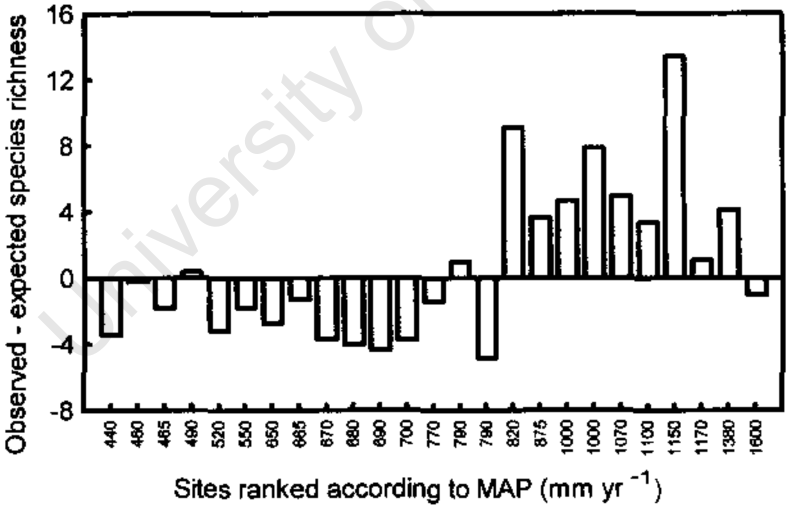


Figure 4.3 Distribution of monocot forbs along a mean annual precipitation gradient, expressed as the difference between the observed mean number of species and that expected from the mean across all sites.

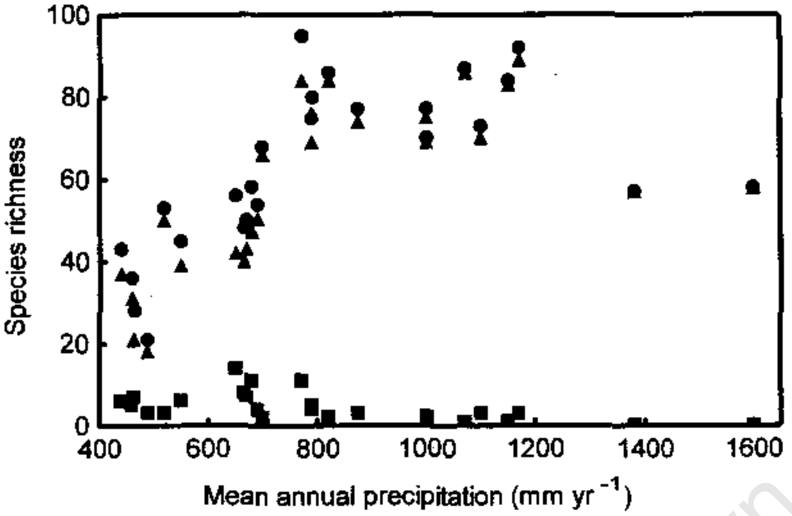


Figure 4.4 Relationship between mean annual precipitation and the total number of forbs (s), number of perennial forbs (A), and number of annual forbs (U) sampled in 2 x 1000 m2quadrats at each site.

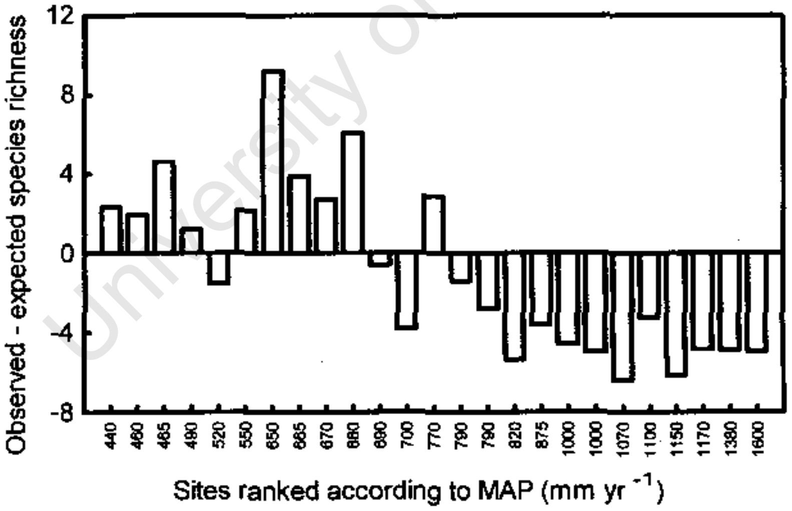


Figure 4.5 Distribution of annual forbs along a mean armual precipitation gradient, expressed as the difference between the observed mean number of species and that expected from the mean across all sites.

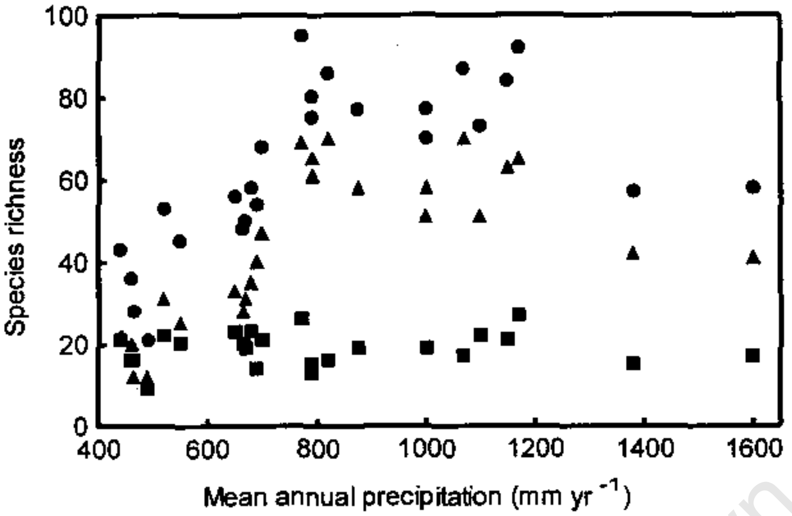


Figure 4.6 Relationship between mean annual precipitation and the total number of forbs (•), number of sprouting forbs (A), and number of non-sprouting forbs (•) sampled in 2 x 1000 m^2 quadrats at each site.

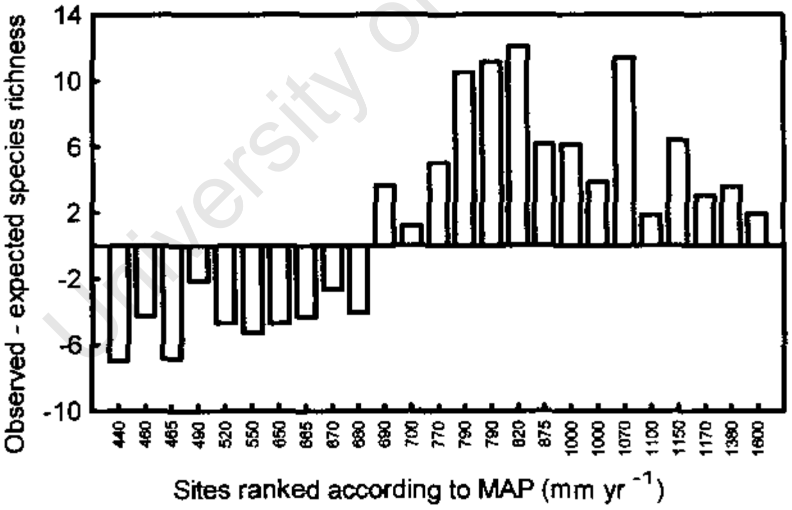


Figure 4.7 Distribution of sprouting forbs along a mean annual precipitation gradient, expressed as the difference between the observed mean number of species and that expected from the mean across all sites

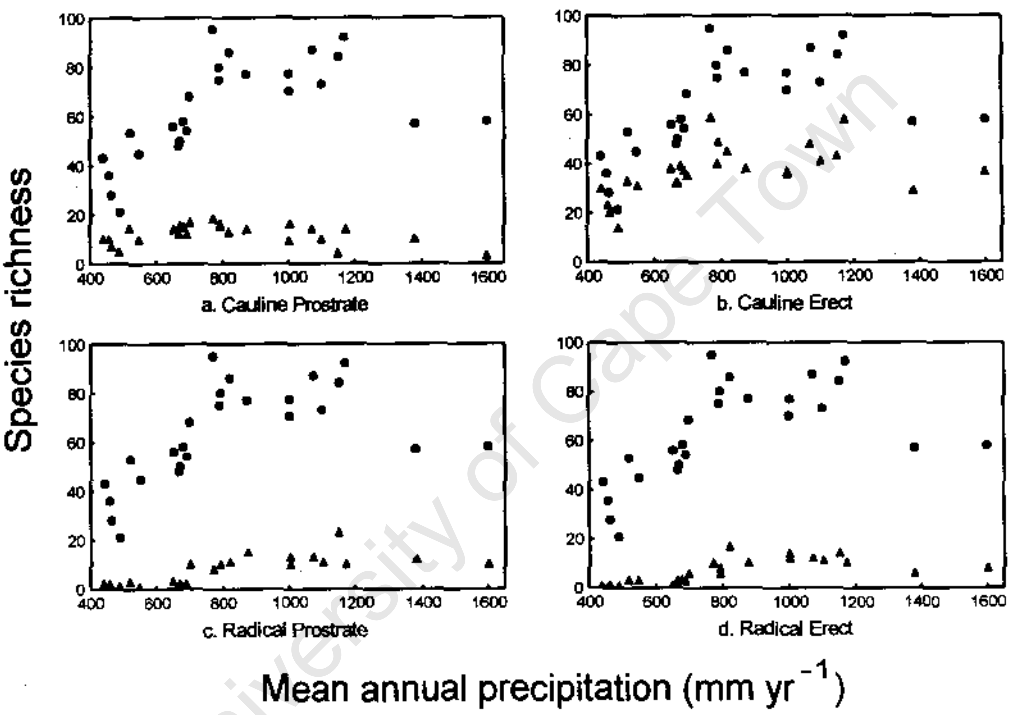


Figure 4.8 Relationship between mean annual precipitation, the total number of forb species Noy and the number of forb species representing each of the four growth forms (A) sampled in 2 x 1000 m^2 quadrats at each site.

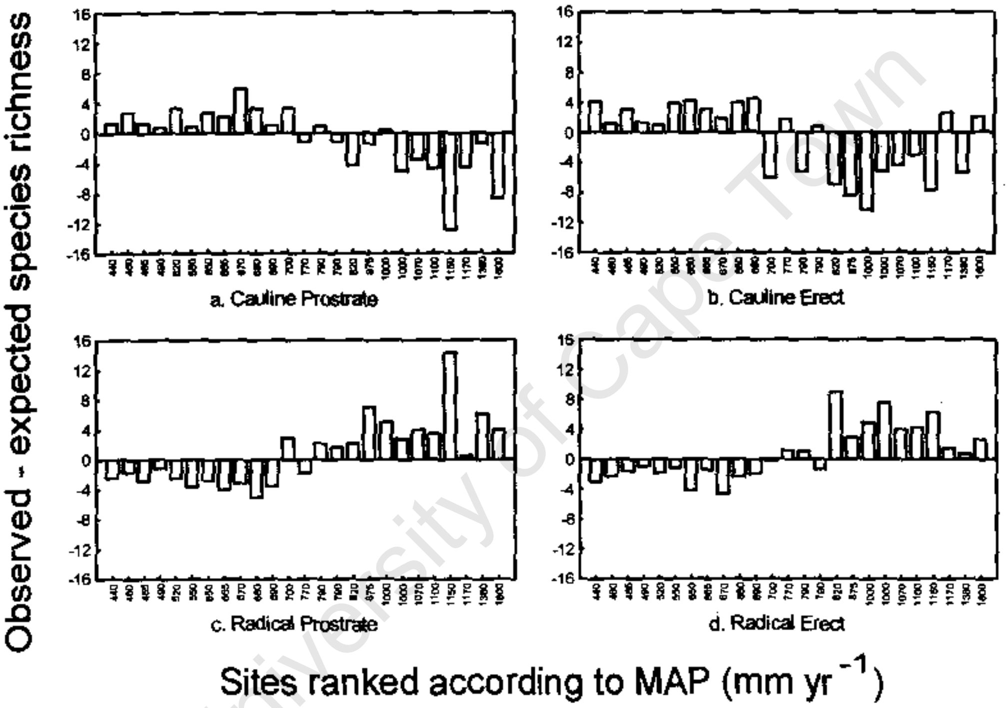


Figure 4.9 Distribution of the four forb growth forms along a mean annual precipitation gradient, expressed as the difference between the observed mean number of species and that expected from the mean across all sites.

4.4 Discussion

44.1 Patterns of fire and drought tolerance

The shift in functional trait composition from the mesic to semi-arid rangelands of southern Africa suggests that distinct fire- and drought-tolerant floras exist across these ecosystems, respectively. Most of the forbs encountered were long-lived, resprouting, dicots, displaying cauline erect growth forms; functional traits that characterise rangeland forb floras around the world (Asia - Wang *et al,* 2002; Australia - Lunt and Morgan, 2002; North America - Freeman, 1998). The increase In short-lived taxa into the semi-arid rangelands suggested a shift towards a drought tolerant flora with decreasing mean annual precipitation (MAP). Conversely, the increase in re-sprouting forbs with MAP, supports the presence of a fire-adapted flora dominating the mesic rangelands of this region. This suggests that, as with the grazing potential of these rangelands (Ellery *et al.,* 1995; Bond, 1997; Hardy *et al,* 1999), disturbance responses differ between mesic and semi-arid areas, with a midpoint around 800 mm MAP.

4.4.2 How forbs survive in grass-dominated ecosystems

Although forbs represent most of the floral richness of rangelands, grasses can constitute up to 90 % of the biomass in these ecosystems around the world (Tremont, 1994). Evidence points to this grass dominance having an overwhelming influence on the diversity of rangeland forbs (Freeman, 1998; Lunt and Morgan, 2002). Forbs appear to have adopted strategies that enable them to persist in dominant grass swards. In fact, short-lived species appeared to be quite the exception in all but the driest rangelands studied. Consequently, one might predict that these floras would not be particularly responsive to disturbances that remove the adult plant. Underground organs confer the ability to resprout after the removal of aboveground parts. The predominance of such organs also appears to allow this rangeland forb flora to remain dormant for several years under moribund swards that prevent sufficient heat from reaching the soil surface to stimulate growth. Forb alpha-diversity has thus been found to persist largely intact for at least five years under a moribund grass sward in a South African fire trial (Uys *et al,* 2004).

Nevertheless, after twenty years and more of fire protection without grazing there was a loss of fire-tolerant species and a compositional shift to fire-intolerant, primarily woody taxa (Uys et *al,* 2004). These gains and losses of taxa under fire protection have, however, yet to be explored more widely for the southern African rangelands. It is essential that this be done to understand the disturbance responses of this flora and so promote informed fire management strategies that will maintain both the fire-tolerant and fire-intolerant floras.

Forbs appear to display four broad growth forms, with varying abilities to compete with the grass sward for light, namely radical and cauline forms of erect and prostrate growth. Radical forms were predominantly represented by monocot taxa and the cauline forms exclusively by dicots. Most of the forbs encountered were cauline erect dicots, but these were seldom observed to be taller than the grass sward. Forbs flower throughout the growing season, while the grasses seem to concentrate their flowering in mid to late summer (Bews, 1925; West, 1951; Bayer, 1955). Thus, some of these cauline erect forts (the early season taxa) appear to avoid being shaded out by the grasses by emerging and flowering before the sward becomes too dense or once it has begun to collapse. Cauline prostrate forbs do not have this problem as they are able to grow up over the grass canopy. These creeping taxa showed a proportionate increase with aridity, which may be due to their other advantage; namely the ability to grow away from grass tufts into inter-tuft spaces. Inter-tuft distances generally increase with aridity so presenting an explanation for the increasing proportion of creeping taxa with increasing aridity.

The poor representation of radical growth forms reflected the paucity of monocot forbs, particularly in the semi-arid grasslands. Unlike the erect dicots though, radical erect monocots were generally as tall or taller than the surrounding grass sward, particularly those in the Iridaceae. Taxa displaying radical prostrate growth forms all had large flat leaves whose whorled positioning creates gaps of > 10 cm in the sward. The proportionally greater abundance of these taxa in the mesic rangelands was probably due to their having been largely represented by monocots whose abundance declined dramatically in the semi-arid areas. Many of these forbs appeared to flower late in the growing season, using the orientation of their leaves *to maintain* a gap in the grass canopy (Pers. Obs.). It was interesting to note that the monocot geophyte growth form, often linked to increased drought-tolerance over their forest dwelling relatives (Goldblatt, 1978), was most prevalent in the mesic rangelands. This might suggest that the geophytic growth form, so widely diversified in the Cape Flora (fynbos) [Goldblatt, 1978], may in some cases confer fire- rather than drought-tolerance. In support of drought-tolerance, the Hyacinthaceae were relatively evenly distributed across the mesic to semi-arid rangelands and therefore relatively more common in the drier areas (Figure 3.8g). In contrast, the Iridaceae, that are centred in the fire-prone Cape Floral Kingdom, were most abundant in the similarly fire-prone mesic rangelands (Figure 3.8h).

4.5 Conclusions

Southern Africa's rangelands appear to be dominated by a similar suite of forb functional types to those found in other rangelands around the world. The distribution of these functional types suggested a clear gradient from fire-adapted taxa in the mesic grasslands to drought-adapted taxa in the semi-arid areas. This has important implications for the way in which we manage and develop our rangelands. Conservationists, especially, need to take this into account and not extrapolate the results of disturbance studies conducted in mesic areas to the management of semi-arid systems.

5 Role of disturbance in forb recruitment

Abstract

I initiated six field trials to examine the effects of animal diggings, drought and fire on the numbers of seedlings and seedling species richness along a rainfall gradient across the rangelands east of the escarpment in southern Africa. Seedling recruitment patterns matched those of the adult sward across the rainfall gradient, both numbers and richness increasing with mean annual precipitation. Seedling numbers and richness were proportionately greatest for fire in the mesic grasslands, shifting to proportionately dominate the animal digging and drought treatments in the semi-arid sites. I also attempted to germinate seed from 60 soil cores collected at each site, but failed to get significant germination from any site. Furthermore, seedlings recorded in the trials did not reflect the flora, suggesting that many species may not recolonise lands transformed by cultivation.

5.1 Introduction

Recruitment is an essential stage in the formation and maintenance of plant communities and is therefore central to our understanding of forb dynamics in grass-dominated ecosystems (Grubb, 1977). Seedling recruitment is not a single event, but rather the culmination of germination, the emergence of the cotyledons above the leaf litter, and the survival of seedlings to the next life-stage (Bullock, 2000). The success of these stages relies on the availability of resources, the absence of chemical and mechanical barriers, and the avoidance of predation (Silvertown, 1980; Bergelson, 1990; Bosy and Reader, 1995; Bullock, 2000). Such conditions are created through the removal of plant material by disturbances, which are subsequently believed to be responsible for mediating recruitment (Platt, 1975; McConnaughay and Bazzaz, 1987).

Disturbance effects differ in the conditions they provide for recruitment according to the component of the sward they affect (*i.e.* above or below ground and living or dead material). Disturbances that kill plants, so generating competitor-free spaces, *may* still not promote recruitment if they do not remove the dead plant material. Although not competing, dead material alters the physical environment, obstructing the availability of resources. This is best demonstrated by the effect that leaf litter has on heat and light, decreasing their availability for germination and growth (Thompson et *al.,* 1977; Silvertown, 1980; Pons and van der Toom, 1988; Facelli and Pickett, 1991; Bosy and Reader, 1995). Dead material may also mechanically impede the emergence and growth of seedlings (Kucera and Dahlman, 1967; Al-Mufti *et al.,* 1977; Grime, 1979), and even present a chemical barrier to recruitment. Thus, it has been found that the leachate produced by the leaf litter of some taxa inhibits the germination of other taxa (Rice, 1972; Werner, 1975; Bosy and Reader, 1995). Although vegetation structure has been shown to affect seed and seedling predation, the role of disturbance in mediating this interaction is less well understood (Bergelson, 1990).

Spatial and temporal variation in disturbance patterns also provides different environments for recruitment that fall into two broad categories: gaps and patches. Gaps are characterised by their short-lived nature, lasting from less than one to seldom more than three generations of the dominant/canopy species. Such spaces are usually created by single event disturbances, as typified by drought, fire or grazing (Weaver and Mueller, 1942; Platt, 1975; Gibson, 1989; Rogers *et* al., 2001). In contrast, patches are longer-lived, being maintained through recurring disturbances, such as those that occur on leks, termitaria or wallows (Platt, 1975; Gibson, 1989). Patches are further characterised as supporting distinct communities to those of the surrounding vegetation, while gap colonizing plants are rapidly assimilated into the sward (Bullock, 2000). While patches generate distinct communities that increase landscape heterogeneity, an understanding of gap dynamics is necessary to provide insight into the formation and maintenance of the community at large (Platt, 1975; Rogers *et al,* 2001).

5.1.1 Disturbance effects

Grasses generally dominate the biomass of rangelands, suggesting that forb recruitment in these ecosystems should be mediated by disturbances that generate gaps in the grass sward. The dominant gap-forming disturbance in southern Africa's rangelands appear to be animal diggings, drought, fire and grazing. Although there are marked spatial and temporal differences, both within and between these disturbances, their most striking difference lies in the manner in which they impact the sward. The effects of fire and grazing are generally confined to the above ground parts, while severe droughts result in both above- and belowground mortality, and animal diggings remove or cover entire grass tufts. As I lacked the resources to thoroughly investigate the spatial and temporal differences within and between these disturbances, I focussed on the different mechanical impacts that the various disturbances had on recruitment.

Grazing has the least physical effect compared to animal diggings, drought and fire. This is due to grazing generally being selectively applied to the living aboveground parts of plants, ignoring the moribund litter. This selectivity, however, presents a methodological challenge, as replicating grazing patterns would require repeat visits to simulate the activities of native grazers. As I was unable to do this on a regular enough basis, I concentrated my efforts on comparing the effects of animal diggings, drought and fire (but see Chapter 6 for the effects of grazing on forb diversity).

The extent of animal diggings is primarily determined by the animal species present and the densities at which they occur. In comparison to drought and fire, animal excavations are far less extensive, but provide some of the largest gaps in the sward. Although both the spatial and temporal distribution of these gaps is often seemingly random, animal diggings provide important sites for the establishment of many rangeland plant species (Platt, 1975; Tilman, 1983; Hobbs and Mooney, 1985; Hobbs and Hobbs, 1987; Gibson, 1989; Rogers and Hartnett, 2001; Rogers *et al.*, 2001). As with grazing, the spatial and temporal unpredictability of diggings makes their experimental replication difficult. Moreover, the range of disturbance sizes and their often unknown time since last disturbance render natural experimentation impractical. I simulated animal diggings by excavation, producing digging sites of known age, standardised size and extent of soil turnover. Studies into the effect of gap-size suggest that plants can germinate and emerge irrespective of gap-size, but that seedling survival increases with gap-size (Grime et al., 1981; Rapp and Rabinowitz, 1985; McConnaughay and Bazzaz, 1987, 1991; Coffin and Lauenroth, 1988; Morgan, 1997, 1998b). I used 1 m^2 plots as these approximate the size of the soil mound outside an aardvark (antbear; *Orycteropus afer)* or pangolin (scaly anteater; *Manis temminckii)* burrow; the most common largish animal-diggings observed in the rangelands in which I was working. The majority of seed of grassland plants has also been found to settle within 1 m of the parent plant, making 1 m2 plots an appropriate size to capture the seed rain (Verkaar *et al.,* 1983; Spence, 1990; Snyman, 2004).

Severe droughts occur at semi-regular, approximately decadal, intervals in southern Africa (Tyson and Dyer, 1978), with less severe droughts occurring more frequently across the region (Le Houerou, 1984; Schulze, 1997). Persistent, severe droughts not only result in the death of most of the sward but extend beyond the point at which all available litter has been decomposed, leaving the ground bare when the drought breaks (Weaver and Albertson, 1936, 1943; Walker *et a*/., 1987). With less severe droughts, gap-size is determined by the inter-tuft distances and the extent to which tufts are reduced by the drought. As sward density decreases with mean annual precipitation across southern Africa (O'Connor and Bredenkamp, 1997; Rutherford, 1980), drought-induced gaps should increase in size with decreasing rainfall. Concurrently, rainfall becomes increasingly erratic as mean annual precipitation decreases, leading to minor droughts being experienced more frequently in the semi-arid parts of southern Africa's rangelands. Thus, one might expect to find taxa with drought-adapted recruitment strategies occurring more frequently in the semi-arid than mesic regions. Drought, however, presents its own methodological problems. Considerable resources are required to simulate drought conditions using rain-out shelters and comparisons to the effects of other gap-forming disturbances are not ideal under natural drought conditions. I attempted to replicate the physical impact of drought on the sward, killing both above- and belowground parts of the sward, and leaving them *in situ.* In doing this, I assumed that the drought had broken and climatic conditions had returned to 'normal', a fair assumption given that attempts at recruitment during drought often results in seedling mortality (Ryser, 1993; Wied and Galen, 1998).

As with drought, severe fires have the ability to clear landscapes of their vegetation, while the size of gaps created by moderate fires is determined by the inter-tuft distances of the sward. In addition to gap-creation, the heat and smoke generated by fires may also facilitate the alleviation of dormancy and the initiation of germination (Cushwa *et at,* 1968; Keeley, 1987; Auld and O'Connell, 1991; Dixon *at Ed,* 1995; Pierce et *al.,* 1995; Auld and Bradstock, 1996; Keeley and Bond, 1997; Keeley and Fotheringham, 1997, 1998; Roche *et al.,* 1997; Morgan, 1998a; Van Staden *et* at, 2000). Ignition sources and appropriate weather conditions aside, the incidence of fires in southern Africa's rangelands is determined by the availability of biomass to burn. As the rate of biomass accumulation increases with mean annual precipitation across these ecosystems (O'Connor and Bredenkamp, 1997; Rutherford, 1980), fire occurs more frequently in the mesic than semi-arid grasslands (Siegfried, 1981; Van Wilgen *et at,* 2000; Balfour and Howison, 2001).

Consequently, I predicted that taxa in semi-arid rangelands should have adapted to recruit under drought conditions and that recruitment at the semi-arid end of the rainfall gradient should be highest for the drought treatment. Conversely, taxa in the mesic rangelands should have adapted to recruit under frequent fires and therefore have the highest recruitment in the fire treatment at the mesic end of the rainfall gradient. To test this, I simulated animal diggings, drought and fire disturbances across six sites representing the transition from the mesic to semi-arid rangelands east of the escarpment in southern Africa. I then recorded the emergence of seedlings across the following two growing seasons to examine the influence these disturbance treatments had on the numbers of emerging seedlings and their taxonomic richness.

5.1.2 *Seed* sources

Available seed is the basis for seedling recruitment (O'Connor, 1991; Tilman, 1997). Therefore, to understand seedling recruitment patterns, it is necessary to distinguish the contribution of seed from parent plants as seed rain from dormant seed-banks (Schott and Hamburg, 1997). For example, *Themeda triandra (a* dominant grass) has no long-term seed bank in southern African savannas, seed only remaining viable for two to three years. This species will go locally extinct if the parent plants are excluded from the system for several years, as occurs under cultivation (O'Connor, 1991).

It is also important to note the composition of the seed-bank as this suggests what the composition of the system might shift to given a severe disturbance that eliminates the parent plants. A number of studies have shown that while the composition of ecosystems dominated by annual taxa is closely reflected in their seed-banks, this is often not the case with perermials (Champness and Morris, 1948; Major and Pyott, 1966; Thompson and Grime, 1979; Donlan and Thompson, 1980; Rabinowitz, 1981; Rabinowitz and Rapp, 1985; Thompson, 1986; Abrams, 1988; Coffin and Lauenroth, 1989; Thompson, 1992; Gilfedder and Kirkpatrick, 1993; Jutila b. Erkkiiä, 1998; Maranón, 1998). Where this occurs, the composition of perennial rangelands may be irreversibly altered by extensive severe disturbances such as ploughing or strip-mining.

Given that such a large proportion of the forb flora displays persistent life-history traits (Chapter 4), I predicted that recruitment would be very low in these rangelands. The starting point for understanding recruitment is quantifying the allocation of reproductive material. As I was unable to revisit all my sites on a regular enough basis to collect the seed myself, I looked to some measure of quantifying the seed-rain. This is often achieved using seed traps placed on the ground. However, this would not have been practical given the abundance of large mammals at each of my six (unfenced) study sites. I therefore focussed on quantifying the presence and composition of seed-banks. Seed-banks are often quantified through sieving and sorting soil cores, but as I felt that I would not get a reasonable measure of the small-seeded grassland flora, I followed Thompson and Grime (1979) and opted to germinate the seed from soil cores.

5.2 Study sites

Trials were initiated at six sites to represent the transition from mesic to semi-arid rangelands east of the escarpment in southern Africa (Table 5.1). All six sites were located in KwaZulu-Natal, the four most arid of which, Pongolapoort (650 mm MAP), Mkuze (665 mm MAP), lmfolozi (680 mm MAP) and Hluhluwe (770 mm MAP), were in the north-eastern Acacia savanna. The next wettest site, Midmar Dam (875 mm MAP), was located in the medium to tall grasslands (0.5 - 1 m) of the midlands and the extreme mesic site, Highmoor (1150 mm MAP), in the short-grasslands (< 0.5 m) of the escarpment foothills (Figure 2.1). Soils across these sites ranged from red clays overlying rhyolite at Pongolapoort and Mkuze; to black clayey soils overlying shales at lmfolozi, Hluhluwe and Midmar Dam; to humic soil overlying basalt at Highmoor.

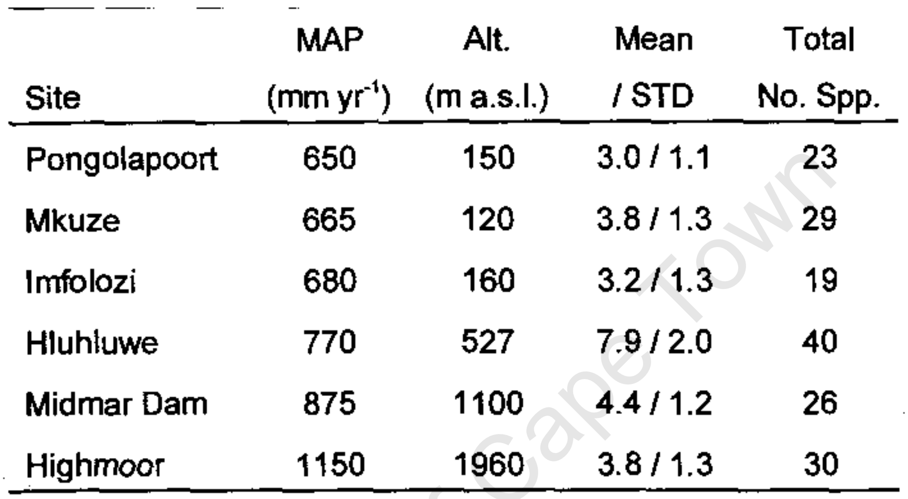
Tallgrass swards of the four savarma grassland sites were all dominated by *Themeda triandra* and *Panicum* spp.. The sward was similar in the midlands except that *Hyparrhenia hirta* replaced the *Panicum* spp. as the co-dominant with *T. triandra.* The shortgrass sward at the montane site, Highmoor, was also dominated by *T. triandra,* but with Heteropogon *contortus* and *Tristachya leucothrix* as co-dominants. Inter-tuft space decreased with increasing MAP across the sites and it became increasingly difficult to locate big enough gaps between the tufts in which to place the 10 cm x 10 cm soil core.

Although the four most arid sites were all located in savanna, trees were only present in the trials at lmfolozi and Pongolapoort. The lmfolozi trial was covered by a short (< 1.5 m), sparse (trees at - 2 m intervals) stand of *Dichrostachys cinerea* that had been reduced to skeletons by the treatment burn. At Pongolapoort there was a small, dense clump (with overlapping canopies) of *D. cinerea (-* 2.5 m) at one end of the plot with several shorter (< 1.5 m) scattered individuals throughout the plot, and a large (- 6 m) *Acacia nilotica* in the opposite corner to the bush clump. Despite the presence of trees at these two sites, there were only two plots (1 m ^{2}) at Pongolapoort that were located under a tree canopy, that of the *Acacia nilotica.*

Further details on the study area, study sites and location of trials at each site are given in Chapter 2 and the following Sub-chapters: Highmoor, 2.5.19; Hluhluwe,

2.5.11; Imfolozi, 2.5.12; Midmar Dam, 2.5.15; Mkuze (clay), 2.5.10; and Pongolapoort, 2.5.8.

Table 5.1 Site characteristics, including the mean and standard deviation (STD) species richness of the sward at 1 m^2 and the total pre-treatment species richness recorded from the 60 x 1 m^2 quadrats sampled at each site.



Site	MAP (mm yr^{-1})	Alt. (m a.s.l.)	Mean / STD	Total No. Spp.
Pongolapoort	650	150	3.0 / 1.1	23
Mkuze	665	120	3.8 / 1.3	29
Imfolozi	680	160	3.2 / 1.3	19
Hluhluwe	770	527	7.9 / 2.0	40
Midmar Dam	875	1100	4.4 / 1.2	26
Highmoor	1150	1960	3.8 / 1.3	30

5.3 Methods

5.3.1 Plot design and sampling

All six trials were initiated at the onset of flowering in the mid to late spring (October / November 2001) in areas where the sward had been burnt at the end of winter (August / September 2001). Ideally, each site should have been sampled at several locations, however, because the research was conducted in conservation areas, I was limited to a single trial per site. Each trial consisted of a grid of 60 plots (each 1 m x 1 m), spaced at 5 m intervals, in six rows of ten plots each (Figure 5.1). Each plot was marked with two steel pins (one of which had a numbered tag) placed at diagonally opposite corners, so that it was possible to re-position a 1 m^2 quadrat over the plot along the direction of the length of the row. The three treatments (animal diggings, drought and fire) were each assigned to 20 plots, based on a random numbers table, with the design being recalculated for each trial. Before applying the drought and animal digging treatments I recorded all the taxa in each plot to provide a measure of the species richness at the site (Table 5.1).

To replicate the die back of both the above- and belowground parts of the sward that occurs with severe drought, I sprayed plots with a 1.5 % solution (as per manufacturer's suggestion) of the non-selective, Glyphosate (Phosphonic acid 360 gfi a.e) based herbicide, Mamba 360 SL (Sanachem (Pty) Ltd; UN No. 3018; Reg. No. L 4817; Act 36 / 1947), that has no to slight soil activity. This killed all the grasses and the majority of the forbs in the plots as a drought would do, but should have had little effect on any buried seed. As the sites had recently been burnt prior to spraying, negligible moribund material was left on the ground as would occur under a severe drought. To replicate animal diggings, I dug all the grass tufts out of a plot to a depth of - 5 cm, dumping these well away from the trial, and turned the remaining soil to a depth of 20 cm.

I sampled the trials at the end of the first flowering season in the period after the plants in the surrounding sward had begun to set seed and before the onset of winter (March / April 2002). I then re-sampled the trials at the end of the following flowering season (March / April 2003). In each plot, I recorded the number of seedlings and attempted to identify species where I could. Matching seedlings to adult taxa was not always possible, especially where seedlings had only recently emerged, and these were grouped as unknowns. Ideally, individual seedlings should have been marked in the first season and followed through to the second season to ensure that they were surviving to the next life-stage and thus recruiting. This was, however, not possible as the research was conducted in reserves with healthy populations of medium-to-large mammals *(e.g.* antelope, baboon, elephant, rhino, and warthog) that would have disturbed such tags. As it was, a number of the steel pins marking the corners of the plots had to be located using a metal detector as they had been trampled into the earth; a resident herd of buffalo being the prime suspects at the Imfolozi site. Fencing these plots to prevent such disturbances was, neither desirable (see the vegetation changes that occurred with grazer exclusion reported in chapter 6) nor financially feasible.

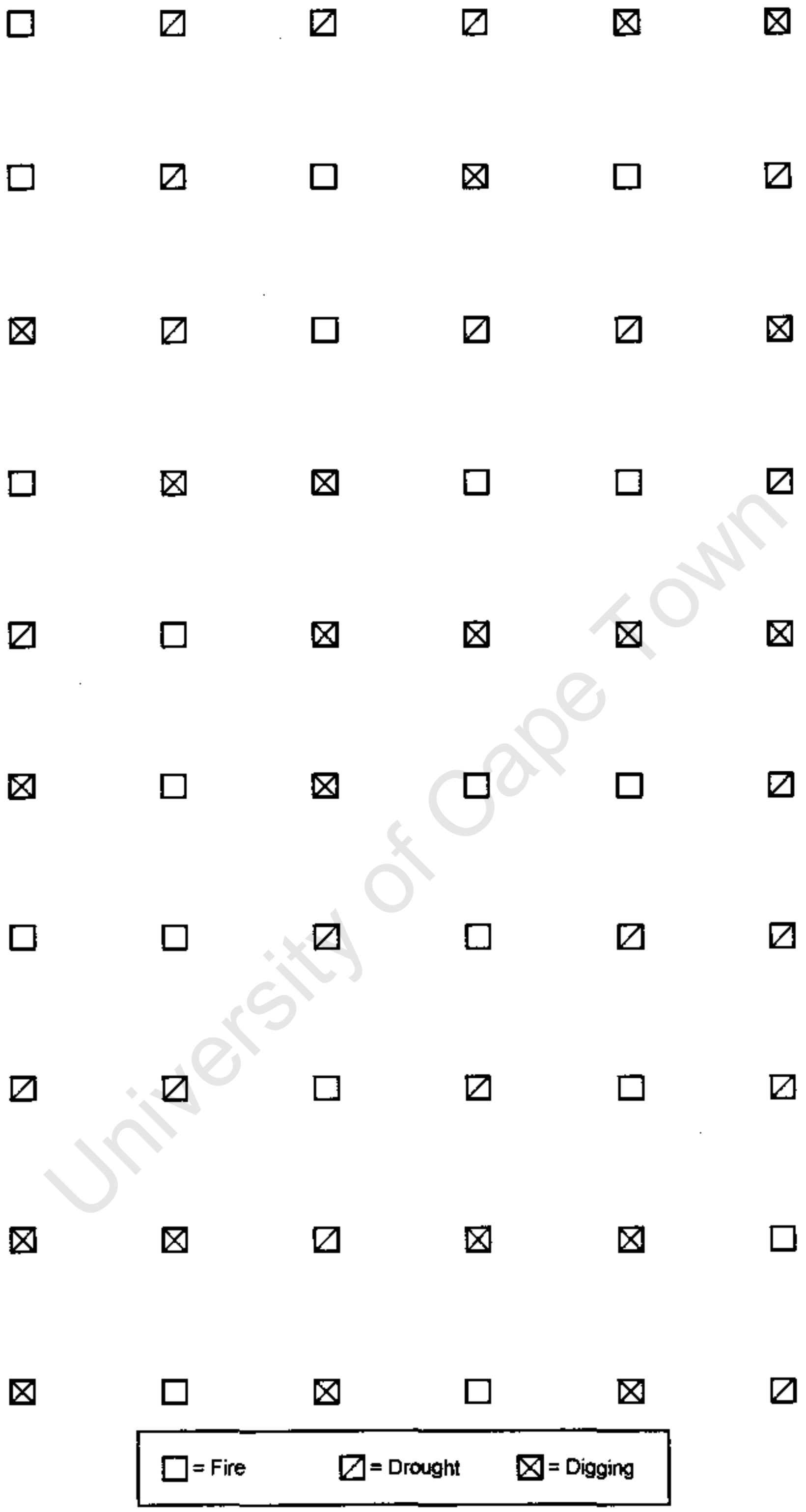


Figure 5.1 Scale diagram of the forb recruitment trial laid out at Highmoor, illustrating the layout of the plots (1 m x 1 m) at 5 m intervals and the random allocation of the treatments to plots.

5.3.2 Seed bank sampling

To test for the presence of a soil seed bank I took 60 soil cores (10 x 10 cm to a depth of - 5 cm) in 6 rows of 10 cores, evenly spaced at 5 m intervals between the 1 m^2 plots. I spread each core over a - 2 cm layer of rinsed and autoclaved coarse sand in a 22.5 cm x 15.5 cm plastic seedling tray. Trays were placed in a glass house where they were maintained at ambient light and temperature, and the soil kept moist with tap water. I monitored the trays three times a week for 6 months when watering. During this time I rotated the trays around the glass house every second week in batches according to their sites. This was done to account for any microclimatic differences that may have existed within the glass-house.

I did not analyse emergence patterns as only 11 seedlings, representing four species (one grass and three forts), emerged seemingly randomly from the 360 samples collected across all the sites. Unfortunately, these seedlings did not survive to the point where they might have been identified, as they succumbed to heat stress due to the cooling apparatus of the glass-house malfunctioning over a weekend.

5.3.3 Data analysis of the plots

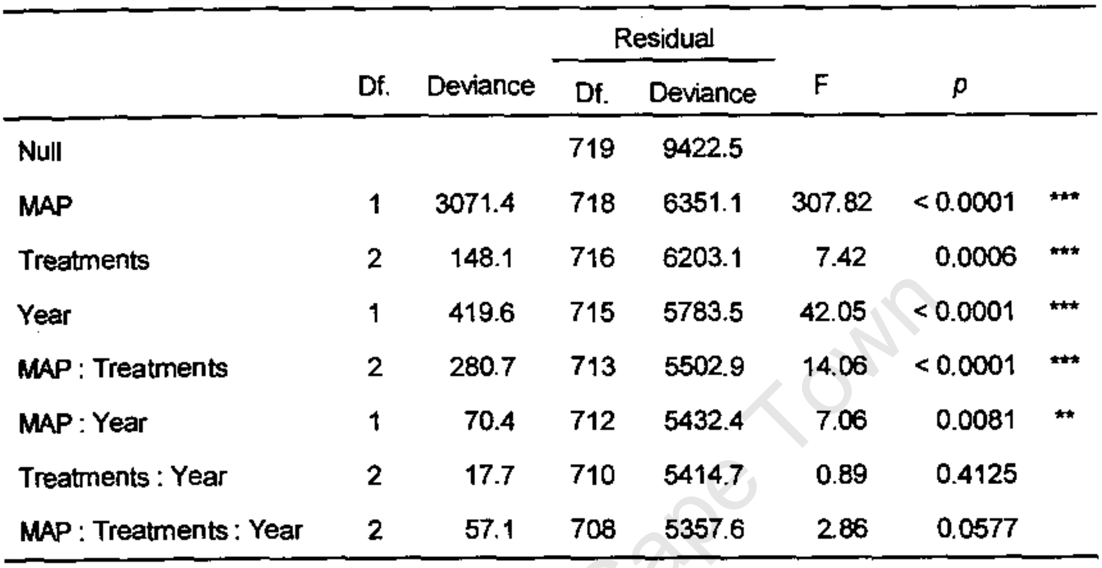
In the sampling design I located plots at three semi-arid and three mesic sites with the intention of comparing treatment responses between mesic and semi-arid grasslands. Examining the data with box and whisker plots, however, suggested that, rather than there being clear treatment distinctions between semi-arid and mesic grasslands, treatment effects slowly shift across the precipitation gradient. To account for this, I examined the effects of MAP, treatments and the time since the treatments were applied (years) on individual and seedling species richness using Generalised Linear Models in R 1.6.0 (The R Development Core Team, 2003). As neither of the data sets were normally distributed I applied a quasi-Poisson distribution to the individual seedling richness data to account for the high level of deviation in this data and Poisson error distribution to the seedling species richness data which was-more

6A Results

Both the numbers of seedlings and seedling species richness significantly ($p < 0.001$) increased with mean annual precipitation (MAP) across the sites (Tables 5.2 and 5.3). This increase was, however, more readily apparent for the numbers of seedlings (Figures 5.2 and 5.3). The numbers of seedlings and seedling species richness were also both significantly ($p < 0.001$) influenced by the time since the treatments were applied, with richness declining in the second year of sampling (Tables 5.2 and 5.3). Treatments only had a significant influence on the numbers of seedlings ($p < 0.001$; Table 5.2), not the richness of seedling species (Table 5.3). Despite this, treatments significantly ($p < 0.001$) interacted with MAP, indicating a shift in treatment effects on both the numbers of seedlings and seedling species richness from the semi-arid to mesic grasslands. The number of seedlings ($p < 0.01$) and seedling species richness ($p < 0.001$) declined significantly from the first to second sampling season across the MAP gradient Yet, despite this decline, there was no significant ($p > 0.05$) interaction between treatments and year suggesting that treatment effects were similar across sampling seasons.

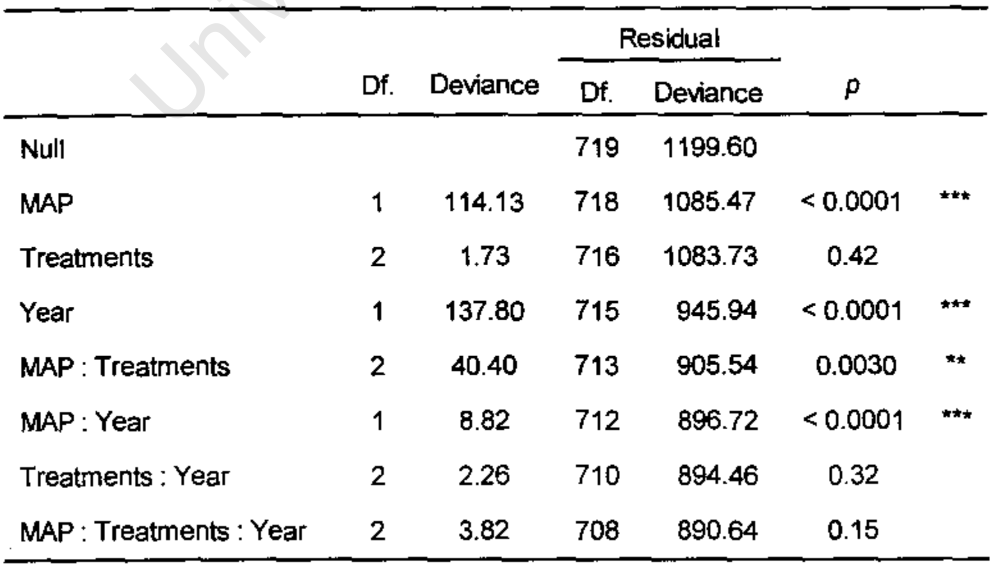
Amongst the emerging seedling species, it was interesting to note that several of the most successful species were not recorded in the pre-treatment sward. Of these, the *Bidens* sp., *Chromolaena odorata, Conyza* sp., *Oxalis* sp. and *Phyllanthus* spp., are short-lived and, besides the *Oxalis* spp., seldom encountered in 'natural' rangelands (Appendices 6.1 to 6.6). Some of the other successful recruiting species, that are regular features of rangeland swards, including *Blepharis integrifolia, Chamaechrista* sp., *Hibiscus pusillus, Sida* sp. *Solanum panduriforme, Spermacoce natalensis, Vernonia* sp. and *Zomia capensis,* are more commonly associated with heavily disturbed areas such as communal rangelands and road verges (Appendices 6.1 to 6.6). Thus, the species with the highest numbers of emerging seedlings appeared to broadly represent gap colonizing specialists, rather than the matrix species that constituted the bulk of the pre-treatment sward.

Table 5.2 Analysis of deviance of the numbers of seedling using a Generalised Linear Model with quasi-Poisson error distribution and log link function. (* = p < 0.05; ** = *p < 0.01; *** = p < 0.001)*

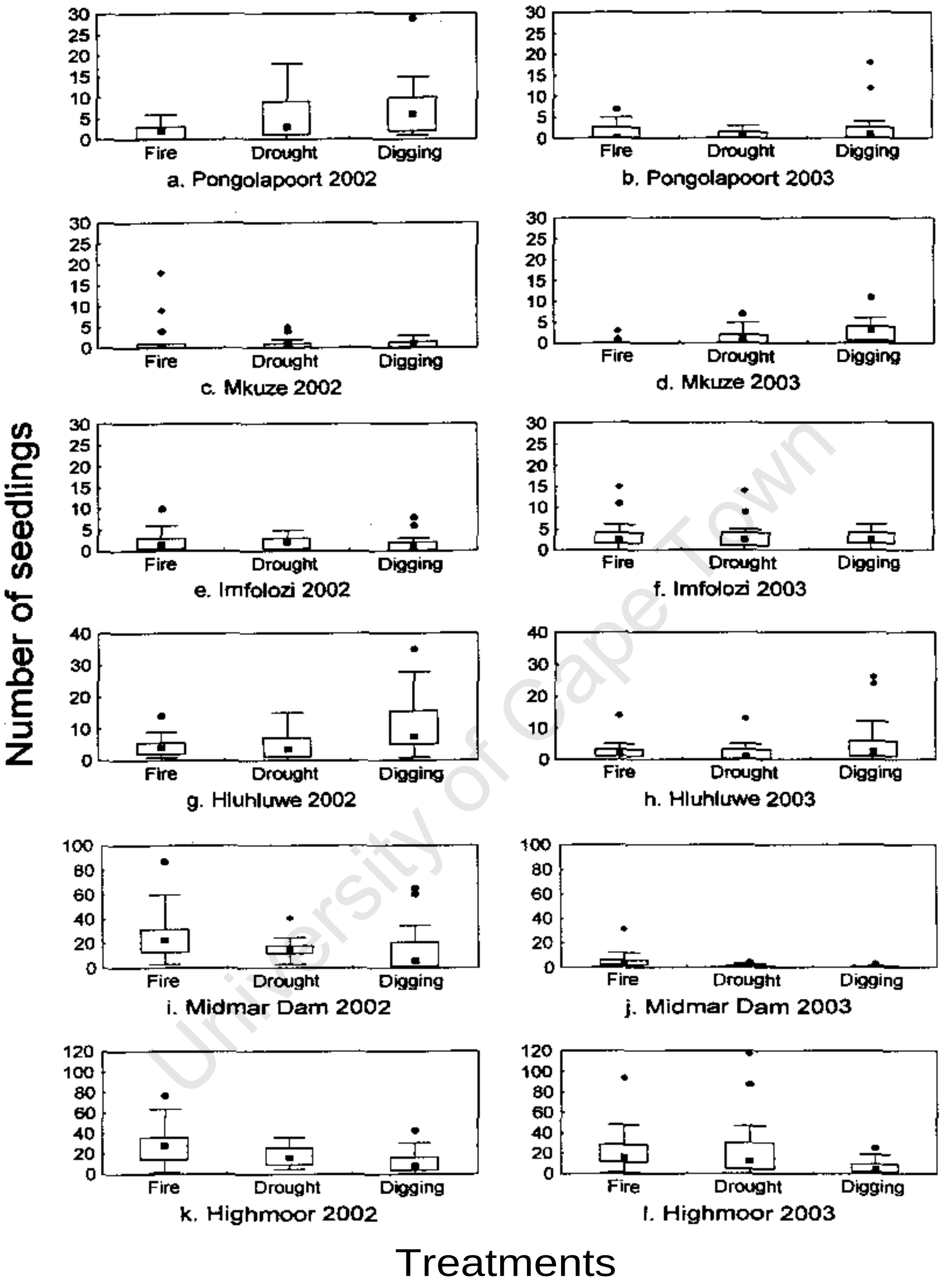


			Residual				
	Df.	Deviance	Df.	Deviance	F	p	
Null			719	9422.5			
MAP	1	3071.4	718	6351.1	307.82	< 0.0001	***
Treatments	2	148.1	716	6203.1	7.42	0.0006	***
Year	1	419.6	715	5783.5	42.05	< 0.0001	***
MAP : Treatments	2	280.7	713	5502.9	14.06	< 0.0001	***
MAP : Year	1	70.4	712	5432.4	7.06	0.0081	**
Treatments : Year	2	17.7	710	5414.7	0.89	0.4125	
MAP : Treatments : Year	2	57.1	708	5357.6	2.86	0.0577	

Table 5.3 Analysis of deviance of the seedling species richness using a Generalised Linear Model with Poisson error distribution and log link function. (* = p < 0.05; ** = *p*< 0.01; *** = *p* < 0.001)



			Residual			
	Df.	Deviance	Df.	Deviance	p	
Null			719	1199.60		
MAP	1	114.13	718	1085.47	< 0.0001	***
Treatments	2	1.73	716	1083.73	0.42	
Year	1	137.80	715	945.94	< 0.0001	***
MAP : Treatments	2	40.40	713	905.54	0.0030	**
MAP : Year	1	8.82	712	896.72	< 0.0001	***
Treatments : Year	2	2.26	710	894.46	0.32	
MAP : Treatments : Year	2	3.82	708	890.64	0.15	



a. Pongolapoort 2002
b. Pongolapoort 2003
c. Mkuze 2002
d. Mkuze 2003
e. Imfolozi 2002
f. Imfolozi 2003
g. Hluhluwe 2002
h. Hluhluwe 2003
i. Midmar Dam 2002
j. Midmar Dam 2003
k. Highmoor 2002
l. Highmoor 2003

Figure 5.2 Median (•) numbers of seedlings recorded over successive years after the application of treatments (each to 20 x 1 m^2 plots) at each of the six sites, along with the upper and lower quartiles (D), non-outlier range (1), outliers *(S)* and extremes (t). Sites ordered from top to bottom according to increasing mean annual precipitation. Note the changing scale of the y-axis from semi-arid to mesic sites.

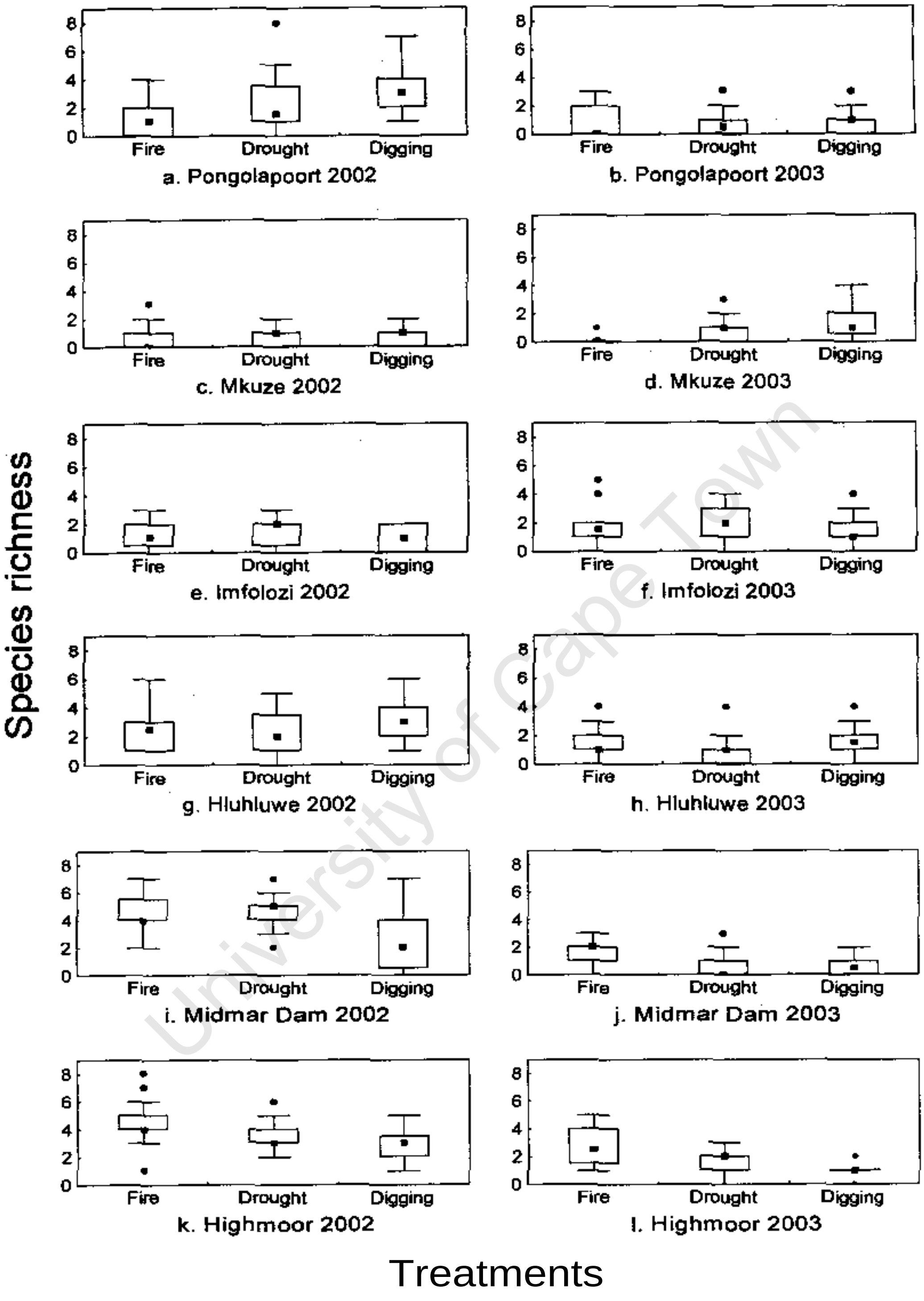


Figure 5.3 Median (•) seedling species richness recorded over successive years after the application of treatments (each to 20 x 1 m^2 plots) at each of the six sites, along with the upper and lower quartiles (D), non-outlier range (I), outliers (•) and extremes (•). Sites ordered from top to bottom according to increasing mean annual precipitation.

5.5 Discussion

5.5.1 Recruitment across the mesic to semi-add rangelands

The most striking result of this study was the dramatic increase in the numbers of seedlings and seedling species richness with mean annual precipitation (MAP) across the sites. This matched the pattern of species richness displayed by the adult plants across the broader MAP gradient sampled across the grass-dominated ecosystems east of the escarpment (Chapter 3). The main aim of this study, however, was to examine how recruitment responses to the three disturbances differed from the mesic to semi-arid rangelands. These patterns were somewhat obscured by the overriding effect of MAP. Yet, there was a relative shift in the effect that disturbance treatments had on the numbers and species richness of recruiting seedlings across the mesic to semi-arid sites. Seedling recruitment in the fire treatment was highest in the extreme mesic rangelands, proportionately decreasing in relation to the animal digging and drought treatments as sites became progressively drier. Thus, seedling recruitment strategies weakly reflected the distribution of plant functional types across the region, with fire-adapted strategies dominating in the mesic grasslands, shifting to drought-adaptation in the semi-arid ecosystems (Chapter 4).

Despite the decline in seedling recruitment in the second season after the application of the treatments, treatment patterns still held across the MAP gradient. This decline may have been due to the generally lower rainfall experienced throughout that growing season or the exhaustion of the seed bank. Seed production, germination and seedling survival are highly dependent on rainfall over critical periods. Thus rainfall, along with seed(ling) predation, appears to be the major factor limiting recruitment in these systems (Weaver and Mueller, 1942; Comelius, 1950; Knapp, 1984; Dye and Walker, 1987; O'Connor, 1995; Wilson and Witkowski, 1998; Barnes, 2001). The increasingly erratic nature of rainfall with aridity may therefore account for the accompanying decline in both the numbers of seedlings and seedling species richness.

1.5.2 Importance of seed for forb recruitment

The remarkably poor germination from the soil cores suggests that this flora -does not maintain a significant soil seed bank, an observation supported by O'Connor and Pickett (1992) and Everson (1994). Alternatively, the experimental conditions may not have been optimal for the germination of this flora. Having, however, struggled to find seed off these rangeland forbs, I feel that the former explanation should not be excluded on the basis of experimental procedure. If this is the case, and these forbs are not contributing to a soil seed bank, it holds serious implications for the utilization of these ecosystems. The forb flora of these ecosystems is dominated by long-lived taxa, the majority of which appear able to recover from disturbance by resprouting from underground organs (Chapter 4). Nevertheless, despite the abundance of underground storage organs, few taxa appear able to reproduce vegetatively, making the flora ultimately reliant on seedling recruitment. Seedling recruitment does not, however, appear to be maintaining these communities. My observations suggest that the fraction of the community that is recruiting from seed does not reflect the dominant taxa in the sward. A similar situation is reflected in Australian grasslands where seed recruitment of the native perennial forbs is rare, despite over 70 96 of these forbs being reliant on seed regeneration (Morgan, 1998a, 1999). Thus, southern Africa's rangelands appear to have a limited capacity to recover their original composition after major soil disturbances such as ploughing. This conclusion is supported by the floral composition of old-lands in the South African Highveld grasslands which had not recovered from cultivation after 70 years of lying fallow (Roux, 1969).

5.6 Conclusions

Seedling richness and disturbance response patterns matched those of the sward, reinforcing the need for mesic and semi-arid rangelands to be managed differently. The results of the seed germination trial, although far from conclusive, were not contradictory to the results of similar studies conducted in rangelands around the world. Thus, although the southern African rangeland forb flora can tolerate natural disturbances such as fire and grazing (Chapter 6; Uys et *al.,* 2004), poor seedling recruitment may reduce the ability of forbs to recover from disturbances that remove the parent plant. This suggests that the diversity of these rangelands may be retained under livestock grazing, but that the expansion of cultivated lands could result in serious, potentially irreversible, losses. The seed biology of the grassland forts requires further study, with emphasis on their modes of dispersal, as these may help explain the poor ability of this flora to recolonise disturbed areas.

6 Effects of grazing on forb diversity

Abstract

I examined the effects of unhindered grazing, rhino exclusion and the complete exclusion of native vertebrate herbivores on forb diversity across the rainfall gradient in Hluhluwe-lmfolozi Park. Species and family composition and richness were not significantly affected by treatments at either the **1** m^2 scale or across the 100 x 1 m^2 quadrats sampled in each treatment across ten sites. Richness declined with rainfall across the park, matched by a shift in species composition. This, however, was not reflected in the proportion of life-form or life-history traits. Compositional shifts were also noted between the first (unburnt) and second (burnt) sampling years, with the greater total richness suggesting turnover in the emergence of this predominantly long-lived flora. Vertebrate herbivory increased under burnt conditions, but invertebrate herbivory appeared independent of burning. Few forbs appeared to be preferentially grazed or avoided.

6.1 Introduction

Since their emergence in the Miocene (-10 m.y.a.) the structure and composition of C, rangeland floras has been influenced by grazing. The current distribution of rangelands is believed to be a post glacial phenomenon, being attained since the last glacial maximum, starting around 15 000 BP (Webb, 1977, 1978; Clayton, 1981; Stebbins, 1981; Mack and Thompson, 1982; Axelrod, 1985; Janis, 1993; Cerling *Oat,* 1997; Jacobs et *at,* 1999; Scott, 2002; De Vivo and Carmignotto, 2004). In this time, and particularly in the last 2000 years, many of the herbivore assemblages that influenced the structure and composition of rangeland floras around the world, have gone extinct (Owen-Smith, 1989; Flannery, 1995). In Africa, however, the grazing fauna has remained largely intact throughout the Holocene (last -10 000 yrs) [De Vivo and Carmignotto, 2004], being recently preserved in a number of wildlife sanctuaries. This allows us to examine the impacts of grazing by intact native herbivore communities on the structure and composition of rangeland plant communities. In doing so we are able to test theories developed to describe grazing effects and challenge our understanding of the processes that have shaped these plant communities.

Grazing effects have received considerable attention around the world, with some emerging generalizations. Grazer exclusion generally favours taller perennial species and results in a decline in species richness compared to communities that are moderately grazed (Stuwe and Parsons, 1977; McNaughton, 1983; Collins and Barber, 1985; Smart et *at,* 1985; Noy-Meir *et al.,* 1989; Belsky, 1992; Mclntyre *et al.,* 1993; Trémont and Mclntyre, 1994; Wahren *et al.,* 1994; Noy-Meir, 1995; Zhang, 1998; Lavorel et *al.,* 1999; Lunt and Morgan, 1999; Noy-Meir and Sternberg, 1999; Oba *et at,* 2001). At the other end of the grazing spectrum, intense grazing (as perceived according to local commercial livestock grazing norms) is often seen to favour shorter species, particularly annuals, and result in a decrease in species richness (McNaughton, 1983; Collins and Barber, 1985; Kucera, 1986; Collins, 1987; Noy-Meir et at, 1989; Belsky, 1992; Milchunas and Lauenroth, 1993; Trémont, 1994; Wahren *et al.,* 1994; Mclntyre et *al,* 1995; Altesor *et al.,* 1998; Fensham *et al,* 1999; Fensham and Skell, 1999; Hadar, 1999; Lunt and Morgan, 1999; Noy-Meir and Sternberg, 1999; Fynn and O'Connor, 2000; Bullock et a/., 2001). Grazing is therefore seen to support the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978; Huston, 1979) across a coarse intensity gradient (exclusion - moderate - intense) [Milchunas *et al.,* 1988; Noy-Meir *et* a/., 1989; Milchunas and Lauenroth, 1993; Olff and Ritchie, 1998; Oba *et al.,* 2001]. Nevertheless, not all studies have displayed such intermediate responses and the shape of the response appears to vary according to environmental factors and disturbance-history (McNaughton, 1983; Milchunas *et al.,* 1988; Noy-Meir et al., 1989; Milchunas and Lauenroth, 1993; O'Connor, 1994; Olff and Ritchie, 1998; Proulx and Mazumder, 1998; Fensham *et at,* 1999; Lunt and Morgan, 1999; Bullock et at, 2001; O'Connor *of at,* 2003). Accordingly, two sets of authors, Milchunas *et* al. (1988) and Olff and Ritchie (1998), have attempted to synthesize the wealth of existing studies into models that describe grazing responses under different environmental and disturbance-history conditions.

6.1.1 Milchunas et *at* (1988) grazing model

Milchunas *et al.* (1988) developed a four-state model based on the evolutionary history of grazing and the availability of environmental moisture to explain grazing effects over a range of communities. They reasoned that the rangeland flora evolved under grazing pressures that have had a marked impact on the physiognomy of these ecosystems. These authors argue that grazing and water stress result in common tolerance mechanisms in floras, as both forms of disturbance result in the partial or total loss of organs. They further argue that grazing avoidance mechanisms *(e.g.* below-ground meristems that allow perennial species to survive heavy grazing [Noy-Meir *et al.,* 1989]) may also confer greater water use efficiency. In support of convergent selection pressures, they cite an increase in such avoidance and tolerance mechanisms with decreasing environmental moisture and increasing evolutionary history of grazing. Subsequently, they present a four-state model based on the extremes of long and short evolutionary grazing history, and semiarid and subhumid environmental moisture conditions (Figure 6.1). They used existing studies to derive the following relationships for the effects of grazing intensity on diversity under each of these four states. (1) Semiarid rangelands with a long grazing history experienced little compositional or physiognomic changes with increasing grazing intensity. This was reported to be due to the generally short stature of these rangelands and their floras having been selected for rapid regrowth following defoliation so that there is lithe relaxation of competitive interactions. A slight decline in species richness was predicted to account for the loss of rare species under intense grazing regimes. (2) Semiarid rangelands with a short grazing history were also found to be dominated by short grasses. Increases in grazing intensity were, however, found to promote grass dominance and so result in a decrease in species richness. This was attributed to the short grazing history of these systems not having conferred the competitive ability required for the forb component of this flora to respond rapidly to defoliation and maintain an equal competitive footing with the grasses. (3) Subhumid rangelands with a long grazing history were found to be represented by a mosaic of short to tall grasses. Tall grasses dominated in the absence of grazing, out-competing the generally shorter forbs, and so resulting in a decline in species richness. Moderate grazing promoted a mosaic of short to tall species, so increasing diversity. Short grasses dominated at higher grazing intensities, leading to Milchunas et *al.* (1988) displaying the effects of grazing intensity on diversity as a classic hump-backed curve. (4) All the subhumid rangelands with a short grazing history examined were dominated by taligrasses that did not tolerate grazing or aridity. Consequently, this grassland state was considered to be the most likely to be altered by grazing. Inferior canopy competitors increased at low grazing intensities, but grazing mortality overshadowed the effects of competitive relaxation on diversity, resulting in a decline in richness at even moderate grazing intensities.

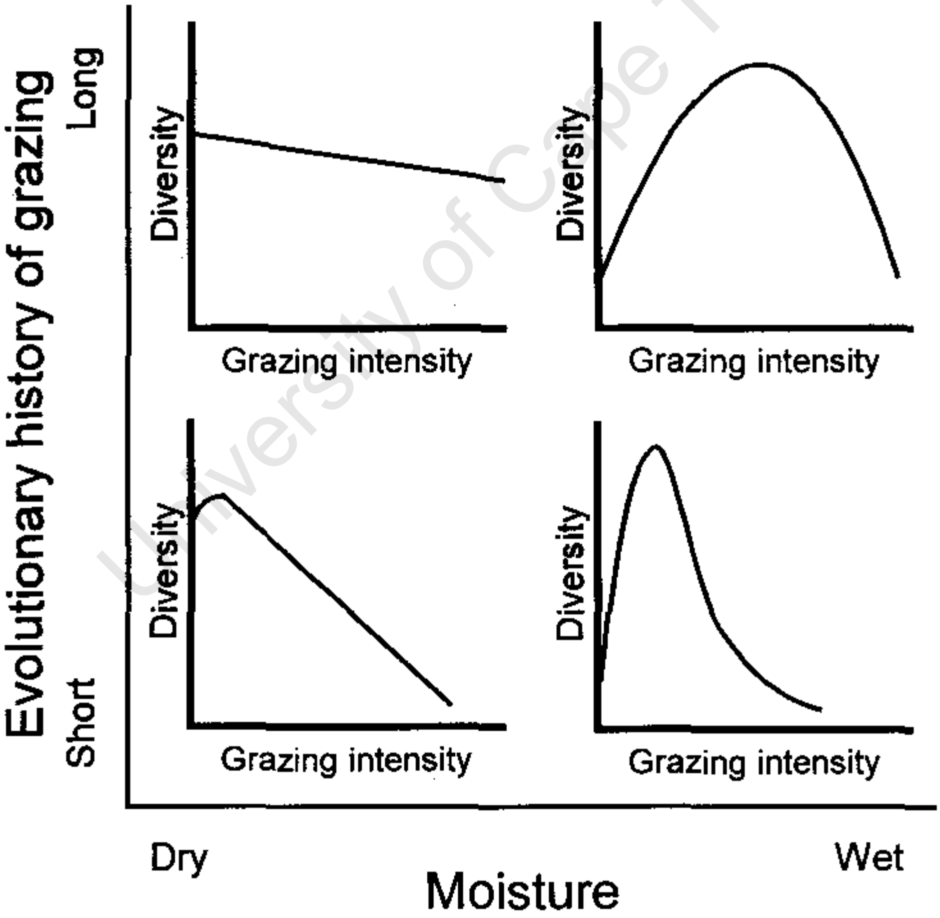


Figure 6.1 Hypothesized four-state model of Milchunas *et al.* (1988) displaying their predicted effects of grazing intensity on rangeland plant diversity under extremes of environmental moisture and evolutionary history of grazing.

8.1.2 Olff and Ritchie (1998) grazing model

Olff and Ritchie (1998) used a similar approach to Milchunas *et al.* (1988), but did not attempt to examine the effect of grazing intensity on diversity. Instead, they focussed on the net effect of colonizations and extinctions experienced as a result of the differential effects of grazing by large and small herbivores. Diversity is accordingly expected to be maximised by disturbances that favour colonization and minimize extinctions. As with the Milchunas et a/. (1988) model, Olff and Ritchie (1998) also invoke an environmental moisture component, namely precipitation. They, however, examined soil fertility on their second axis rather than evolutionary history of grazing. Olff and Ritchie (1998) argue that the ratio of supply of these two resources (nutrients and water) determines the productivity and palatability of the dominant plant species and so whether herbivores will mediate plant colonization and extinction rates. Accordingly, they used existing studies that conformed to the availability of these two resources to predict the effects that large and small herbivores would have on colonization and extinction, and the subsequent net effect (Table 6.1). (1) Dry rangelands on infertile soils were found to have low productivity and to favour species able to compete for the scarce nutrients and water in the absence of herbivory. The same morphological traits that make these species good competitors also often deter herbivory. Consequently, grazing results in few extinctions or is confined to rare, palatable taxa. Grazing also has little effect on colonization due to the low productivity, resulting in a slightly negative or no net effect. (2) Dry rangelands on fertile soils promoted palatable competitive dominants and subsequently supported high herbivore densities. Yet, despite the negative impact these diverse herbivore assemblages were seen to have through extinctions, their removal of the plant canopy may provide regrowth opportunities. Herbivores are therefore predicted to only have a moderately negative net effect on diversity in such ecosystems. (3) Wet rangelands (where precipitation is non-limiting) on infertile soils supported dominant species with low tissue nutrient concentrations. This makes them only palatable to large herbivores that can tolerate low plant tissue quality. It is thus hypothesised that grazing by such large herbivores might shift plant competition from light availability to soil nutrients, and so promote species coexistence. Under such conditions, small herbivores would be forced to target rare palatable taxa, resulting in extinctions, but their soil disturbing activities may mitigate against this by promoting recruitment. Consequently, grazing, especially by large herbivores, could dramatically increase diversity in such ecosystems. (4) Wet rangelands with fertile soils are highly productive, resulting in competition for light being the major limiting factor to plant diversity. Again, high stem : leaf ratios render the plants of such mesic ecosystems only palatable to large herbivores. Reduction of the tall canopy plants by large herbivores increases diversity by favouring a few grazing-tolerant plant species. The introduction of such species that are capable off quick regrowth may, however, encourage higher grazer densities. This, in turn, may result in high mortality of grazing intolerant plants and thus a decline in species richness. Consequently, it is hypothesised that grazing effects in such ecosystems may be either negative or positive depending on the herbivores present.

Table 6.1 Hypothesized four-state model of Olff and Ritchie (1998) displaying their predicted negative (-) and positive (+) effects of grazing by different sized herbivores on colonization and extinction, and the net effects of these under extremes of precipitation and soil fertility.

		Effects on plant diversity				
Environment		Through colonization		Through extinction		Net effects
Precipitation	Soil	Large herbivores	Small herbivores	Large herbivores	Small herbivores	
Dry	Infertile	–	+	– –	–	0 / –
Dry	Fertile	+	+	– –	– –	–
Wet	Infertile	+	+	+ +	–	+ +
Wet	Fertile	+	+	+	–	+ / –

6.1.3 Testing the 'four-state' grazing models

Both 'four-state' models were based on a range of studies, but none from southern Africa as the effects of grazing on plant diversity in these rangelands remains to be explored. Fire effects, however, have recently received some attention and suggest that southern Africa's rangelands show different disturbance responses to similar ecosystems around the world (Fynn *et al,* 2004; Uys *et al.,* 2004). This raises the question of whether the 'four-state' grazing models of Milchunas *et at* (1988) and Olff and Ritchie (1998) are able to predict grazing effect on plant diversity in the southern African rangelands.

Grazing exclusion trials initiated across the precipitation gradient in Hluhluwe-Imfolozi Park in northern KwaZulu-Natal provided the opportunity to test some of the predictions of the two hypothetical models in a southern African context. Fire was included as a response variable across the trials, allowing the relationship between grazing effects and burning to be examined. The broad precipitation gradient across the Park accounts for two of the conditions (semiarid / dry [Imfolozi] and subhumid / wet [Hluhluwe]) represented in the models. The Park, however, represents a fairly uniformly fertile landscape (Whateley and Porter, 1983) whose vegetation has also uniformly experienced a long evolutionary history of grazing (Scott, 2002). Consequently, only two of the four states of each model could be tested.

To review: Milchunas *et al.* (1988) predict that increasing grazing intensity in semiarid rangelands with a long evolutionary history of grazing *(ie.* Imfolozi) should result in a linear decline in species richness. Subhumid rangelands with a long evolutionary history of grazing *(i.e.* Hluhluwe) should display a classic hump-backed response to grazing intensity, species richness peaking at an intermediate intensity. Olff and Ritchie (1998) also predict a decrease in richness when dry / fertile grasslands *(i.e.* Imfolozi) are grazed. In wet / fertile grasslands *(i.e.* Hluhluwe) they predict that species richness may either increase or decrease depending on whether grazers target the quick-regrowth species (whose presence would increase the richness) predicted to be favoured by the removal of the tall canopy.

The Milchunas *et at* (1988) and Olff and Ritchie (1998) grazing *models* both focus on species richness and do not consider how either taxonomic or functional type composition may vary in response to grazing under each of their four states. My analysis of diversity patterns across southern Africa's rangelands (Chapters 3 and 4) suggests that moisture gradients, as applied in both grazing models, may have a significant impact on the functional type composition of the rangelands. ln general, studies suggest that grazing encourages annuals and shorter taxa at the expense of taller perennials (McNaughton, 1983; Collins and Barber, 1985; Kucera, 1986; Collins, 1987; Noy-Meir *et al.,* 1989; Belsky, 1992; Milchunas and Lauenroth, 1993; Tremont, 1994; Wahren et al., 1994; Mclntyre *et al.,* 1995; Fensham *et al.,* 1999; Fensham and Skell, 1999; Hadar, 1999; Lunt and Morgan, 1999; Noy-Meir and Stemberg, 1999; Fynn and O'Connor, 2000; Bullock *et al.,* 2001). Life-form and life-history strategy may therefore determine community grazing responses, but these observations have yet to be reviewed in an environmental context.

To gain insight into grazing effects we need to understand how individual species are affected by, and respond to, defoliation. Grazing responses can, to some extent, be predicted from plant functional traits, but ultimately grazing effects will be determined by the type and density of herbivores present. Their mode of feeding and dietary preferences will determine which species are targeted and the extent of damage. Selective herbivory of the southern African rangeland fort flora has received little attention for both native mammalian and invertebrate herbivores. To address the impact of grazing on individual species, I examined the proportional frequency of forbs displaying various life-forms and life-history strategies and the degree to which the taxa present were damaged by invertebrates, and selective and bulk mammalian herbivores.

6.2 Study sites

Hluhluwe-lmfolozi Park (900 km') is located in northeastern KwaZulu-Natal on the eastern seaboard of South Africa (28° 00'-28° 26'S, 31° 43'-32° 09'E) [Chapter 2.5.11 and 2.5.12; Figure 2.1 and 6.2]. Situated in the foothills of the first escarpment on the western side of the Zululand Coastal plain, the park spans an attitudinal gradient of 60 - 700 m a.s.l. across undulating to hilly terrain. This terrain causes a strong orographic gradient from - 990 mm mean annual precipitation (MAP) in the north (Hluhluwe) to < 635 mm MAP in the south (lmfolozi). Armual precipitation displays an unimodal seasonal pattern, with most of the rain falling in summer; the wettest period being from October to March (70 % of the MAP) and the driest between June and August. Long-term, the rainfall pattern is typical of the region, displaying extended periods of above- and below-average precipitation that last for an average of between four to ten years (Brooks and MacDonald, 1983; Balfour and Howison, 2001). The climate is moderated by the warm Mocambique Current (Indian Ocean), with mean daytime temperatures ranging from 13.2 °C to 25.3 °C in mid-winter (July) and 21.8 °C to 32.6 °C in mid-summer (January) [Owen-Smith, 1988]. Soils across the park are eutrophic, generally being derived from underlying shales and sandstones with interspersed doleritic intrusions (see Whateley and Porter, 1983 for a more detailed description of the pedology and geology).

Besides Eland *(Trarotragus onyx)* and Oribi *(Ourebia ourebi)* which might be expected to occur in the region (Rowe-Rowe, 1994), the park maintains the full complement of medium to large herbivores expected for the region. This included, as of the 2003 game census estimate, approximately: 300 Black (hook-lipped) Rhinoceros *(Diceros bicomis),* 2980 Blue Wildebeest *(Connochaetes taurinus),* 3020 Buffalo *(Syncerus caller),* Bushbuck *(Tragelaphus scriptus),* Bushpig *(Potamchoerus porous),* Common Reedbuck *(Redunca arundinum),* Elephant *(Loxodonta africana),* 750 Giraffe *(Giraffe camelopardalis),* Grey Duiker *(Sylvicapra grimmia),* 23660 Impala *(Aepyceros melampus),* 1375 Kudu *(Tragelaphus strepsiceros),* Mountain reedbuck *(Redunca fulvorufula),* 8050 Nyala *(Tragelaphus angash),* 810 Waterbuck *(Kobus ellipsiprymnus),* 3870 Warthog *(Phacochoerus aethiopicus),* 1710 White (square-lipped) Rhinoceros *(Ceratotherium simum)* and 3430 Zebra *(Equus burchelli).*

The vegetation of the park is broadly described as Natal Lowveld Bushveld (Low and Rebelo, 1996: Vegetation type 26). Plant communities range from open grassland to savanna and woodland, with isolated patches of forest in the wetter northern parts of Hluhluwe. Grasslands in the park are dominated by tall C_4 andropogonoid bunch-grasses, characterised by *Themeda triandra. Sporobolus pyramidalis* dominates patches in the mesic northern parts, possibly due to localized intense grazing and trampling. Stoloniferous lawn-grasses occur throughout the reserve, but the extent of grazing lawns increases with aridity (Archibald, 2003; Archibald *et al.,* 2005), as was found to be the case for the Serengeti (McNaughton, 1985). Grazing lawns in the park are dominated by *Dactyloctenium australe, Digitaria longiflora* and *Urochloa mossambicensis.* Other characteristic bunch-grasses in the park include: *Anstida congests, Bothriochloa insculpta, Cymbopogon excavatus,* C. *plurinodis, Eragrostis curvula, Heteropogon contortus, Hyparrhenia fillipendula, H. hirta, Panicum coloratura* and *P. maximum.* Savanna and woodland communities are variously characterized by the following tree species: *Acacia burkei, A. caffra, A. gerrardii, A. karroo, A. nigrescens, A. nilotica, A. tortilis, Cornbreturn apiculatum,* C. *molle, Euclea divinorum* and *Spirostachys africana,* with *Dichrostachys cinema* occurring as a sub-dominant in several of these communities (Whateley and Porter, 1983).

The Zululand Grass Project, under which this research was conducted, was initiated to explore the role of White Rhino, a supposed keystone megaherbivore (Owen-Smith, 1988), in creating and maintaining the grazing lawns on which they preferentially feed. Exclusion trials were initiated in 1999, with five sites identified in Hluhluwe, at the mesic end of the rainfall gradient, and five sites in lmfolozi, at the semi-arid end. Sites were selected across a grazing intensity gradient, to represent heavily grazed forb dominated areas (Klazana in Hluhluwe; Mona in Imfolozi), lawn-grasses (Seme in Hluhluwe; Thobothi in lmfolozi), mixed lawn and bunch grasses (Maquanda and Nombali in Hluhluwe; Goyeni and Mbuzane in lmfolozi) and lightly grazed bunch grasses (LeDube in Hluhluwe; Sokwezela in Imfolozi) at each end of the precipitation gradient (Figure 6.2 and 6.3). Three treatments (40 m x 40 m plots) were applied at each site: an unrestricted grazing control; a partial exclosure to exclude only the rhino; and a full exdosure intended to exclude all mammals larger than mice. The partial exclosure consisted of a single cable strung - 500 mm off the ground which, because rhinos struggle to lift their knees, is too high for them to cross. In theory this should not have restricted other grazing mammals, but it was found that wildebeest and zebra spent significantly less time in this treatment than they did in the unfenced control (0lff, H., pers. comm.). The full exdosure was erected with a 2 m tall Bonox fence (200 mm x 150 mm rectangular wire mesh decreasing at the bottom to 50 x 150 mm) supplemented by a 800 mm high band of chicken mesh (12 mm hexagonal wire mesh) sunk - 300 mm into the ground to discourage burrowing rodents. The sites and the area around them were burnt in 2000 and 2002 to simulate management burns and to determine the effects of the different exclusion treatments on fire response. Grids of 400 pins (20 x 20 pins) were laid out at 2 m intervals across each plot to provide fixed points to resurvey treatment effects on the vegetation.

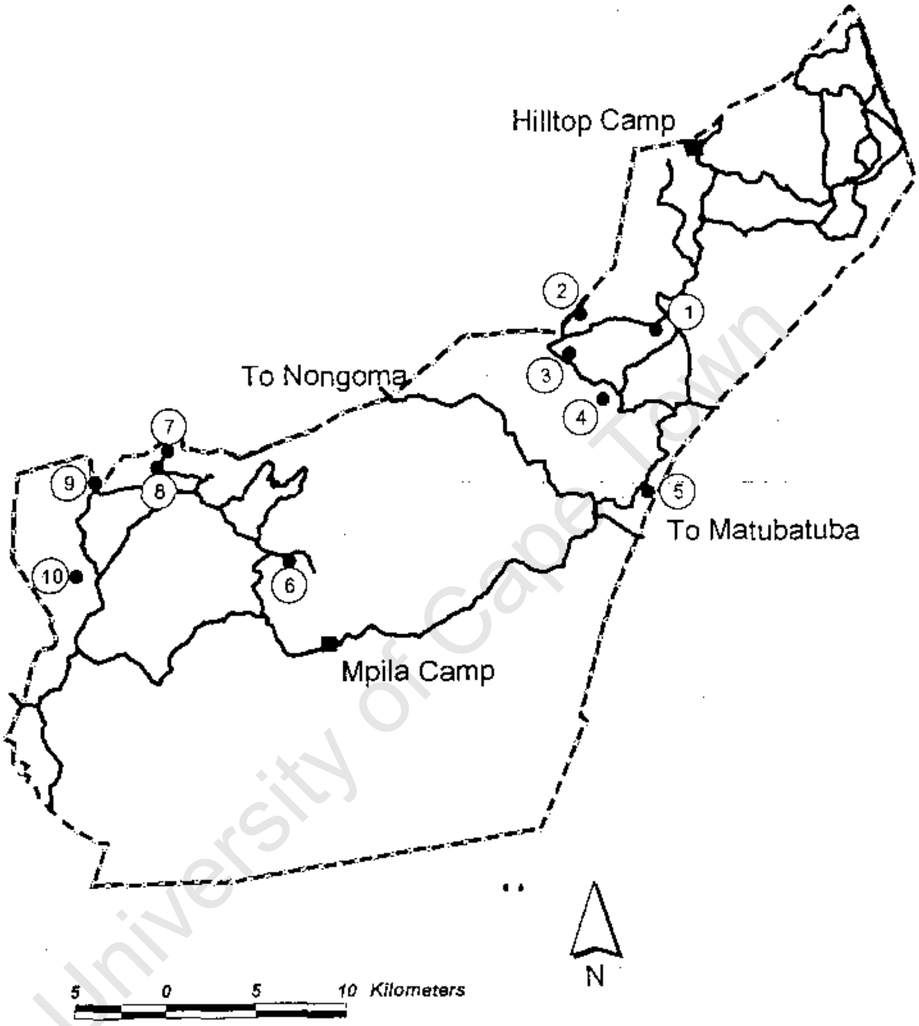


Figure 6.2 Map of Hluhluwe-lmfolozi Park showing location of study sites. Hluhluwe sites: 1 = Nombali (mixed grass), 2 = Klazana (forb dominated area), 3 = Seme (short grass), 4 = Maquanda (mixed grass), 5 = LeDube (tall grass); Imfolozi sites: 6 = Goyeni (mixed grass), 7 = Mona (forb dominated area), 8 = Mbuzane (mixed grass), 9 = Thobothi (short grass), 10 = Sokwezela (tall grass).

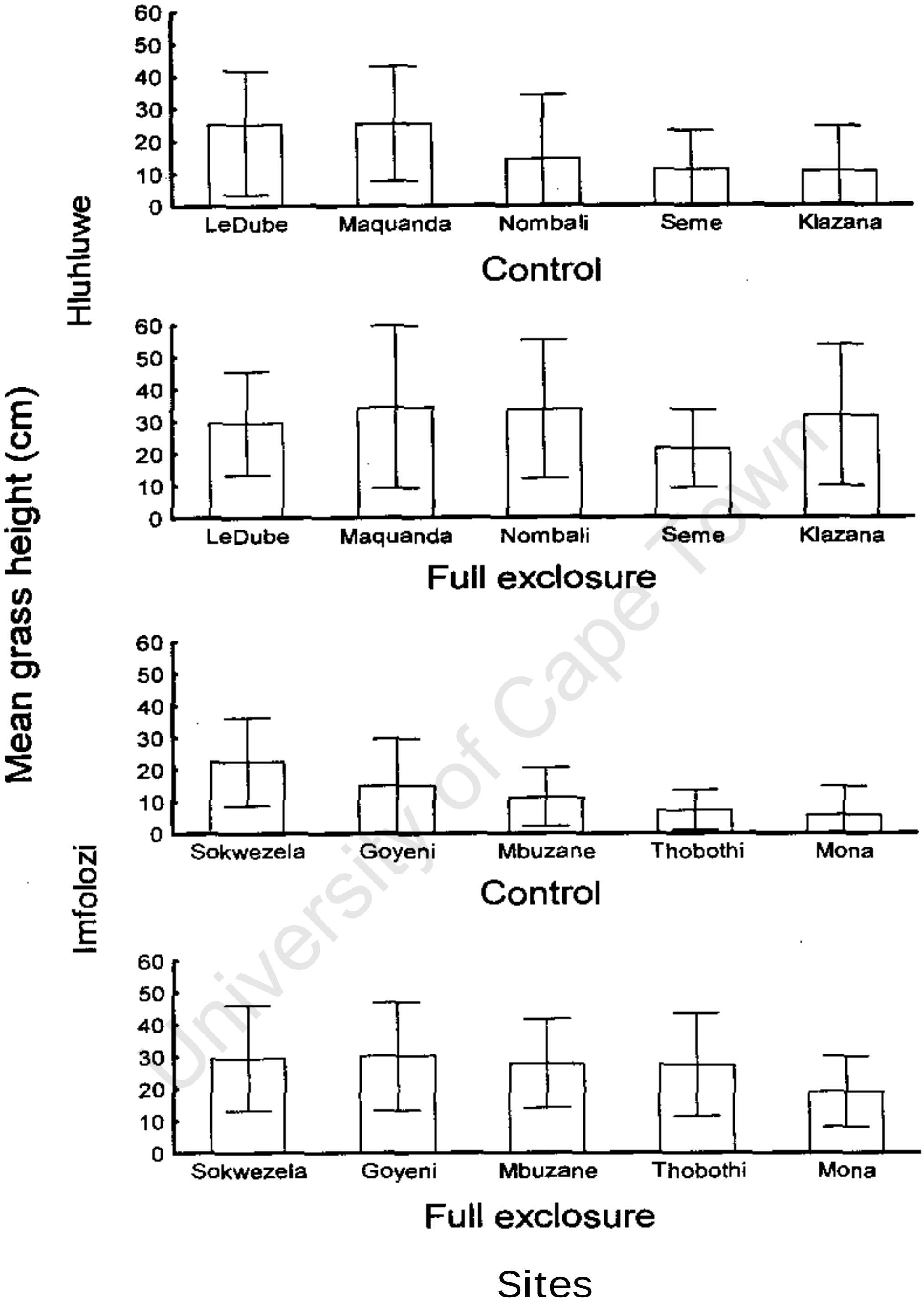


Figure 6.3 Mean and standard deviation in grass height from annual surveys conducted from 2000 to 2003 in the control and full exclosure treatments at each of the five sites at Hluhluwe and Imfolozi (Bond, W.J., unpublished).

6.3 Methods

To capitalize on the application of fire as a response variable, I sampled treatments in the grazing exclusion trials over two flowering seasons. Sites had not been burnt for a year at the time of the first sampling season (2001), but were subsequently burnt before the second sampling (2002). Both surveys were conducted at the peak of the flowering season (November / December), with the second starting four to six weeks after the plots had been burnt at the end of September. I was able to combine the results of both seasons to create a total species list as I sampled the same 1 m^2 quadrats in each plot across the two years. To do so, I used the permanent grid of pins laid out in each plot, centring 100 x 1 m^2 quadrats over the pins in a 10x 10 quadrat block. This resulted in a grid of 1 m^2 quadrats spaced at 1 m intervals as the pins were located 2 m apart. Instead of attempting to randomly select 100 pins of the 400 in each plot, I chose to use a block of pins (10 x 10 pins) as this made it easier for me to re-find pins that were often hidden in long grass and / or covered by soil due to trampling.

I recorded all the forb species within each quadrat, noting their life-form and life-history strategies. Functional traits that were examined included whether the forbs were dicots or monocots, long-lived (perennials) or short-lived (annuals and biennials), sprouters or non-sprouters (according to their underground organs), and their aboveground growth form as described in Chapter 4. I also recorded whether the aboveground parts of each species showed any damage by invertebrates or mammalian grazing.

I compared the mean unburnt, burnt and total species richness in the control, partial and full exclosure treatments (Treatment) across both sampling seasons (Year) between Hluhluwe and Imfolozi (Reserve) at 1 m^2 (n = 500) and 100 m^2 (n = 5) using a generalised linear model in Statistica 6.1 (Anon, 1984). I also graphed the mean and standard deviation of the species richness at 1 m^2 and 100 m^2 for comparison. I then calculated the frequency at which species occurred across the 100 x 1 m^2 quadrats sampled in each plot. Rather than assuming that treatments were having an effect, I used an unconstrained ordination on this data to examine the composition under different grazing treatments across the park. As the initial correspondence analysis showed an arch effect I applied the detrended correspondence analysis in Canoco 4.02 (Ter Braak and Smilauer, 1997). Based on the initial ordination of sites across the park, I subsequently reviewed the sites across each reserve separately. I further reviewed the distribution of species across the treatments and reserves by conducting an analysis of similarities (Anosim) on the combined data set of both sampling seasons of the total species recorded in the 100 x 1 m^2 quadrats in each plot using Primer 5 (Clarke and Gorley, 2001). Subsequently, I also reviewed the Bray-Curtis dissimilarity percentages in a SIMPER analysis of the floras of the two reserves (Primer 5; Clarke and Gorley, 2001).

I recorded the family richness in the treatments across the sites at Hluhluwe and Imfolozi in a table, noting whether families represented divots or monocots. As with the species richness, I examined the distribution of the forb families in ordination space using the detrended correspondence analysis in Canoco 4.02 (Ter Braak and Smilauer, 1997).

I graphed the mean and standard deviation in the species richness of the various forb life-form and life-history strategies recorded as a total from the 100 x 1 m^2 quadrats (100 m^2) sampled at each site. The species richness of traits was compared across the various treatments at each reserve using an analysis of variance (ANOVA) in Statistica 5.1 (Anon, 1984) with the total forb richness at each site factored out as a co-variable to allow for differences between sites. A post-hoc Tukey HSD ANOVA was then conducted to highlight significant differences in trait richness across the treatments and reserves.

I plotted the frequency of each species in each treatment against the number of times the species was grazed to determine whether selective grazing by invertebrates and mammals was occurring. I then used the mean percentage of times that species were being grazed, according to their frequency, to predict what the relationship between frequency and grazing would be if forbs were damaged at random. This assumed a linear relationship between species abundance and the frequency at which they are damaged by grazing. Forb species that were damaged considerably more or less than this average were then believed to have been selected for or against, respectively.

6.4 Results

6.4.1 Forb species richness

The total forb species richness sampled across all sites was consistently higher in Hluhluwe than lmfolozi across the unburnt year, burnt year and total years (combination of both sampling years) [Table 6.2]. Similarly, higher fort species richness was recorded across both reserves in the burnt than unburnt year (Table 6.2). The total of both sampling years was, however, greater than either year alone, suggesting some degree of species turnover within reserves between years (Table 6.2). Turnover was also reflected at smaller sampling scales (1 m^2 and 100 m^2), the total species richness being higher than the richness for either sampling year alone. There was very little difference in species richness among treatments at Hluhluwe. At Imfolozi species richness in the control and partial exclosure was very similar but fewer species were recorded in the exclosure treatment. Differences in species richness between Hluhluwe and Imfolozi (Table 6.2) were, however, not found to be significant at 1 m^2 ($p > 0.05$), only becoming apparent at 100 m^2 ($p < 0.001$) [Tables 6.3 and 6.4; Figures 6.4 and 6.5; Appendix 6.1]. Grazing treatments did not significantly ($p > 0.05$) influence fort species richness across either the reserves, sampling years or sampling scales (1 m^2 or 100 m^2) [Tables 6.3 and 6.4; Figures 6.4 and 6.5].

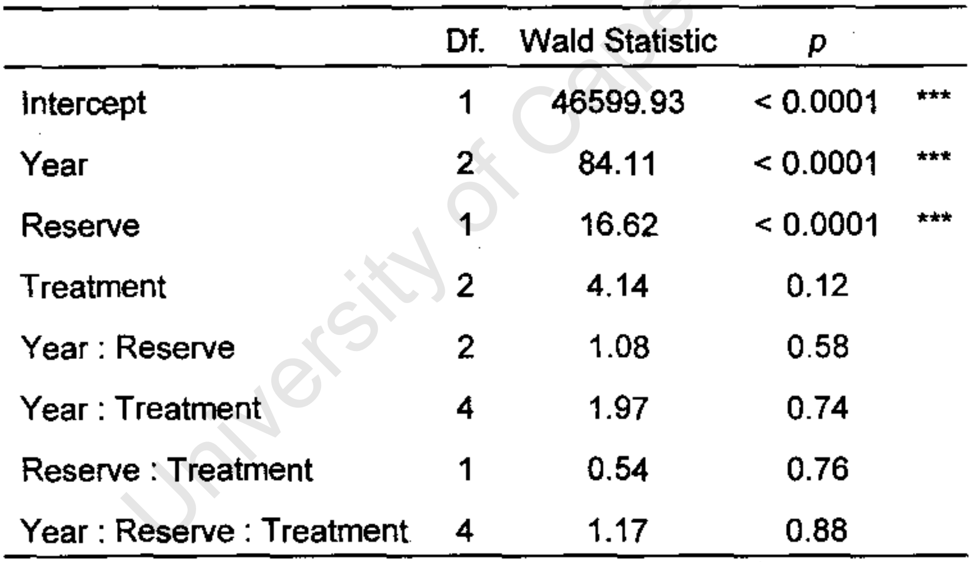
Table 6.2 Numbers of forb species recorded across the five sites of three treatments each (100 x le per treatment plot = 1500 x 1m2 per reserve), sampled in each of Hluhluwe and lmfolozi reserves in the unburnt and bumt sampling years, with the total number and number of common species recorded across the reserves and sampling years.

	Sampling years			
Reserves	Unburnt	Burnt	Total	Common
Hluhluwe	112	131	158	85
Imfolozi	73	81	96	58
Total	125	152	174	101
Common	60	60	78	N/A

Table 6.3 Analysis of deviance of the numbers of forb species recorded at **1 m**^{2} in 100 quadrats surveyed in the unburnt and burnt years and the total over both years (Year) in the control, partial exclosure and full exclosure treatments (Treatment) at each of the five sites in Hluhluwe and imfolozi (Reserve) using a Generalised Linear Model with Poisson error distribution and log link function. (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$)

	Df.	Wald Statistic	*p*	
Intercept	1	1350.85	< 0.0001	***
Year	2	32.95	< 0.0001	***
Reserve	1	0.07	0.78	
Treatment	2	4.42	0.11	
Year : Reserve	2	0.26	0.88	
Year : Treatment	4	0.11	1.00	
Reserve : Treatment	1	3.72	0.16	
Year : Reserve : Treatment	4	0.19	1.00	

Table 6.4 Analysis of deviance of the numbers of forb species recorded at $100\ m^2$ in the unburnt and burnt years and the total over both years (Year) in the control, partial exclosure and full exclosure treatments (Treatment) at each of the five sites in Hluhluwe and Imfolozi (Reserve) using a Generalised Linear Model with Poisson error distribution and log link function. (* = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$)



	Df.	Wald Statistic	*p*	
Intercept	1	46599.93	< 0.0001	***
Year	2	84.11	< 0.0001	***
Reserve	1	16.62	< 0.0001	***
Treatment	2	4.14	0.12	
Year : Reserve	2	1.08	0.58	
Year : Treatment	4	1.97	0.74	
Reserve : Treatment	1	0.54	0.76	
Year : Reserve : Treatment	4	1.17	0.88	

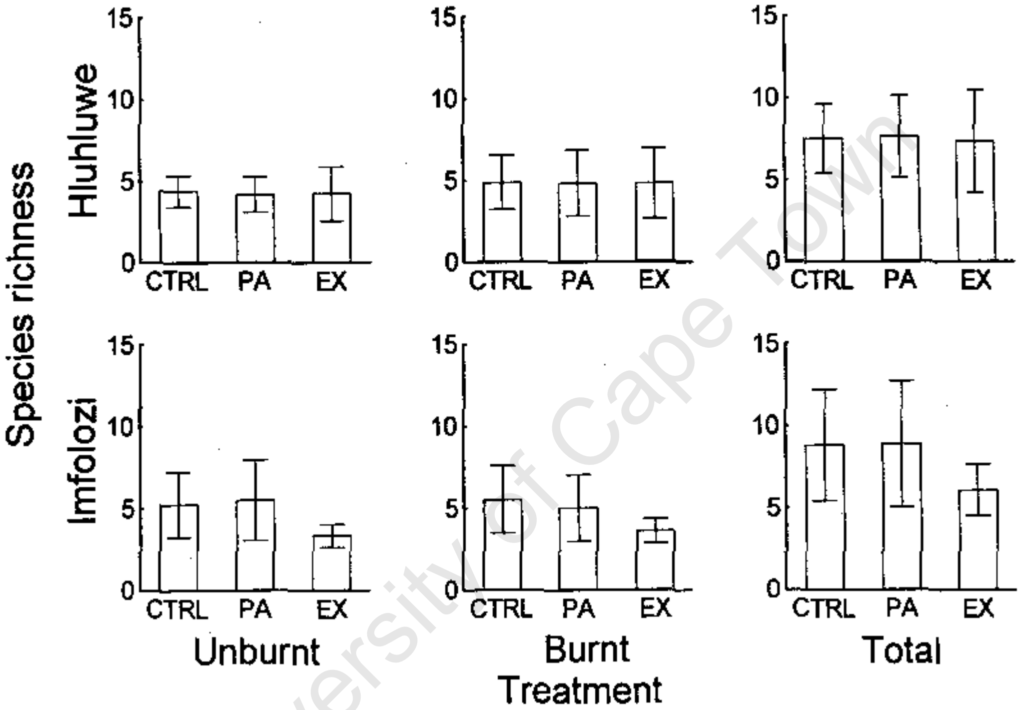


Figure 6.4 Mean and standard deviation in the forb species richness recorded at 1 m^2 (n = 500) in the unburnt and burnt years, and the combined total of both years, from the control (CTRL), partial exclosure (PA) and full exclosure (EX) treatments at each of the five sites in Hluhluwe and Imfolozi.

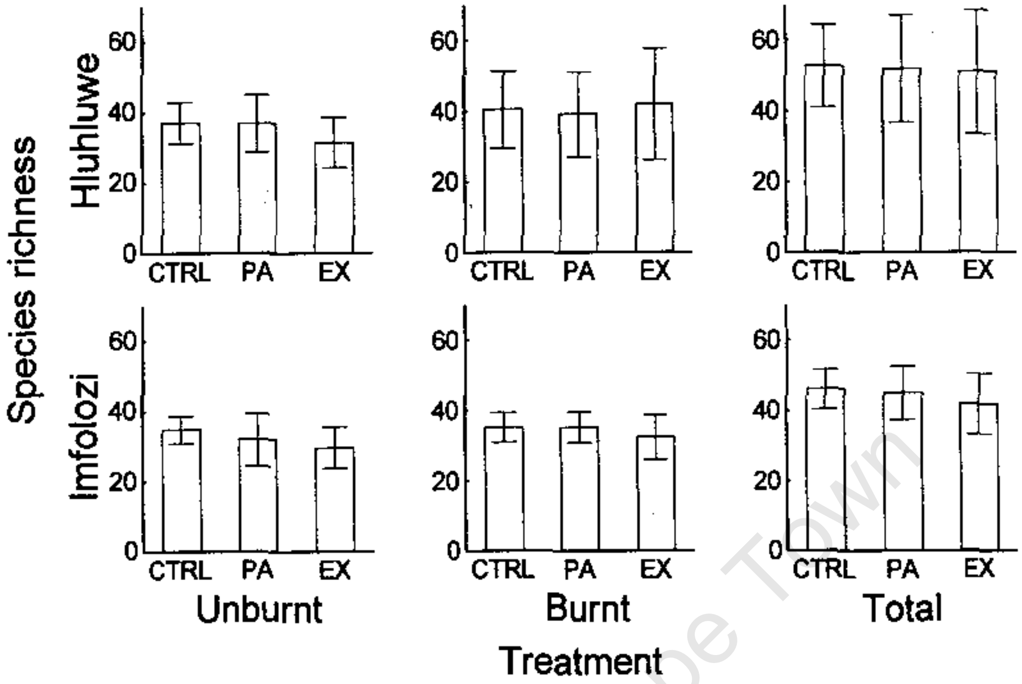


Figure 6.5 Mean and standard deviation in the forb species richness recorded at 100 m² (n = 5) in the unburnt and burnt years, and the combined total of both years, from the control (CTRL), partial exclosure (PA) and full exclosure (EX) treatments at each of the five sites in Hluhluwe and lmfolozi.

6.4.2 Forb species composition

Treatments primarily separated out along the first and strongest axis according to whether they were from the mesic (Hluhluwe) or semi-arid (lmfolozi) sites, in a combined detrended correspondence analysis of the treatments across Hluhluwe and Imfolozi based on the fort frequency (Figure 6.6). Subsequent separation appeared to group plots according to site rather than treatment, as was particularly apparent for the LeDube and Seme plots (Figure 6.6). When reserves were treated individually, plots remained clustered according to sites, but the separation along the first axis appeared more clearly according to the sward height / biomass of sites (Chapter 6.2; Figure 6.3), decreasing from left to right for both reserves (Figures 6.7a and 6.7b). Thus, for Hluhluwe, sites separated out from left to right on the first as: LeDube (tall bunch-grass site), Maquanda and Nombali (intermediate mixed lawn- and bunch-grass sites), and Seme (short lawn-grass site), with Klazana (forb dominated site) intermediate to the mixed- and short-grass sites (Figure 6.7a). For Imfolozi, sites separated out from left to right on the first axis as: Sokwezela (tall bunch-grass site), followed closely by Goyeni and Mbuzane (intermediate mixed lawn- and bunch-grass sites) and Thobothi (short lawn-grass site), with Mona (forb dominated site) quite separate (Figure 6.7b).

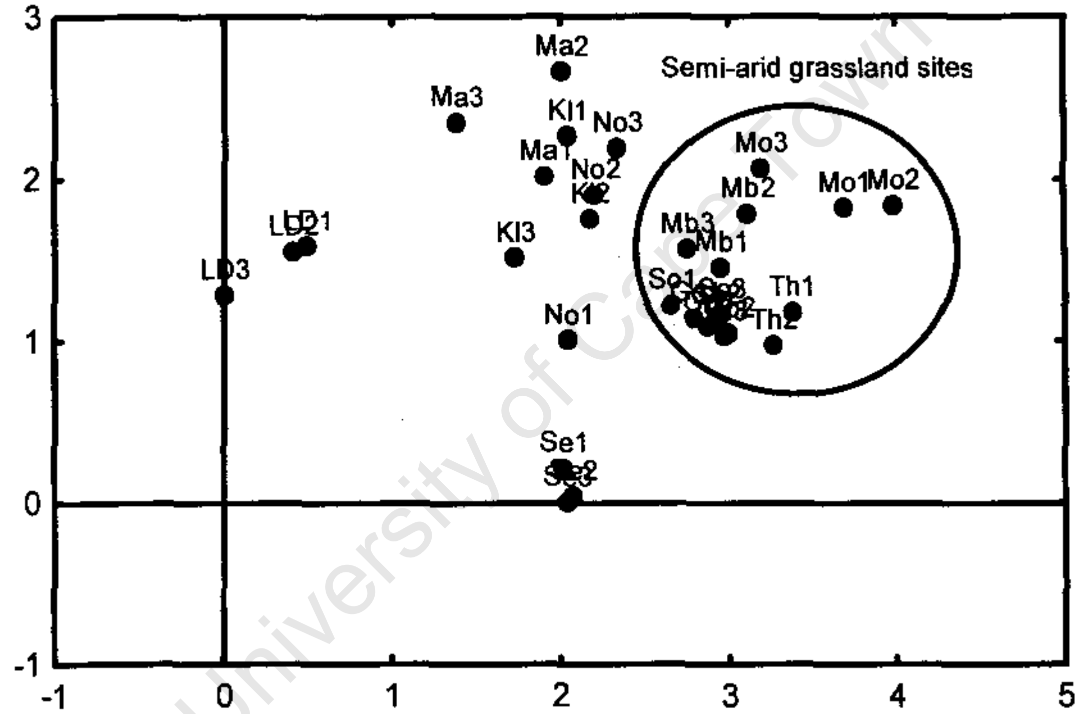
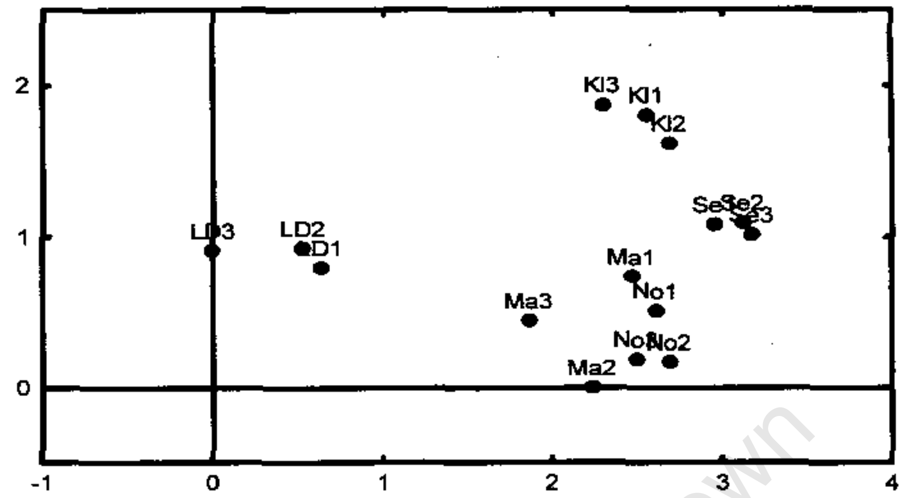
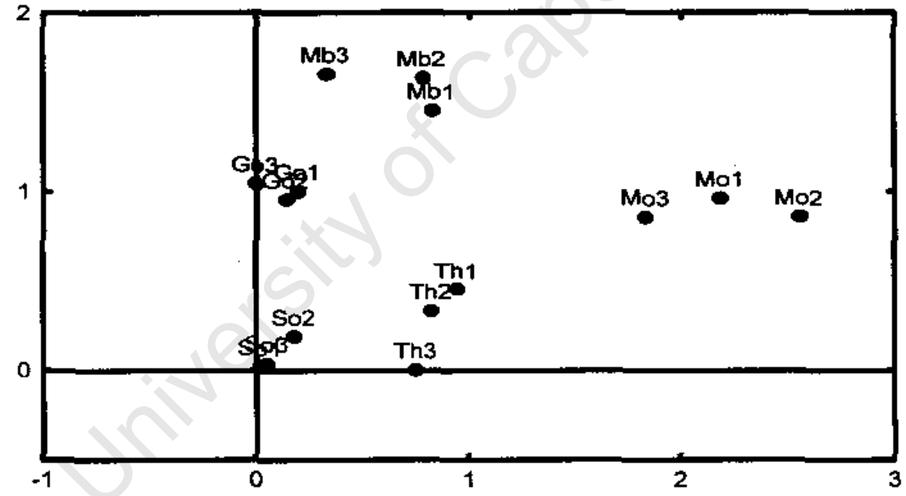


Figure 6.6 Detrended correspondence analysis of the treatments represented in the grazing exclusion trials across Hluhluwe and Imfolozi, based on the total (combined burnt and unburnt) forb species lists. Treatments: 1= control, 2= partial exclosure, 3 = full exclosure. Hluhluwe sites: Kl = Klazana, LD = LeDube, Ma = Maquanda, No = Nombali, Se = Seme. Imfolozi sites: Go = Goyeni, Mb = Mbuzane, Mo = Mona, So = Sokwezela, Th = Thobothi.



a. Hluhluwe



b. Imfolozi

Figure 6.7 Individual detrended correspondence analyses of the treatments represented across Hluhluwe (6.7a) and Imfolozi (6.7b), based on the total (combined burnt and unburnt) forb species lists for each reserve. Treatments: 1 = control, 2 = partial exclosure, 3 = full exclosure. Hluhluwe sites: Kl = Klazana, LD = LeDube, Ma = Maquanda, No = Nombali, Se = Seme. Imfolozi sites: Go = Goyeni, Mb = Mbuzane, Mo = Mona, So = Sokwezela, Th = Thobothi.

As with the sites, ordination of the forb species recorded across Hluhluwe-Imfolozi Park found them separating out from left to right along the first axis according to their distribution across the mesic (Hluhluwe) to semi-arid (Imfolozi) rangeland gradient (Figure 6.8). Species clustered into distinct mesic (55 taxa; 8 monocots; 3 short-lived taxa; 42 sprouters) and semi-arid (45 species; 7 monocots; 9 short-lived taxa; 17 sprouters) groups at either end of the gradient (Figure 6.8; Appendix 6.1) as supported by an analysis of compositional similarity (Table 6.5; Appendix 6.2). The cluster of 14 species at the bottom of the ordination (Figure 6.8) notably contained six monocots: *Anthericum cooperi, A. fasiculatum, Blaine capitata, Cyanotis speciosa, Dipcadi viride* and *Schizobasis* sp. (Appendix 6.1). These six monocots were only commonly found in the treatments sampled at Seme, a short lawn-grass site that was similarly positioned as an outlier in the initial overall site ordination for both Hluhluwe and Imfolozi (Figure 6.6). No pattern could be determined for the spread of species on the second axis, but it is assumed that this relates to environmental gradients across the treatments (Figure 6.8). Despite the significant differences in forb composition noted between reserves and sites ($p < 0.01$), treatments did not appear to be favouring significantly different suites of species (Table 6.5).

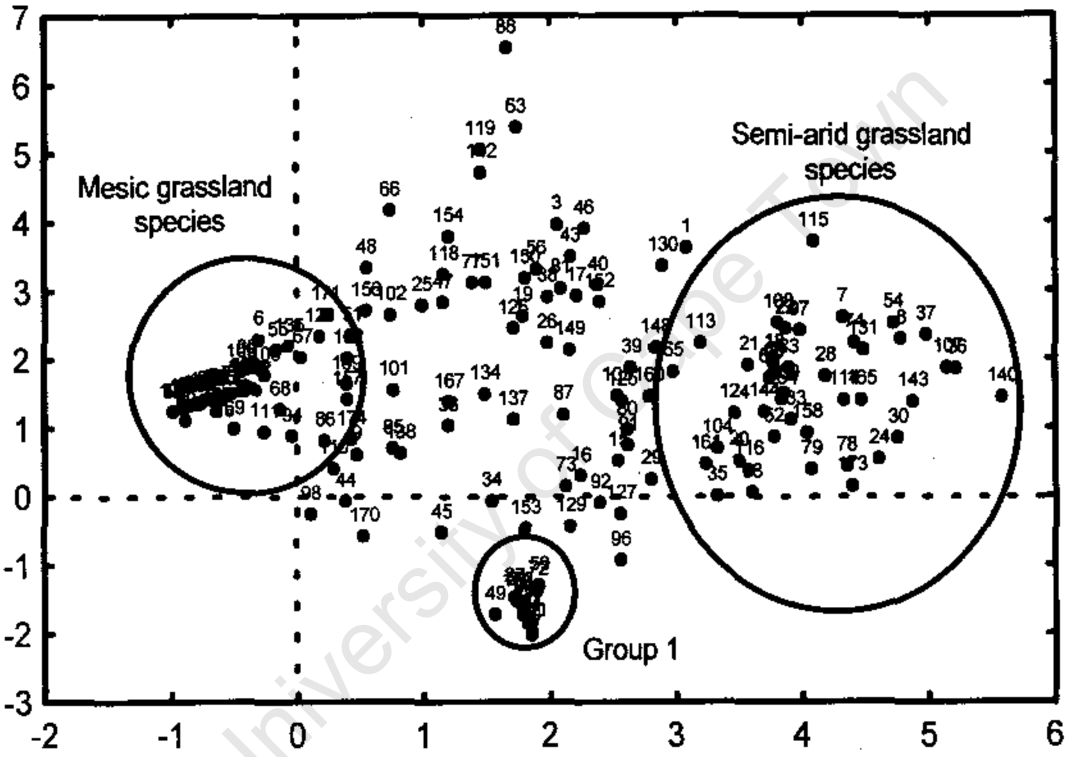
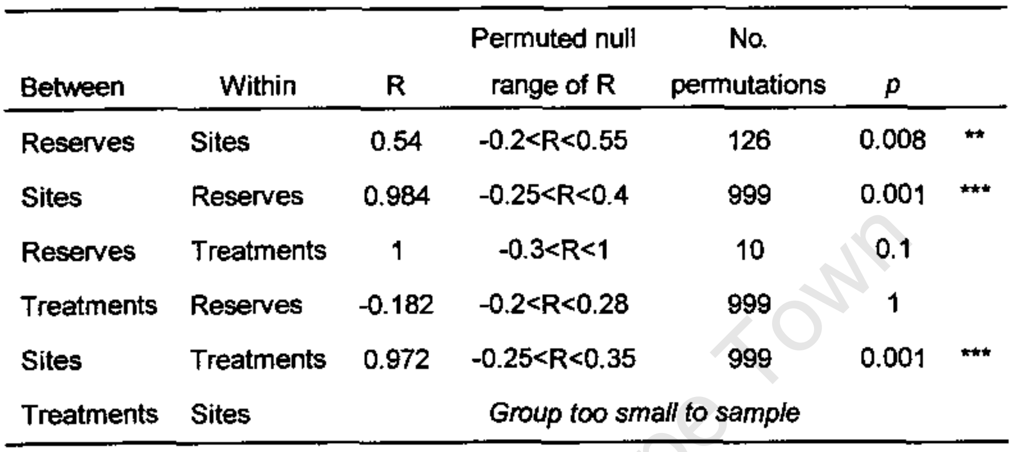


Figure 6.8 Detrended correspondence analysis of the total (combined burnt and unburnt) forb species recorded across the grazing exclusion trials in Hluhluwe and Imfolozi. See Appendix 6.1 for a key to the species and groups, and Appendix 6.2 for an analysis of forb species frequency.

Table 6.5 Two-way nested analysis of the (Bray Curtis, log transformed) similarity in forb composition between and within reserves, sites and treatments of the grazing trials across Hluhluwe-lmfolozi Park, comparing the true value of R to a randomly permuted range of R values expected when the null hypothesis is true. (` = $p < 0.05$; n= $p < 0.01$; *** = $p < 0.001$)



Between	Within	R	Permuted null range of R	No. permutations	*p*	
Reserves	Sites	0.54	-0.2<R<0.55	126	0.008	**
Sites	Reserves	0.984	-0.25<R<0.4	999	0.001	***
Reserves	Treatments	1	-0.3<R<1	10	0.1	
Treatments	Reserves	-0.182	-0.2<R<0.28	999	1	
Sites	Treatments	0.972	-0.25<R<0.35	999	0.001	***
Treatments	Sites		*Group too small to sample*			

6.4.3 Forb family richness

Of the 44 families recorded across Hluhluwe-lmfolozi Park, the Asteraceae (30 spp.) and Fabaceae (24 spp.) were by far the dominant (Table 6.6). Interestingly, the next six dominant families (Acanthaceae [11 spp.], Convolvulaceae [8 spp.], Lamiaceae [8 spp.], Euphorbiaceae [6 spp.], Malvaceae [6 spp.] and Verbenaceae [5 spp.]) were all dicots, followed by the monocotyledonous Hyacinthaceae (5 spp.). In agreement with the forb species richness (Table 6.2 and 6.4; Figure 6.5), the sites in Hluhluwe represented more families on average (37 families) than those in Imfolozi (32 families). There was, however, little variation in the average number of families represented by each treatment across Hluhluwe (CTRL = 37, PA = 36, EX = 38) or lmfolozi (CTRL = 33, PA = 33, EX = 31) [Table 6.6].

Table 6.6 Total number of species (out of 176 spp.) for each of the 44 families recorded in the grazing exclusion trials in Hluhluwe-lmfolozi Park (10 sites [5 per reserve] x 3 treatments x 100 x 1 m^2 quadrats) and the average number of species per family for each treatment, calculated across the sites at Hluhluwe and Imfolozi from the combined pre- and post-burn species lists (5 sites x 100 x 1 m^2 quadrats). Dominant families (based on their average number of taxa) in bold. Asterisks denote families that were only (*) or mostly (**) recorded from the sites in Hluhluwe and only (***) or mostly (****) recorded from the sites in lmfolozi. The two unknown taxa are due to their specimens having been lost before they were identified.

Family	Monocot / Dicot	Total No. of taxa	Hluhluwe			Imfolozi		
			CTRL	PA	EX	CTRL	PA	EX
Acanthaceae	**D**	**11**	**6.8**	**7.8**	**6**	**5.4**	**5**	**5**
Aizoaceae	D	1	0.4	0	0.4	0.8	0.6	0.4
Amaranthaceae	D	3	0.8	1	0.4	0.6	1	0.6
Amaryllidaceae	M	1	0.2	0	0	0	0.2	0
Anthericaceae *	D	1	0.2	0	0.2	0	0	0
Araceae	D	1	0.6	0.6	0.8	0.4	0	0.4
Asclepiadaceae	D	7	1.6	1.2	0.6	0.4	0.8	0.8
Asparagaceae	D	4	0.8	0.6	0.8	1.6	1.4	1.8
Asphodelaceae	M	4	1	0.6	0.6	0.8	1	0.8
Asteraceae	**D**	**30**	**5.6**	**5.8**	**7**	**4**	**4.4**	**3**
Boraginaceae **	D	2	0	0.2	0	1	1.4	1
Brassicaceae	D	1	0.2	0.4	0.2	0	0.2	0.2
Campanulaceae *	D	1	0.2	0	0	0	0	0
Caryophyllaceae *	D	1	0	0.6	0.2	0	0	0
Chenopodiaceae ****	D	2	0.2	0	0	0.8	0.8	0.2
Clusiaceae *	D	1	0	0.2	0.2	0	0	0
Commelinaceae	M	3	2	1.6	1.8	1.8	1.6	1.8
Convolvulaceae	**D**	**8**	**2.2**	**3**	**2**	**3.2**	**3**	**3**
Curcubitaceae	D	3	0.8	0.8	0.6	0.4	0.6	0.4
Dipsacaceae *	D	1	0	0.2	0.2	0	0	0
Eriospermaceae	M	2	0.2	0	0.2	0.4	0.6	0.4
Euphorbiaceae	**D**	**6**	**2.2**	**2.2**	**2**	**2.6**	**2.4**	**2.8**

Family	Monocot / Dicot	Total No. of taxa	Hluhluwe			Imfolozi		
			CTRL	PA	EX	CTRL	PA	EX
Fabaceae	**D**	**24**	**9.2**	**6.6**	**7.4**	**5.6**	**5.2**	**4.4**
Geraniaceae	D	2	0	0.2	0.2	0.4	0.2	0
Hyacinthaceae	M	5	1	1.2	1.6	0.6	1.2	0.8
Hypoxidaceae *	M	2	1.2	0.4	1	0	0	0
Iridaceae *	M	3	0.2	0.4	0.8	0	0	0
Lamiaceae	**D**	**8**	**3**	**2.4**	**1.8**	**1.8**	**1.4**	**1.4**
Lobeliaceae *	D	1	0.8	0.6	0.4	0	0	0
Malvaceae	**D**	**6**	**3.2**	**4**	**3.4**	**4**	**3.8**	**3.4**
Mesembryanthemaceae	D	1	0.2	0	0	0.2	0.2	0
Nyctaginaceae ***	D	1	0	0	0	0.2	0.4	0
Oxalidaceae *	D	2	0.2	0.4	1	0	0	0
Polygalaceae	D	3	1	1.4	1.2	1	0.8	0.6
Portulacaceae	D	1	0.4	0.8	0.6	1	1	0.8
Rubiaceae	D	5	1	0.8	0.8	0.4	0.2	0.6
Santalaceae	D	1	0.6	0.6	1	0.8	0.8	1
Scrophulariaceae *	D	1	0	0	0.2	0	0	0
Solanaceae	D	3	1.4	1.4	1.4	1.6	0.8	1
Thymelaeaceae **	D	1	0.2	0.2	0.2	0.2	0	0
Tiliaceae **	D	1	0.4	0.6	0.8	0	0	0.4
Verbenaceae	**D**	**5**	**2.4**	**2.4**	**2.4**	**2.2**	**2.2**	**2.6**
Violaceae	D	1	0.2	0.2	0	0.4	0.4	0.6
Vitaceae	D	2	0.2	0.4	0.4	0.6	0.2	0.8
Zygophyllaceae ***	D	1	0	0	0	0.4	0.6	0.6
Unknown		2	0	0.2	0.2	0.4	0.6	0.2
Total number of families			37	36	38	33	33	31

6.4.4 Forb family composition

Ordination of sites according to the distribution of forb families across Hluhluwe and Imfolozi produced a similar result to the ordination of species (Figures 6.6 and 6.9). The initial separation of sites occurred along the first and strongest axis according to whether they were located in Hluhluwe or Imfolozi (Figure 6.9). There was however more overlap between sites than seen in the ordination of sites according to species composition. Secondary separation of plots appeared to be determined by the site to which the plots belonged rather than their treatments. Again, this was best displayed by the treatments at LeDube and Seme, the bunch- and lawn-grass sites in Hluhluwe (Figure 6.9).

As with the ordination of species, families were distributed along the first and strongest axis from mesic (Hluhluwe) to semi-arid (lmfolozi) grasslands (Figures 6.8 and 6.10). Of the 44 families, 11 were only recorded in the mesic rangeland sites of Hluhluwe and two only recorded in the semi-arid rangelands of lmfolozi (Table 6.6; Figure 6.10). These, however, comprised some of the less well represented families (s 3 species), while the better represented families (> 5 species) were all clustered in the middle of the ordination (Table 6.6; Figure 6.10). No clear pattern could be discerned to account for the spread of families across the secondary axis (Figure 6.10).

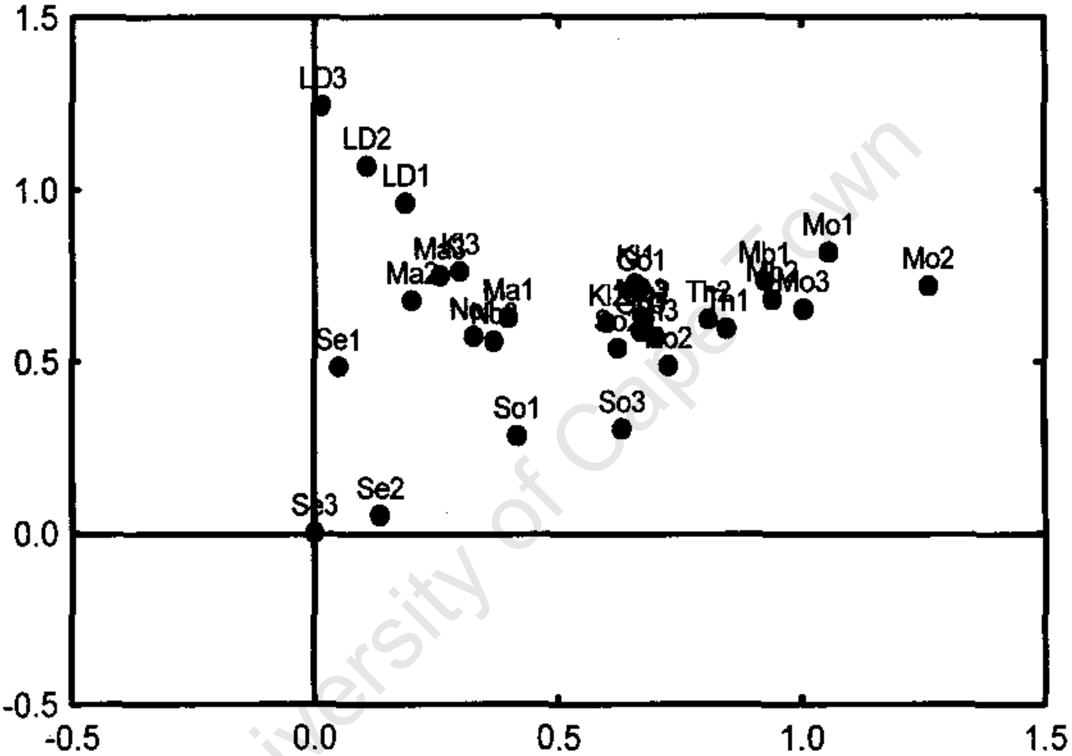


Figure 6.9 Detrended correspondence analysis of the treatments represented in the grazing exclusion trials across Hluhluwe and Imfolozi, based on the total (combined burnt and unburnt) forb family lists. Treatments: t= control, 2 = partial exclosure, 3 = full exclosure. Hluhluwe sites: KI = Klazana, LD = LeDube, Ma = Maquanda, No = Nombali, Se = Seme. Imfolozi sites: Go = Goyeni, Mb = Mbuzane, Mo Mona, So = Sokwezela, Th = Thobothi.

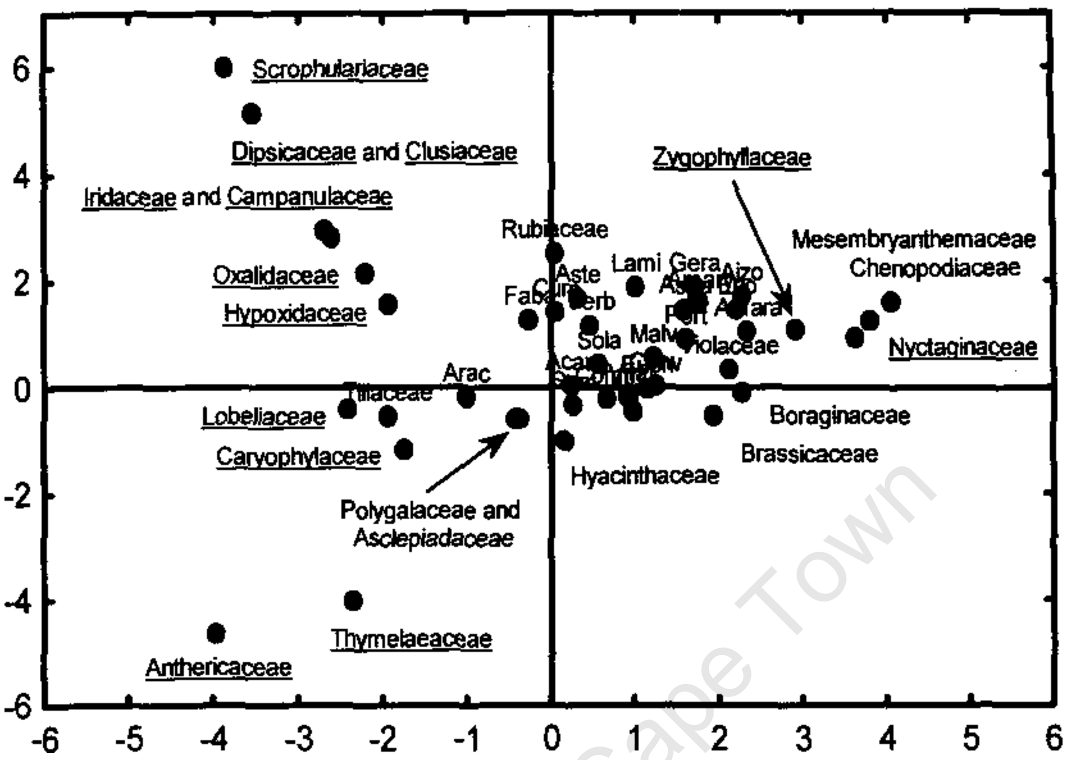


Figure 6.10 Detrended correspondence analysis of the total (combined burnt and unburnt) forb families occurring across the grazing exclusion trials in Hluhluwe and Imfolozi. Underlined families were only recorded in either the mesic grassland sites of Hluhluwe (left of the centroid) or the semi-arid grassland sites of Imfolozi (right of the centroid). Abbreviated family names include: Acan = Acanthaceae, Aizo = Aizoaceae, Amara = Amaranthaceae, Amery = Amaryllidaceae, Arac = Araceae, Aspa= Asparagaceae, Asph = Asphodelaceae, Aste = Asteraceae, Comm = Commelinaceae, Cony = Convolvulaceae, Curc = Curcubitaceae, Erb = Eriospermaceae , Euph = Euphorbiaceae, Faba = Fabaceae, Gera = Geraniaceae, Lami = Lamiaceae, Maly = Malvaceae, Port = Portulacaceae, Sant = Santalaceae, Sola = Solanaceae, Verb = Verbenaceae, Viol = Violaceae, Vita = Vitaceae.

i.4.5 Forb functional type richness

Dicots dominated the flora in both reserves, with approximately five dicot orbs to every monocot forb species recorded (Figure 6.11). There was no significant difference (*p* > 0.05) in the numbers of divots or monocot forbs between reserves Figure 6.11), or in the numbers of dicot or monocot forbs across the treatments at zither Hluhluwe or Imfolozi (Figure 6.11).

Long-lived and short-lived taxa showed a similar pattern to that of dicots and monocots, with long-lived forb species being four to five times more abundant than the short-lived forbs in both reserves (Figure 6.12). Between reserves there was again no significant difference ($p > 0.05$) in the numbers of long-lived and short-lived forbs. In agreement with the broader pattern observed across the rangelands east of the escarpment (Chapter **4),** the semi-arid Imfolozi sites had a greater proportion of short-lived taxa than the mesic Hluhluwe sites, although this was not significant ($p > 0.05$) [Figure 6.12]. Again, no significant difference ($p > 0.05$) was recorded in either the numbers of long-lived or short-lived forbs across the treatments at either Hluhluwe or Imfolozi (Figure 6.12).

While the number of sprouting to non-sprouting forb species did not differ significantly ($p > 0.05$) within reserves, the number of sprouting forbs decreased significantly ($p < 0.05$) from Hluhluwe to Imfolozi (Figure 6.13). Treatments, nevertheless, did not have a significant effect ($p > 0.05$) on the numbers of either sprouting or non-sprouting forb species within either Hluhluwe or Imfolozi (Figure 6.13).

The two radical growth forms (erect and prostrate) were not particularly well represented (< 3 spp. on average) and could not be shown to differ significantly (p 0.05) between treatments, across reserves, or between each other (Figure 6.14). Cauline-prostrate forb taxa were significantly ($p < 0.05$) more numerous than the radical growth forms, but their richness showed no significant difference ($p > 0.05$) between reserves or treatments within reserves (Figure 6.14). Cauline-erect taxa dominated both the mesic (Hluhluwe) and semi-arid (Imfolozi) floras, representing $2/3$ of the forb taxa in each treatment (Figure 6.14). Despite this, there was still no significant difference ($p > 0.05$) in the numbers of these cauline-erect forbs between reserves or treatments within reserves (Figure 6.14).

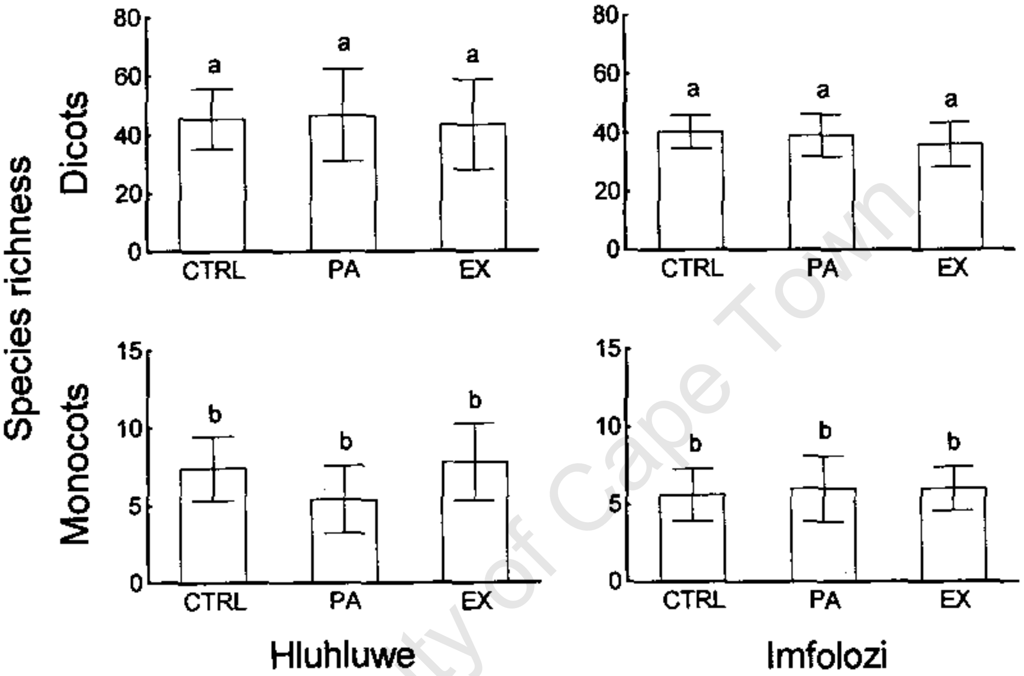


Figure 6.11 Mean richness of dicot and monocot forb taxa sampled in 100 m^2 (100 x 'I m^2 quadrats per plot) in each of the control (CTRL), partial exclosure (PA) and full exclosure (EX) treatments surveyed in each of the five grazing exclosure sites across Hluhluwe and Imfolozi. Mean values were calculated from the total (combined unburnt and burnt sampling years) forb species lists for each plot and compared using an ANOVA with the forb species richness at each site as a covariable (n = 5, df = 11, F = 59.52, $p < 0.001$). Symbols denote statistically similar ($p < 0.05$) levels species richness based on a Tukey HSD ANOVA.

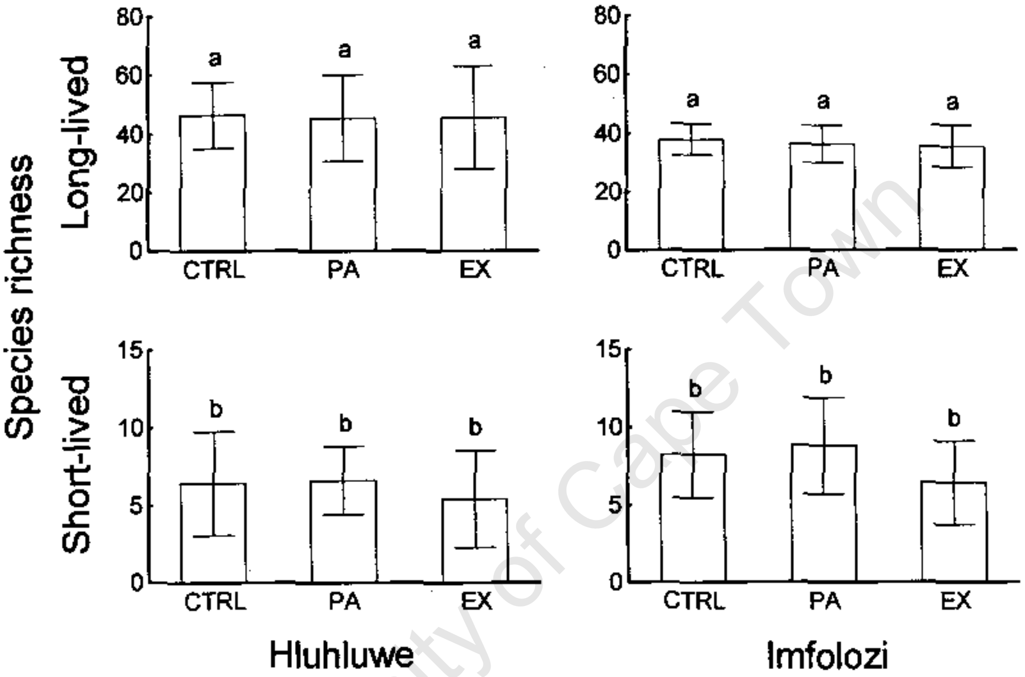


Figure 6.12 Mean richness of long-lived (perennial) and short-lived (annual and biennial) forb taxa sampled in 100 m^2 (100 x 1 m^2 quadrats per plot) in each of the control (CTRL), partial exclosure **(PA) and** full exclosure (EX) treatments surveyed in each of the five grazing exclosure sites across Hluhluwe and Imfolozi. Mean values were calculated from the total (combined unburnt and burnt sampling years) forb species lists for each plot and compared using an ANOVA with the forb species richness at each site as a covariable (n = 5, df = 11, F = 47.52, $p < 0.001$). Symbols denote statistically similar ($p < 0.05$) levels species richness based on a Tukey HSD ANOVA.

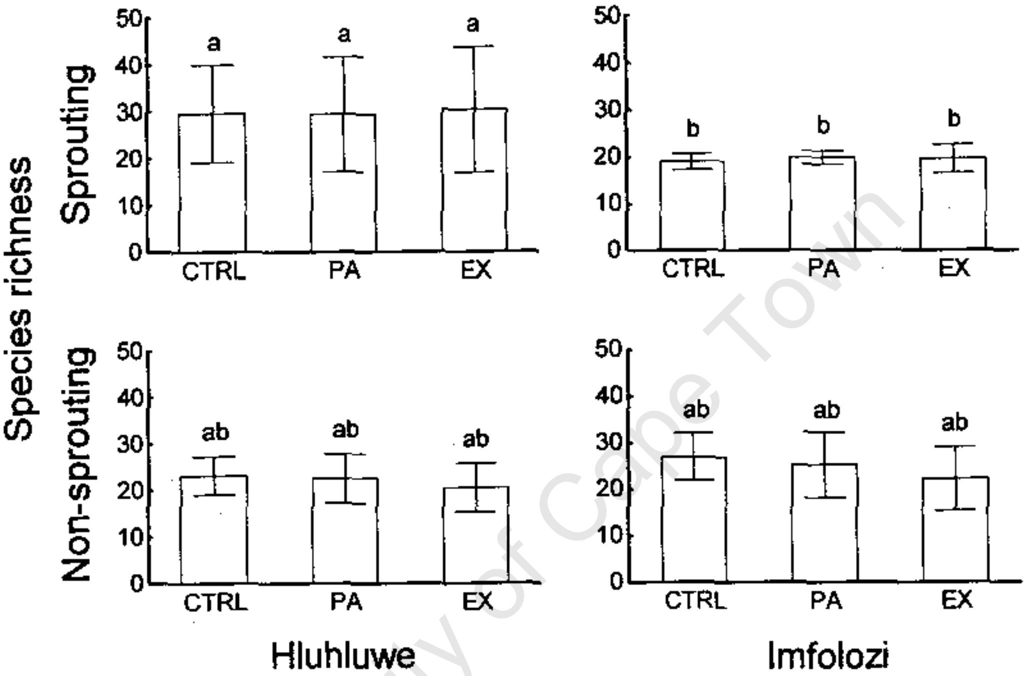


Figure 6.13 Mean richness of sprouting and non-sprouting forb taxa sampled in 100 m^2 (100 x 1 m^2 quadrats per plot) in each of the control (CTRL), partial exciosure (PA) and full exciosure (EX) treatments surveyed in each of the five grazing exclosure sites across Hluhluwe and Imfolozi. Mean values were calculated from the total (combined unburnt and burnt sampling years) forb species lists for each plot and compared using an ANOVA with the forb species richness at each site as a covariable (n = 5, df = 11, F = 3.28, $p < 0.05$). Symbols denote statistically similar ($p < 0.05$) levels species richness based on a Tukey HSD ANOVA.

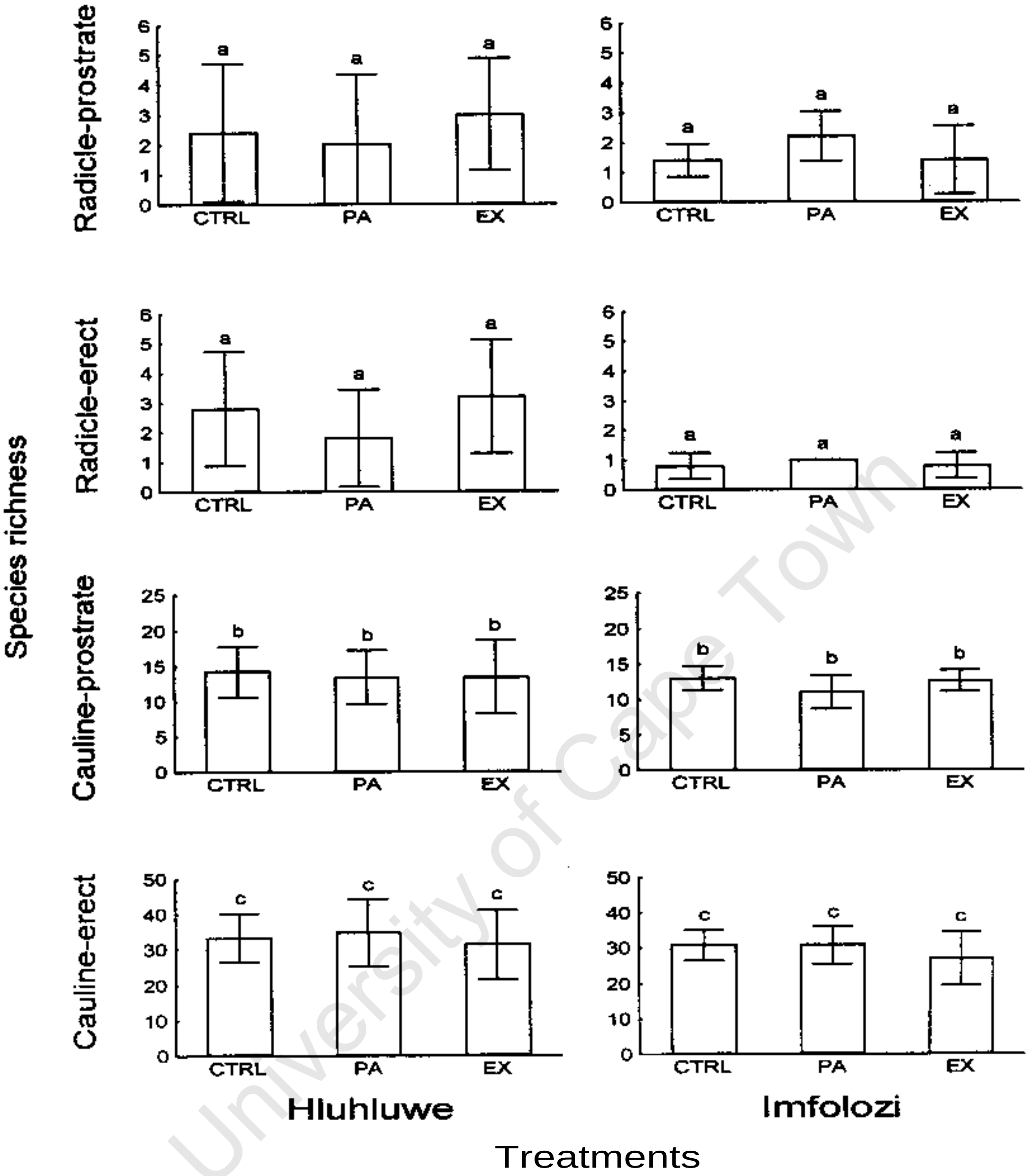


Figure 6.14 Mean species richness of the above-ground forb growth forms sampled in 100 m^2 (100 x 1 m^2 quadrats per plot) in each of the control (CTRL), partial exciosure (PA) and full exciosure (EX) treatments surveyed in each of the five grazing exclosure sites across Hluhluwe and Imfolozi. Mean values were calculated from the total (combined unburnt and burnt sampling years) forb species lists for each plot and compared using an ANOVA with the forb species richness at each site as a covariable (n = 5, df = 23, F = 81.76, $p < 0.001$). Symbols denote statistically similar ($p < 0.05$) levels species richness based on a Tukey HSD ANOVA. Note different scales on y-axes

6.4.6 Forb grazing damage

The extent of mammalian grazing damage increased dramatically between the unburnt and burnt sampling years (Figures 6.15 and 6.16). In contrast, the extent of invertebrate grazing damage was less influenced by burning, displaying a slight decrease (Figures 6.17 and 6.18). It is worth noting that few of the species were represented in > 1/5 (100) of the quadrats sampled across the treatments applied to the five sites at each reserve. In fact, most of the species occurred in < 1/10 (50) of the quadrats, making it difficult to predict whether they were being grazed accidentally or selectively. Despite this, there appeared to be little difference in the amount of post-burn mammal damage between the control and partial exclosure treatments in both Hluhluwe and Imfolozi. Forbs, nevertheless, appeared to be grazed more in Imfolozi than in Hluhluwe. I could not, however, identify any characteristics that might explain why abundant taxa were, or were not, being targeted by mammalian herbivores.

Invertebrate herbivory in the treatments across Hluhluwe appeared to decrease slightly post-burn (Figures 6.17 and 6.18). This, however, corresponded to an increase in damage by mammalian grazers, which may have obscured the impact of invertebrate grazing. Invertebrate damage appeared to be marginally lower in the full exclosure than in the control treatments. Again, I found it difficult to identify plant traits that might explain why particular taxa were being targeted by invertebrate grazers. Amongst those forb species that were apparently selected against, some have small or fine-leaves which would have made it difficult to see when the plant had been damaged by insect herbivores (e.g. *Helichrysum rugulosum, Phyllanthus meyerianus, Thesium* sp. and *Schukuria pinata).* In general though, no taxon was observed to be consistently targeted by invertebrate herbivores across sampling years, reserves or treatments.

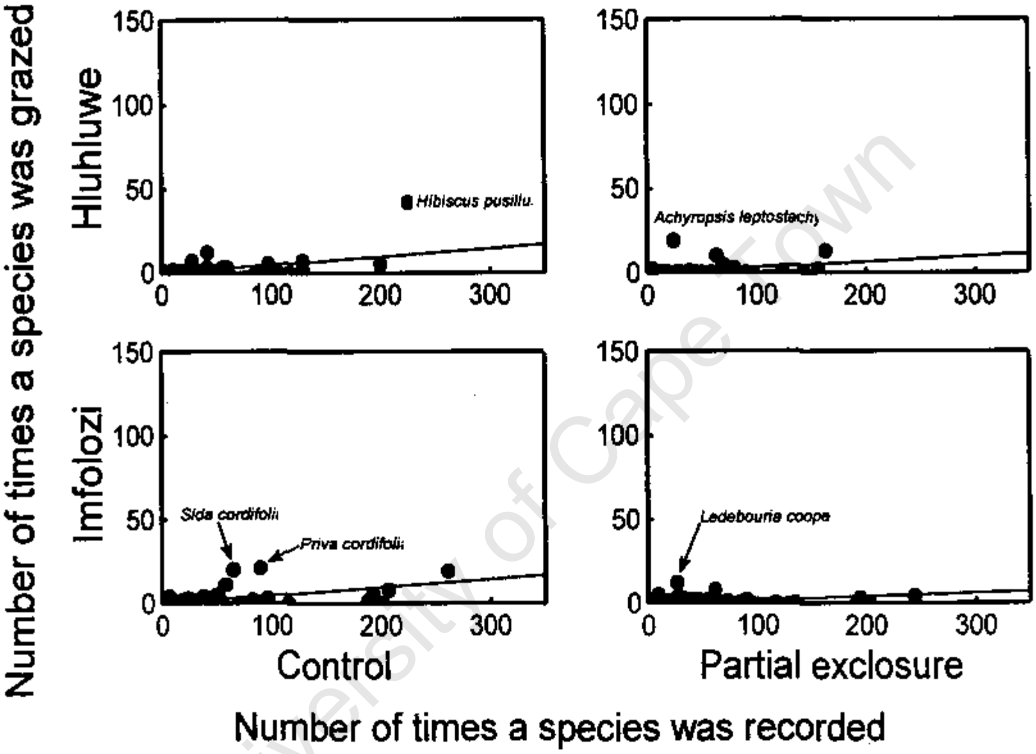


Figure 6.15 Pre-burn relationship between the frequency of species across the sites (5 sites x [100 x 1 m^2 quadrats] per reserve) at Hluhluwe and Imfolozi and the number of times the species were found to have been **grazed by mammals** in the control and partial exciosure treatments; with a regressed line indicating the relationship expected under non-selective grazing.

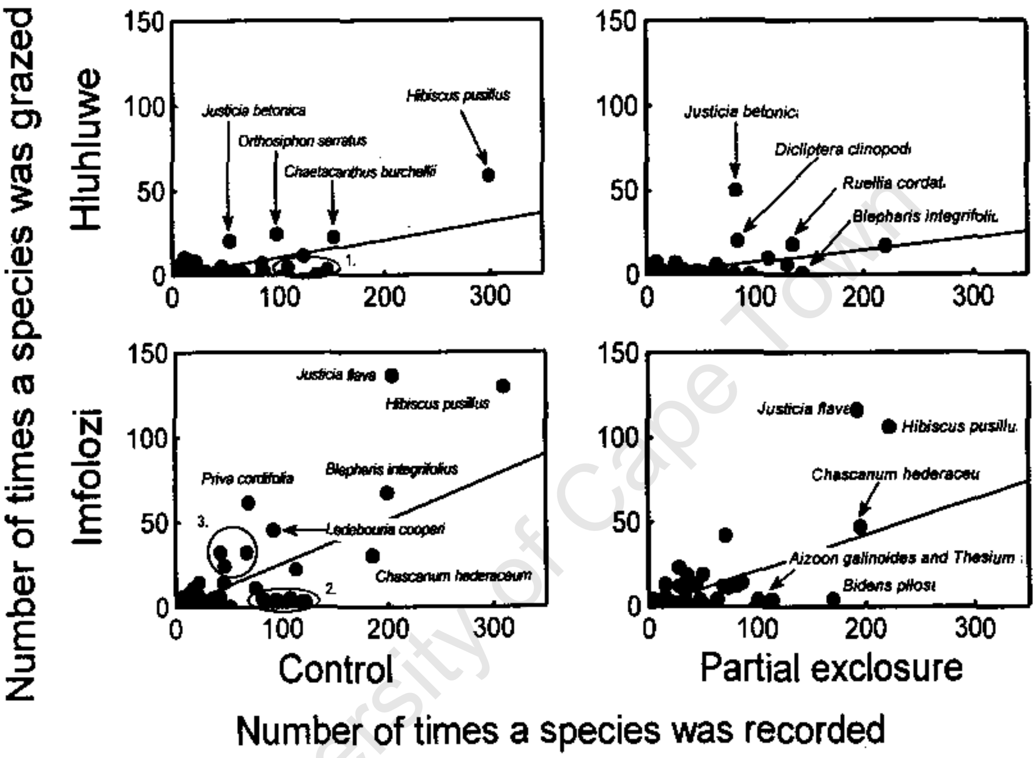


Figure 6.16 Post-burn relationship between the frequency of species across the sites (5 sites x [100 x 1 m^2 quadrats] per reserve) at Hluhluwe and Imfolozi and the number of times the species were found to have been **grazed by mammals** in the control and partial exclosure treatments; with a regressed line indicating the relationship expected under non-selective grazing. 1. *Blepharis integrifolius, Helichrysum rugulosum* and *Solanum pandurifonne;* 2. *Almon galinoides, Bidens pilosa, Indigofera velutiana, Phyllanthes meyerianus* and *Schkuria pinnate;* 3. *Boertravia diffuse, Phyilanthus maderaspatensis* and *Puerile cordate.*

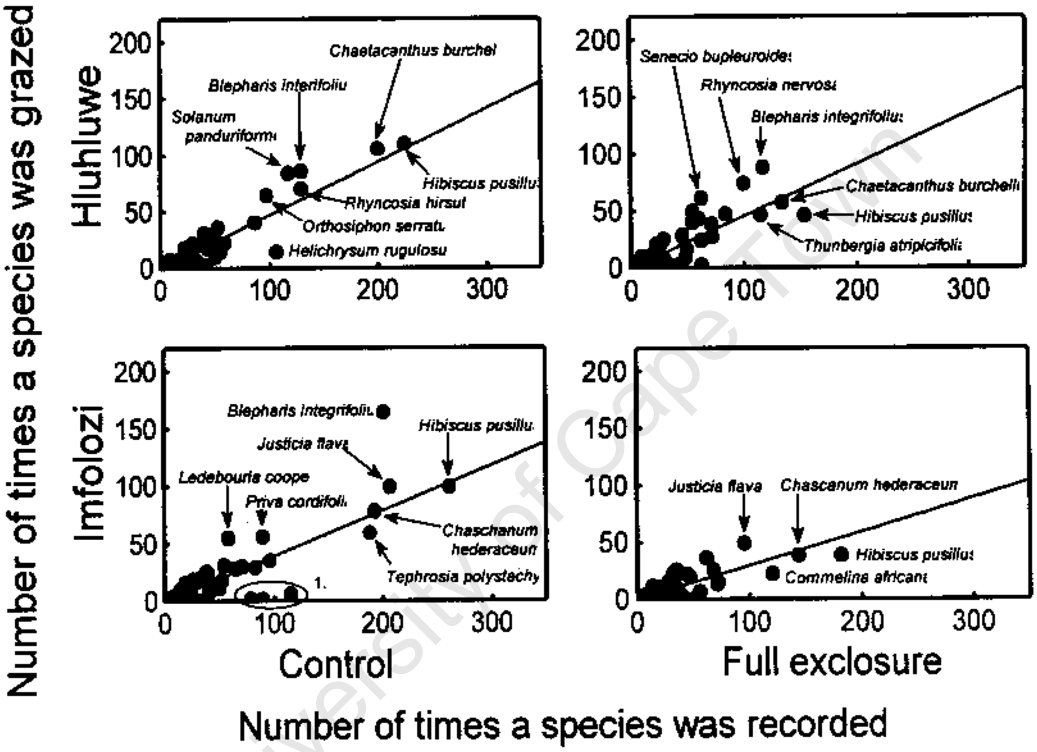


Figure 6.17 Pre-burn relationship between the frequency of species across the sites (5 sites x [100 x 1 m^2 quadrats] per reserve) at Hluhluwe and Imfolozi and the number of times the species were found to have been grazed by invertebrates in the control and full exclosure treatments; with a regressed line indicating the relationship expected under non-selective grazing. 1. *Phylianthus meyerianus, Tagetes minute* and *Thesium* sp..

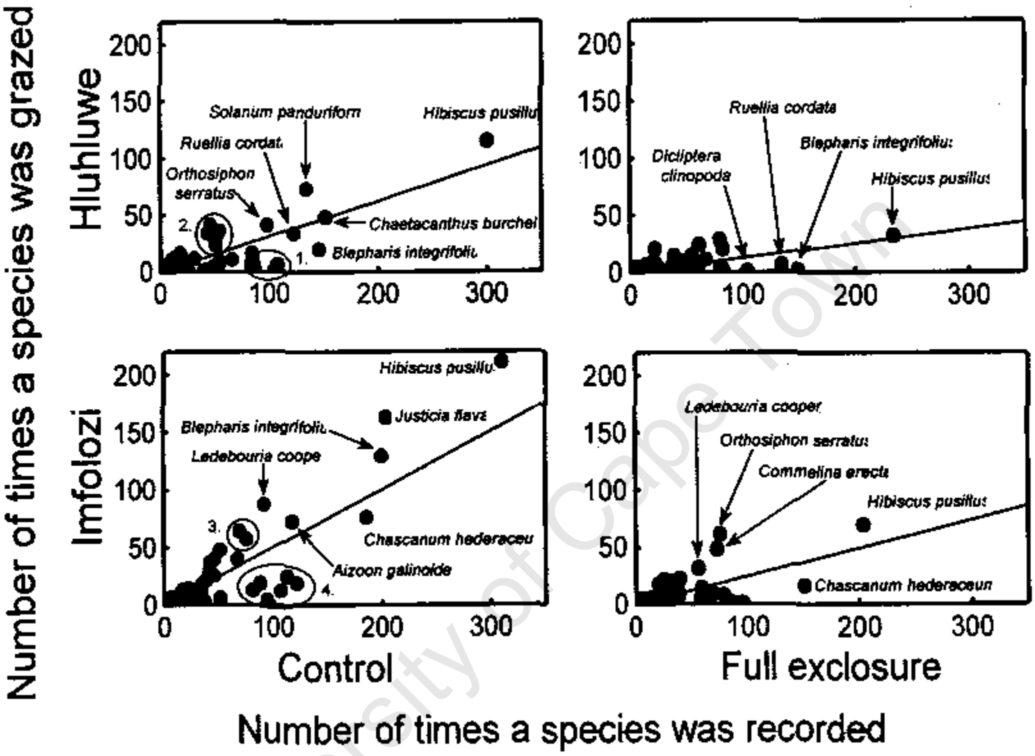


Figure 6.18 Post-burn relationship between the frequency of species across the sites (5 sites x [100 x 1 m^2 quadrats] per reserve) at Hluhluwe and Imfolozi and the number of times the species were found to have been **grazed by invertebrates** in the control and full exclosure treatments; with a regressed line indicating the relationship expected under non-selective grazing. 1. *Acalypha villicaulis* and *Helictuysum rugulosum*; 2. *Aizoon galinoides, Helichrysum oxyphylum, Justicia betonica, Ledebouria* cooped and *Senecio bupleuroides*; 3. *Heliotropium studneri* and *Priva cordifolia*; 4. *Bidens pilosa, Chenopodium mucronatum, Indigofera velutiana, Phyllanthus meyehanus, Schkuria pinnate* and *Thesium* sp..

6.5 Discussion

6.5.1 Sampling scale and the interpretation of results

Contrary to the predictions of both the Milchunas *et al* (1988) and Olff and Ritchie (1998) models, herbivore exclusion did not appear to impact species composition or richness across the trials in Hluhluwe or Imfolozi. Instead, plot composition and richness appeared to be more strongly determined by environmental and disturbance history gradients across the park. This, however, is not unexpected, as I have found similar effects to operate in small-plot fire trials in these rangelands (Uys et *al,* 2004). In all three fire trials, plant composition was more strongly determined by environmental gradients across the trials than the fire treatments applied to the plots. Although species richness did not appear to respond to frequency or season of fire in these small-plots (100 m^2) trials, richness displayed a clear inverse relationship to fire frequency when sampled at the landscape scale (Uys *et al.,* 2004). The scale at which the grazing exclusion treatments were applied and sampled may therefore have also been too small to highlight grazing effects on forb richness. Furthermore, the trial had only been going for two to three years and, although this was enough time to see marked shifts in grass composition, it may not have been sufficient to highlight effects on the forb flora.

Interpretations of species richness are not only influenced by the numbers of species present, but also by how evenly those species are distributed. As species become increasingly rare, clumped, or individual plants increase in size, larger quadrats are needed for them to be recorded (Oksanen, 1996). Thus, species poor communities, whose species are evenly distributed, may appear to have as many species as a richer community whose species are unevenly distributed, if sampled at a small scale. A richer community will only begin to appear to be richer when sampled at a large enough scale to account for the rare or patchy distribution of its species. In examining grazer exclusion I found no significant difference in the species richness between Hluhluwe and Imfolozi when sampling at 1 m^2. However, when I compared taxonomic richness from the 100 x 1m^2 quadrats sampled in each plot and as a total across the reserves, I found both the species and family richness to be significantly greater in Hluhluwe than Imfolozi. Consequently, although the rangelands of Imfolozi than the mesic sites of Hluhluwe.

Subsequent to the separation along the environmental gradient across the park, plots were seen to separate along a gradient from "rightly" grazed tall bunch-grass areas through mixed-grass areas to the "heavily" grazed short lawn-grass areas and forb sites that had little grass. Compared to bunch-grasses, lawn-grasses are better suited to tolerate greater levels of herbivory due to their tiller initials being positioned below graze height, at or close to the ground. In contrast, bunch grasses are more susceptible to grazing damage as they bear their tiller initials well within graze height above the ground where they are less likely to be shaded by accumulating uneaten moribund material (Everson *et al.,* 1988; Uys *et at,* 2004). Thus, while the shorter lawn-grasses appear to rely on grazing to exclude the taller bunch-grasses that would shade them out of the sward, bunch-grasses rely on fire to remove accumulated moribund material that might shade their tillers. As these disturbances are believed to have been operating for some time to maintain the lawn- / bunch-grass matrix, they may also account for the different suites of (orbs encountered across the bunch to lawn-grass gradient. I could, however, not find any evidence that distinct plant functional types were supported in lawn- and bunch-grass areas to explain this pattern.

6.5.3 An alternative model for grazing effects on plant diversity

Both the Milchunas *et al.* (1988) and Olff and Ritchie (1998) grazing models invoke environmental moisture gradients to account for grazing effects, but neither related these to plant life-form or life-history strategies. As I have argued in Chapter 4, the precipitation gradient across the grass-dominated ecosystems of southern Africa influences the types of disturbances driving these ecosystems. Due to the rapid accumulation of biomass (O'Connor and Bredenkamp, 1997; Rutherford, 1980) and greater incidence of lightning to induce fires (Edwards, 1984), I contend that mesic rangelands represent fire driven ecosystems, while increasing rainfall variability results in semi-arid areas being driven by frequent drought (Is Houerou, 1984; Tyson, 1986; Bond, 1997; Schulze, 1997; Bond et at, 2003). Relating this to plant functional types, I further argue that the fire-driven mesic rangelands should favour long-lived sprouting forbs, while the drought driven semi-arid rangelands should favour short-lived non-sprouting species (Chapter 4). If so, the mesic rangeland flora should be suited to tolerate constant moderate levels of grazing, while the semi-arid rangeland flora would be better suited to recover after sporadic bouts of intense grazing. Given the apparent lack of recruiting opportunities in a dominant grass sward (Chapter 5), it makes sense that mesic rangeland forbs should adopt persistent life-history strategies. These characteristics would not, however, favour the recovery of forbs from intense disturbances that kill the parent plant. Short-lived taxa are, by their nature, reliant on recovery from seed. This favours their surviving sporadic intense grazing events that not only destroy the adult plant, but also other plants around it, reducing subsequent competition for seedlings. Obligate seeding, however, requires a constant source of seed, which will not be available under constant grazing that damages the plant's reproductive organs.

Based on the results discussed below, herbivores appear not to target the forbs, apparently favouring the grass component of the sward (Chapter 6.5.5). As grass production is closely linked to available moisture, grazing patterns should naturally match the precipitation characteristics. Rainfall variability is inversely related to mean annual precipitation (Le Houerou, 1984; Tyson, 1986; Schulze, 1997), resulting in sporadic grass production in semi-arid ecosystems. Subsequently, herbivore numbers (and thus grazing) show episodic peaks relating to high rainfall years that favour increased production (Ellis and Swift, 1988; Blois and O'Connor, 1999). By comparison, the mesic rangelands are considered to be closer to equilibrium, their rainfall and grass production being generally more consistent. Herbivore populations therefore naturally fluctuate less, yet their numbers would also be maintained at moderate levels due to the decline in grass palatability in these mesic rangelands over winter (Tainton, 1999). Consequently, the floras of mesic and semi-arid rangelands should display different grazing responses according to their plant functional traits and the production characteristics of these ecosystems. Mesic floras appear well suited to tolerate continuous moderate defoliation, while semi-arid floras should tolerate intense episodic grazing.

Thus, I predict that intense grazing in mesic grasslands or continuous grazing in semi-arid ecosystems will have a negative impact on the diversity of these ecosystems. The design of this study was unfortunately not conducive to testing these hypotheses. To attempt this, I investigated the effects of intense stocking under communal land tenure systems in mesic grasslands in relation to low stocking densities in adjacent conservation lands (Chapter 7).

6.5.4 Interactive effects of fire and grazing

Fire and grazing are the main ecological management tools available for biodiversity conservation. Primarily, both operate to remove biomass, but they do so in different ways, resulting in interactive effects. By sampling over two seasons, under unburnt and burnt conditions, I hoped to explore these interactive effects. Diversity is believed to increase after a burn (West, 1951), as was noted between the first and second sampling season. In addition though, different species emerged under the unburnt and burnt conditions, as indicated by the greater total species richness from both sampling years than either year alone. The majority of taxa in these plots were long-lived, suggesting that it was not their composition that changed, but merely their emergence. The species were most likely present in the system over both years (i.e. negligible immigration) and all that would have changed was whether they remained dormant at the end of winter or emerged in spring. Thus, when quantifying rangeland plant diversity we need to distinguish between the potential diversity that includes plants that are dormant at the time of sampling and the realized diversity that is observed aboveground in the sward at a moment in time.

As I observed in my fire studies (Uys *et al.,* 2004), several of the woody (orbs were only recorded in the unburnt rangelands (namely: *Athrixia phylicoides, Chromolaena odorata, Leonotis intermedia* and *Leucas glabra).* There were some species, however, such as *Thunbergia atripicifolia,* a robust long-lived sprouting dicot, that I expected to encounter in both years, but only encountered in one. This suggests that other factors were influencing forb emergence. The onset of grass production in the mesic rangelands, where water is not limiting, has been shown to be determined by increases in soil temperature (Everson and Everson, 1987). In contrast, water availability has been shown to be a crucial factor in initiating grass production in semi-arid areas where moisture is limiting (Danckwerts *of* al., 1984, 1986; Danckwerts and Stuart-Hill, 1988). Thus, climatological factors may have confounded fire effects on emergence.

6.5.5 Patterns of grazing damage

Few forbs appeared to be preferentially grazed, but it was interesting to note how fire influenced vertebrate, but not invertebrate grazing patterns. Size differences between vertebrate and invertebrate grazers suggest that they would perceive different scales of patchiness in the environment. Consequently, as disturbance effects differ according to scale (Hobbs and Mooney, 1991), one might expect vertebrate and invertebrate herbivores to respond differently to disturbances.

Huhluwe-Imfolozi park is burnt in a mosaic of fire compartments, producing a coarse patchwork of burns at the landscape scale (Balfour and Howison, 2001). Thus, with vertebrate numbers fluctuating little from year-to-year in the park, the post-burn increase in vertebrate grazing suggests that these herbivores are preferentially feeding in the parts of the park that have been recently burnt as has been borne out by other research (Archibald, 2003; Archibald *et al.,* 2005). Consequently, the calculation of vertebrate carrying capacity needs to be reviewed according to the area available for preferential grazing rather than the size of the reserve.

Invertebrate grazing appeared little affected by fire or the exclusion of mammalian grazers. Any effects that these disturbances might have been having, would therefore have been at too coarse a scale to influence invertebrate herbivory. The generally low abundance of forbs, however, meant that I was unable to confidently determine whether these plants were being selected for or damaged by chance. To address this question, we need factorial studies to investigate how fire and rainfall patterns impact the grazing patterns of various herbivore species over spatial and temporal scales.

6.6 Conclusions

Taxon and family richness and composition did not appear to respond to the grazing exclusion treatments at each site, providing no support for the predictions of either the Milchunas *et al.* (1988) or Olff and Ritchie (1998) models. As with fire effects (Uys et *al.,* 2004), however, composition was seen to be influenced by environmental gradients across the park, with an additional influence of grazing history. This lent further support to the notion that mesic and semi-arid rangelands are governed by different sets of environmental variables and therefore require different management strategies. The manner in which we interpret diversity was also highlighted by the turnover in fort species between sampling years. Different portions of the total forb component must have been sampled in each year, as these species are long-lived, presumably slow growing, and therefore must have been in the system to have emerged as adults the following year. Consequently, it does not appear possible to account for all the species present in a single survey. The effects of fire on herbivory were also highlighted, with mammalian grazer activities appearing to be more strongly influenced by the time since last burn than invertebrate grazing. Nevertheless, more detailed studies are required of the feeding preferences of various herbivores and combinations of herbivores under different environmental conditions to develop a better understanding of the influence of grazing on forb diversity.

7 Effects of heavy livestock grazing on plant diversity

Abstract

I examined fence-line contrasts at Ithala Game Reserve and Impendle Nature Reserve to test the prediction that intense grazing effects would decrease species richness and encourage short-lived dicot forbs. At each site, I sampled a transect of quadrats paired between the lightly grazed, regularly burnt reserves and the heavily grazed, infrequently burnt commonages. Richness did not differ consistently at the quadrat scale (10 m^2). However, when compared as a total across the transects, species and family richness was consistently lower on the commonages. At both sites soft-leaved monocot forbs recorded inside the reserve were replaced by short-lived dicot forbs on the commonage. Concomitantly, there was a shift to less palatable grass species and the appearance of alien plant species outside of the reserve. Intense cattle grazing of these mesic grasslands under communal tenure was thus seen to have negative impacts on the plant diversity of these ecosystems as predicted.

7.1 Introduction

Communally grazed rangelands represent a significant proportion of the land-use of the rangelands east of the escarpment in southern Africa. Pasture scientists generally consider these rangelands to be poorly managed and grossly overstocked (Everson and Hatch, 1999). Although individual stock owners tend to have few cattle, collectively animal numbers often add up to stocking rates two or three times that of corresponding commercial systems (Tapson, 1993; Hoffman *et al.,* 1999; Vetter, 2005). With each rancher attempting to maximise their utilization of the commonage (Hardin, 1968), and the majority of animals belonging to absentee stock owners who live and work in urban centres away from the rural areas (De Bruyns, 1998), it is not surprising that such perceptions of poor management on communal lands abound. In their review of over 50 years of southern African rangeland literature, O'Reagain and Turner (1991) showed that stocking rate had the greatest effect on range condition and livestock production and could not be mitigated by the grazing system applied (Ie. continuous grazing versus rotational schemes). This is particularly concerning in the light of the general reluctance of communal pastoralists to voluntarily reduce their individual numbers of livestock (Everson and Hatch, 1999).

Mesic rangelands east of the escarpment have probably never supported the grazing intensities currently experienced in communal rangelands. Despite grass swards in this region being highly productive over the summer growing season, their palatability declines markedly over winter, resulting in their being known locally as "Sourveld" (sour grassland) [Ellery, 1995; Tainton, 1999]. Consequently, native herbivores must have existed at low densities in these grasslands, or have migrated to the "Sweetveld" semi-arid rangelands across the escarpment. Sweetveld grasslands maintain their palatability through winter, but lack the productivity to maintain continuous intense grazing pressure (Ellery, 1995; Tainton, 1999). In support of this, the stocking rate of native herbivores in the Giant's Castle Game Reserve in the Drakensberg Mountains is estimated to have naturally stabilized at 1 AU / 55 ha (628 AU on 34,700 ha) [Rowe-Rowe and Scotcher, 1985]. Cattle grazing recommendations for these same montane rangelands range from 1AU / 5 ha to 1 AU / 1.5 ha (Edwards, 1981). Intense, continued grazing of southern Africa's mesic rangelands (as often occurs under communal grazing) results in smaller grass tufts, declines in basal cover and a shift to less palatable grass species than found under corresponding commercial systems (O'Connor *et at,* 2003). As with most rangeland research in southern Africa, however, the impact on the forb flora remains to be explored. This is of particular concern to conservation as forbs constitute most of the floral richness of these grasslands (Chapter 4).

Exotic livestock may also display different dietary preferences to native herbivores. This relation remains to be fully quantified and collated for southern Africa's native herbivores, but the differences in feeding strategies between cattle and Bison *(Bos bison)* have been well explored for North America's tallgrass prairies. There, exotic livestock were found to consume a greater proportion of forbs in their diets than the native Bison (Schwartz and Ellis, 1981; Krueger, 1986; Plum and Dodd, 1993; Knapp *et al.,* 1999). If the same holds true for southern Africa's rangelands and the forbs being targeted include less abundant, palatable species, intense grazing under communal land tenure may result in the extirpation of taxa, so posing a conservation threat.

In the face of increasing habitat degradation, it is essential that we are able to make informed decisions regarding the contribution of different land-tenure systems to meeting nature conservation targets for southern Africa's rangelands. Communal livestock grazing poses a particular problem in this regard, for although the land has not been obviously transformed *(e.g.* as occurs under ploughing), it is often stocked at rates considered unsustainable in the long-term. Although the effects of such intense grazing are well understood for the composition and production of the grass sward, impacts on overall species composition and richness remain to be explored. Current understanding suggests that such intense grazing should result in a shift from persistent life-history traits to short-lived, taxa with an overall decline in species richness in southern Africa's mesic rangelands (McNaughton, 1983; Collins and Barber, 1985; Kucera, 1986; Collins, 1987; Noy-Meir *et al.,* 1989; Belsky, 1992; Milchunas and Lauenroth, 1993; Trémont, 1994; Wahren *et al.,* 1994; McIntyre *et* at, 1995; Altesor *et at,* 1998; Fensham *et al,* 1999; Fensham and Skell, 1999; Hadar, 1999; Lunt and Morgan, 1999; Noy-Meir and Stemberg, 1999; Fynn and O'Connor, 2000; Bullock *et al.,* 2001). To test this, I examined two fence line contrasts in the mesic rangelands east of the escarpment in southern Africa. At each site I examined the richness and composition of the plant species, families and functional types to determine whether there were significant differences between the reserves that were lightly stocked with native herbivores and the adjacent communal lands that were subjected to heavy cattle grazing.

7.2 Study sites

7.2.1 Ithala Game Reserve

Ithala Game Reserve is located -7 km north of the town of Louwsburg (2732 CB) in the hilly terrain of central-northern KwaZulu-Natal, South Africa (27 °25'-27°36'S, 31 ^{0}10'-31 ^{0}25t) [Chapter 2.5.9; Figure 2.1 and L1]. The reserve supports savanna, tall grassland and short grassland, but only the short grassland (- 30 cm) on the high plateau lay adjacent to a communally grazed area, the Louwsburg commonage. The plateau represents a - 6.5 km^{2} tableland that gently undulates between 1360 - 1450 m a.s.I., receiving 820 mm mean annual precipitation (MAP). The soil on the plateau is a shallow lithosol overlying a basalt base which frequently appears as outcrops. The vegetation is North-eastern Mountain Grassland (Low and Rebelo, 1996: Vegetation type 43), a montane grassland type rich in endemic plant species, but with a highly fragmented distribution limited to plateaus (> 1400 m a.s.I.) of the eastern mountain chain from Limpopo Province, south through Mpumalanga, to KwaZulu-Natal, with outliers in the northern parts of the Eastern Cape (Low and Rebelo, 1996). Across its range, this grassland type is characterized by medium to short C4 grasses, typical of montane grasslands of the main eastern escarpment, such as *Alloteropsis semialata, Diheteropogon filifolius, Loudetia simplex, Michrochloa caffra* and *Trachypogon spicatus.* Interestingly the Louwsburg plateau also maintains Fynbos elements, namely: *Protea simplex* and *Erica* spp.. Grazing inside this part of the reserve is particularly light, with only a single herd of four Mountain Reedbuck *(Redunca fulvorufula)* observed during the study (1 AU / 100 ha). Outside the reserve, the 3.5 km^{2} commonage was stocked with - 280 cattle at the time of sampling (1 AU / 1.25 ha). While this number may vary considerably, the stocking rate remains well above that expected for commercial farms in the area (1 AU / 2 ha) [Camp, 1997]. Although no accurate stocking data exist, these stocking rates have probably existed since the first part of the reserve was proclaimed in 1972.

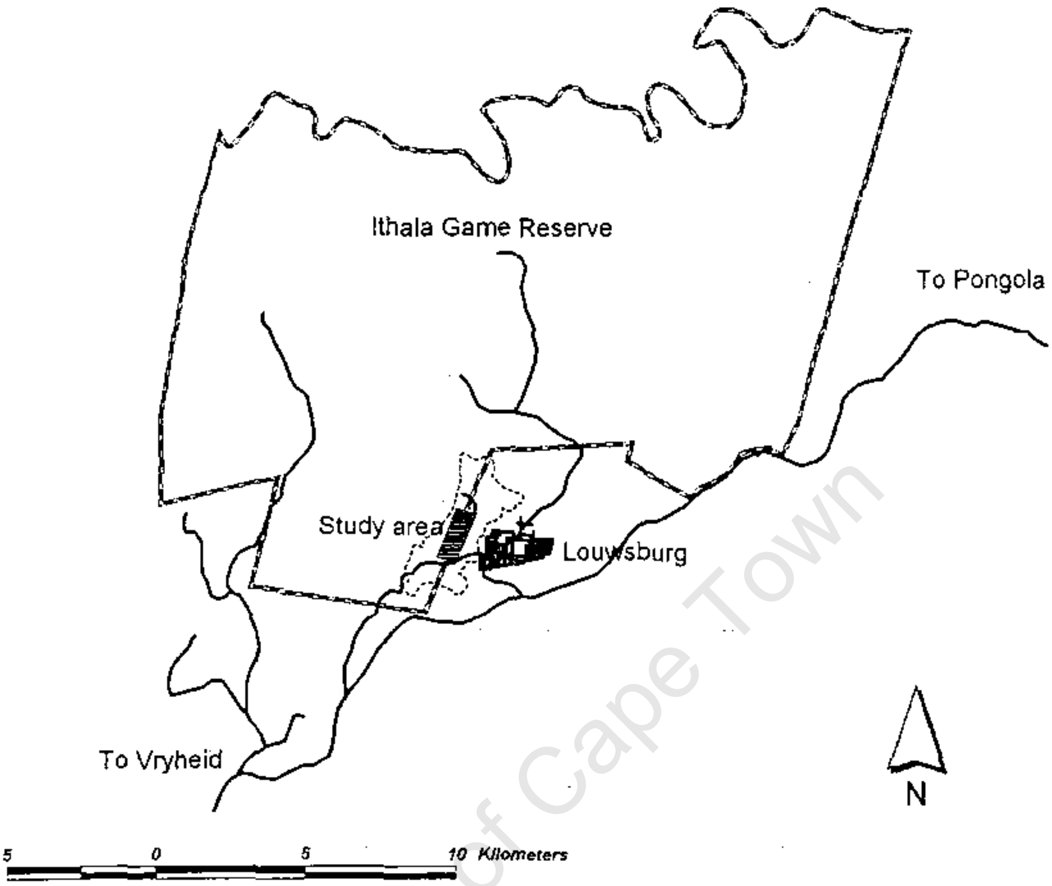


Figure 7.1 Location of conservation versus communal grazing study area (hashed block) on the Louwsburg plateau (dotted line) at Ithala Game Reserve.

7.2.2 Impendle Nature Reserve

Impendle Nature Reserve is located 10 km south of Impendle Village (2929 DB) which is roughly half way between Pietermaritzburg and Underberg in the foothills of the Drakensberg escarpment in KwaZulu-Natal, South Africa (29° 39'-29° 46'S, 29° 45'-29° 59'E) [Chapter 2.5.16; Figure 2.1 and 7.2]. This small reserve (80 km') is composed of old farm lands, but is maintained for its untransformed areas which represent important habitat of the endangered Blue Swallow (*Hirundo atrocaerulea)* [Barnes, 2000]. The reserve covers an altitudinal range from 940 - 1586 m a.s.l., mostly undulating, but dropping off sharply to the Mkomazi River on its southern boundary (940 m Receiving 1100 mm MAP, the region supports

Moist Upland Grassland (Low and Rebelo, 1996: Vegetation Type 42) with patches of Afromontane Forest in the steeper valleys. These medium height (0.3 - 0.5 m) C_4 grasslands are characterized by the grasses *Themeda triandra, Heteropogon contodus* and *Tristachya leucothrix,* with Fynbos elements (namely *Stoebe vulgaris)* and *Protea caffra* and *P. roupelliae* occurring at higher elevations. On the eastern end of its northern boundary the reserve lies adjacent to the Impendle commonage that, according to the overseer of the local dipping tank station, supports -1000 cattle (- 1 AU / 2.5 ha). In contrast, the stocking rate inside the reserve is negligible (< 1 AU / 100 ha). As with Ithala, no accurate stocking records for this area exist, but the fence-line contrast sampled would have been initiated with the setting up of the reserve in 1985.

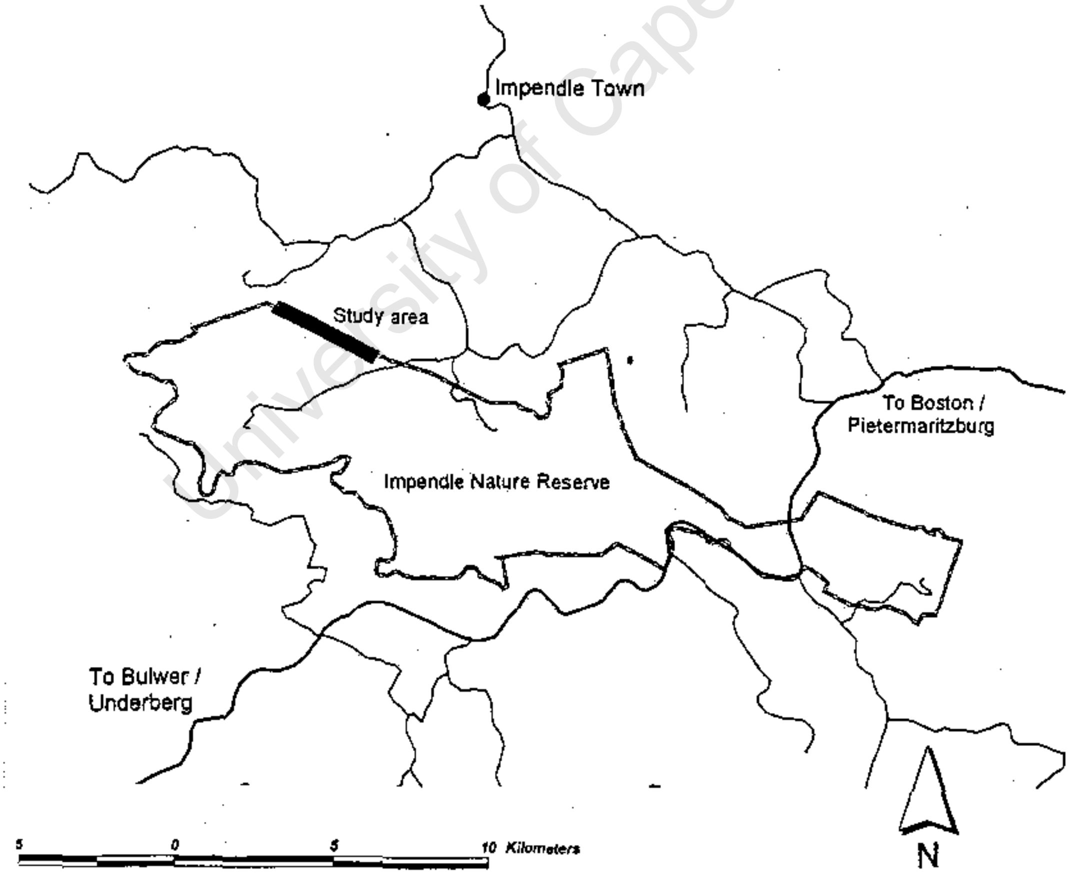


Figure 7.2 Location of conservation versus communal grazing study area (hashed block) at Impendle Nature Reserve.

7.3 Methods

I sampled a series of paired quadrats (5 m x 2 m) spaced at 25 m intervals along the fence-line, approximately 10 m away from either side of the fence, at Ithala Game Reserve (40 pairs of quadrats) and Impendle Nature Reserve (50 pairs of quadrats). This placed my quadrats inside of the reserves in the annually burnt fence-line fire-breaks rather than the biennial burns applied to the rest of the reserves. I have, however, found that environmental heterogeneity has a greater effect on species composition over small scales than differences in fire treatments (Uys *et at,* 2004). This made the close placement of paired quadrats more important than fire treatment concerns. In each quadrat I recorded all the species and classified the forbs according to their life-form and life-history traits, as I had done across the rangelands east of the escarpment (Chapter 4) and for the Hluhluwe-Imfolozi trials (Chapter 6). Traits included whether the forbs were dicots or monocots, long-lived or short-lived, sprouters or non-sprouters (according to their underground organs), and the type of growth form they displayed.

I compared the species richness between the 10 m^2 quadrats sampled inside and outside of Ithala and Impendle using a paired t-test in Statistica 5.1 (StatSoft Inc., 1996). With the same species presence / absence data I examined the distribution of quadrats and species in ordination space for each reserve using the detrended correspondence analysis in Canoco 4.02 (Ter Braak and Smilauer, 1997) to account for the arch effect noted in the initial correspondence analysis of the data.

Family richness was tabulated and reviewed according to the numbers of species, representation of dicots and monocots, and the total number of families recorded inside and outside of each reserve.

As with species richness the representation of life-form and life-history traits in the 10 m^2 quadrats was tested for each trait across the fence-lines using the paired t-test in Statistica 5.1 (StatSoft Inc., 1996). Assumptions of normal distributions were reviewed for all t-tests by examining the distributions of data using histograms.

7.4 Results

7A.1 Species richness

Mean species richness within the $10\ m^2$ quadrats did not respond consistently to grazing treatments across the two reserves (Figure 7.3). Mean richness appeared to be higher outside the reserve at Ithala and lower outside the reserve at Impendle, but neither observation proved to be significant based on the paired t-test (n = 40 and 50, p >0.05). Nevertheless, The total richness recorded across all the quadrats sampled inside and outside of the reserves showed both reserves to support - 20 more species than their adjacent commonages (Figure 7.3).

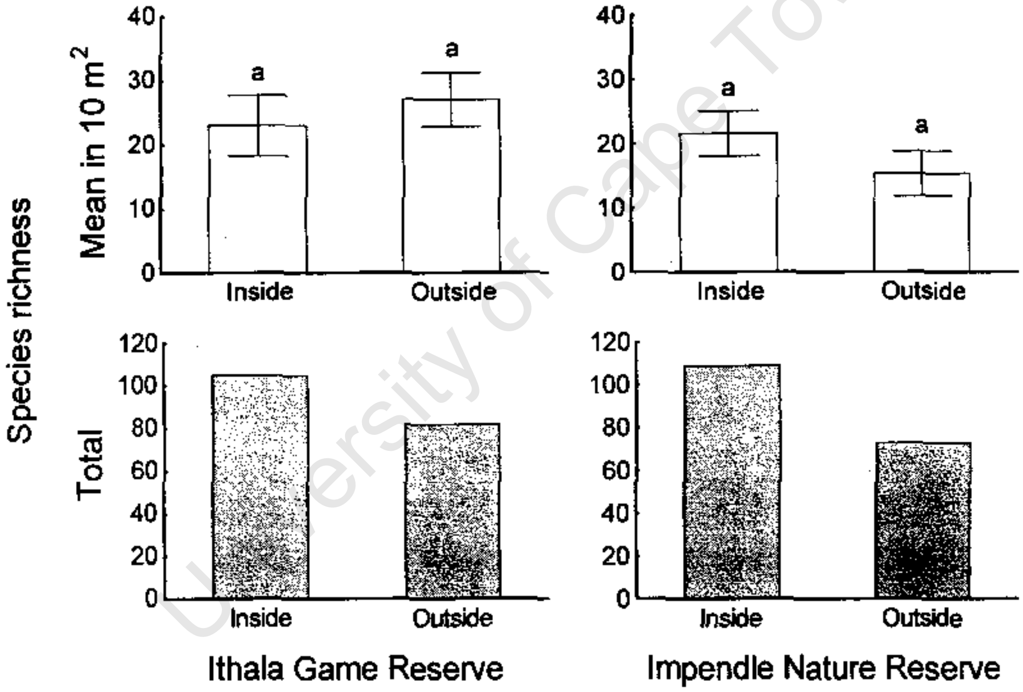


Figure 7.3 Mean (in $10\ m^2$) and total species richness across the quadrats sampled under light grazing inside the conservation areas and heavy cattle grazing on the adjacent communal lands outside Ithala Game Reserve (40 paired $10\ m^2$ quadrats [5 m x 2m], 118 species) and Impendle Nature Reserve (50 paired $10\ m^2$ quadrats [5 m x 2 m], 125 species). Based on paired t-tests, mean species richness at $10\ m^2$ was not significantly different (n = 40 and 50, $p > 0.05$) inside to outside of either reserve.

7.4.2 Species composition

Detrended correspondence analysis of the quadrats surveyed inside and outside of both reserves highlighted distinct compositional shifts between light grazing by native herbivores and heavy cattle grazing (Figures 7.4 and 7.6). Quadrats sampled in both reserves separated out from the quadrats sampled in the adjacent commonages along the first axis. Subsequent separation on the second axis loosely represented the distribution of quadrats along either side of the fence-line, compositional similarity relating to spatial distance (Figures 7.4 and 7.6).

Species composition did not display the clear division according to grazing intensity and type observed in the ordination of quadrats for both reserves (Figures 7.5 and 7.7; Appendices 7.1 and 7.2). Nevertheless, interesting patterns do emerge if we focus on the monocot forbs. At both sites, a group of soft-leaved monocot forbs clustered towards the left hand side of the ordination, which represented the light grazing by native herbivores in the reserves. At Ithala (Figure 7.5) these included *Cyanotis speciosa* (# 39), *Dipcadi virida* (# **41),** *Eulophia* sp. (# 44), *Moraea* sp. (# 83), an unidentified species of orchid (# 84) [my collecting permit did not allow me to remove orchids and the plant was not in flower], and *Scilla nervosa* (# 98). The soft-leaved *Haemanthus* sp. (# 54), *Satyrium* sp. (# 96) and *Trachyandra asperata* (# 109) were located around the centroid of the first axis in the ordination. The two *Ledebouria* spp. (also soft-leaved bulbs) were an exception. *Ledebouria cooped* (# 76) came out in the central group of species to the left of the centroid, suggesting an equal distribution between the reserve and commonage. *Ledebouria ovalifolia* (# 77) [a bulb with its leaves flat on the ground and thus less prone to damage by trampling than those of *L.* cooperi whose leaves stand erect] grouped well to the right of the ordination with the grasses *Eragrostis curvula* (# 6) and *E. plan* (# 7) that are characteristic of high disturbance areas and were observed to characterise the commonage. The grasses *Tristachya leucothrix* (# 17) and *Cymbopogon excavatus* (# 3) [both considered characteristic of low disturbance regimes] were located at the opposite end of the first axis to the *Eragrostis* spp., implying that, to some degree, the flora was separated between the reserve and commonage along the first axis of the ordination.

At Impendle (Figure 7.7) the spread of grass taxa along the first axis of the ordination of species across the reserve and commonage matched that of Ithala (Figure 7.5). The presence of the grasses *Harpochloa falx (#* 12), *Sporobolus africanus (#* 23) and *Trachypogon spicatus (#* 25) on the left hand side, and *Aristide junciformis (#* 2) and *Eragrostis plena (#* 9) on the right hand side of the first axis represented a grazing intensity gradient, from grazing intolerant species on the left to species able to tolerate intense grazing on the right. Again, the soft-leaved monocot forbs were grouped to the left of the ordination. These included: *Corycium nigrescens (#* 49), *Dipcadi marlothi (#* 55), *Eriospermum cooped (#* 58), *Eucomus autumnalis (#* 59), *Eulophia* sp. (# 60), *Kniphofia gracillis (#* 88), an unidentified orchid species (# 93) and *Saila nervosa (#* 108); plus some hard-leaved monocot forbs: *Dierama* sp. (# 54), *Gladiolus ecklonii (#* 66), *Gladiolus* sp.2 (# 68), *Hypoxis argentea (#* 85) and H. *costata (#* 86). Other taxa that were mostly observed on the commonage and not in the reserve included *Sonchus nanus (#* 115) and the alien plants: *Centella asiatica (#* 43), *Ricardia brasilliensis (#* 104), and *Rubus cuneifolius* (# 105).

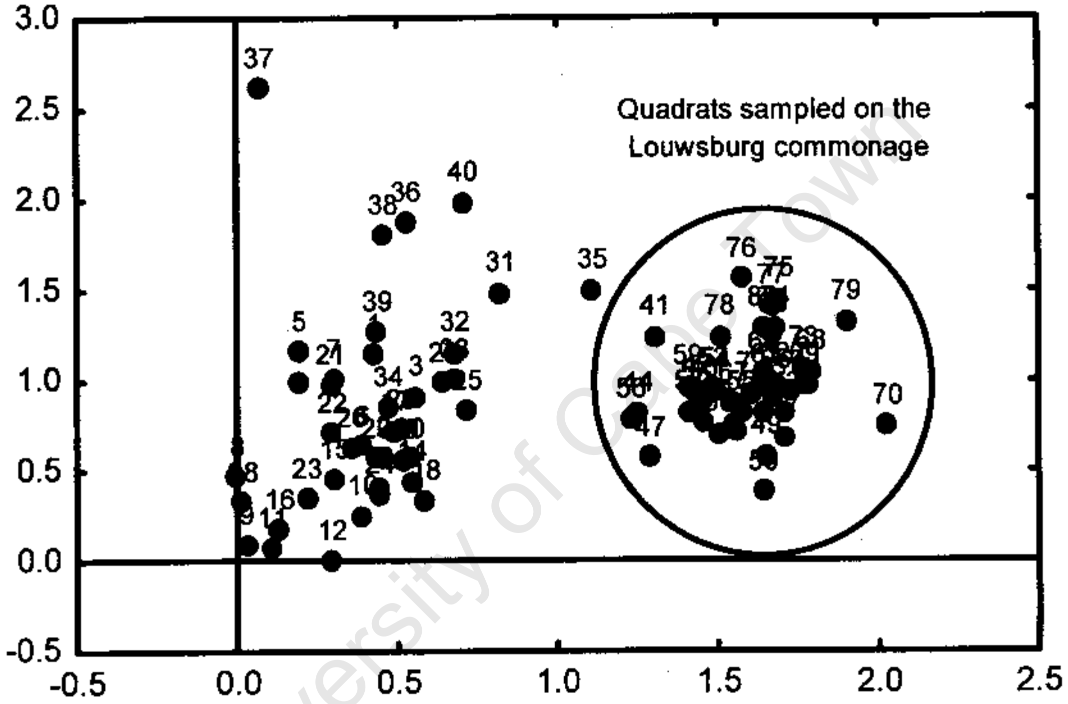


Figure 7.4 Detrended correspondence analysis of the 40 paired $10\ m^2$ quadrats (5 m x 2 m) sampled under light grazing by native herbivores inside Ithala Game Reserve (quadrats 1 - 40) and heavy cattle grazing (- 1 AU / 1.25 ha) outside the reserve on the adjacent Louwsburg Commonage (quadrats 41 - 80), based on the species presence-absence data recorded for each quadrat.

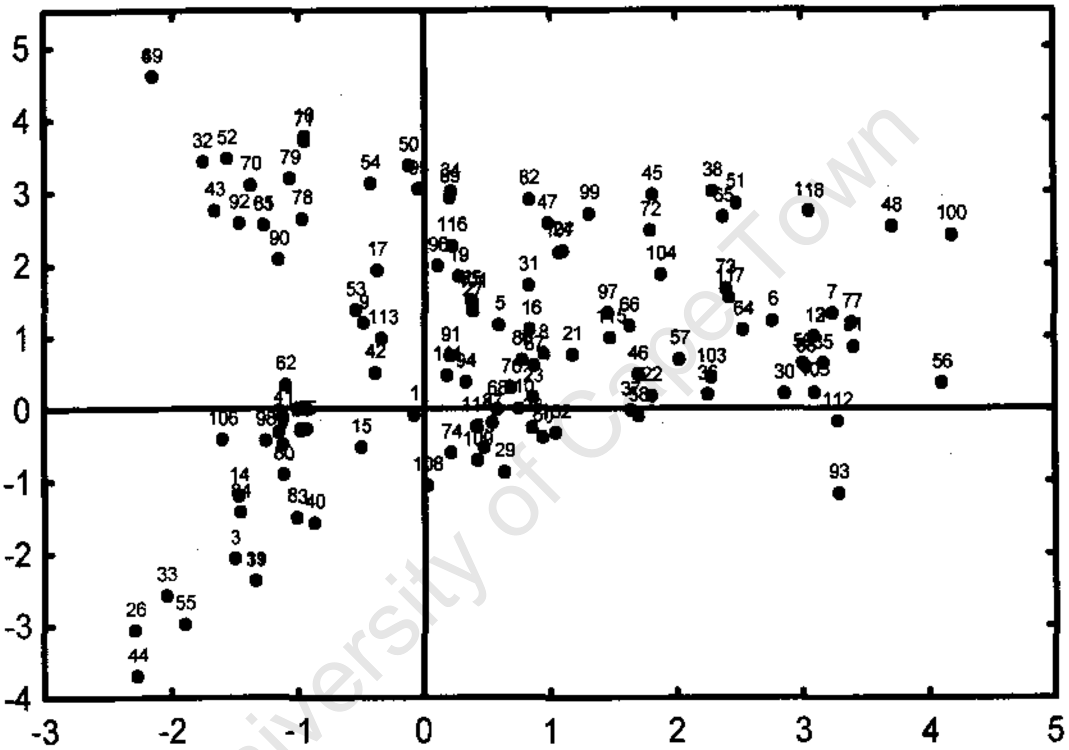


Figure 7.5 Detrended correspondence analysis of the species recorded as present or absent in the 40 paired 10 m^2 quadrats (5 m x 2 m) sampled under light grazing by native herbivores inside Ithala Game Reserve and heavy cattle grazing (- 1 AU / 1.25 ha) outside the reserve on the adjacent Louwsburg Commonage. See Appendix 7.1 for a key to the species.

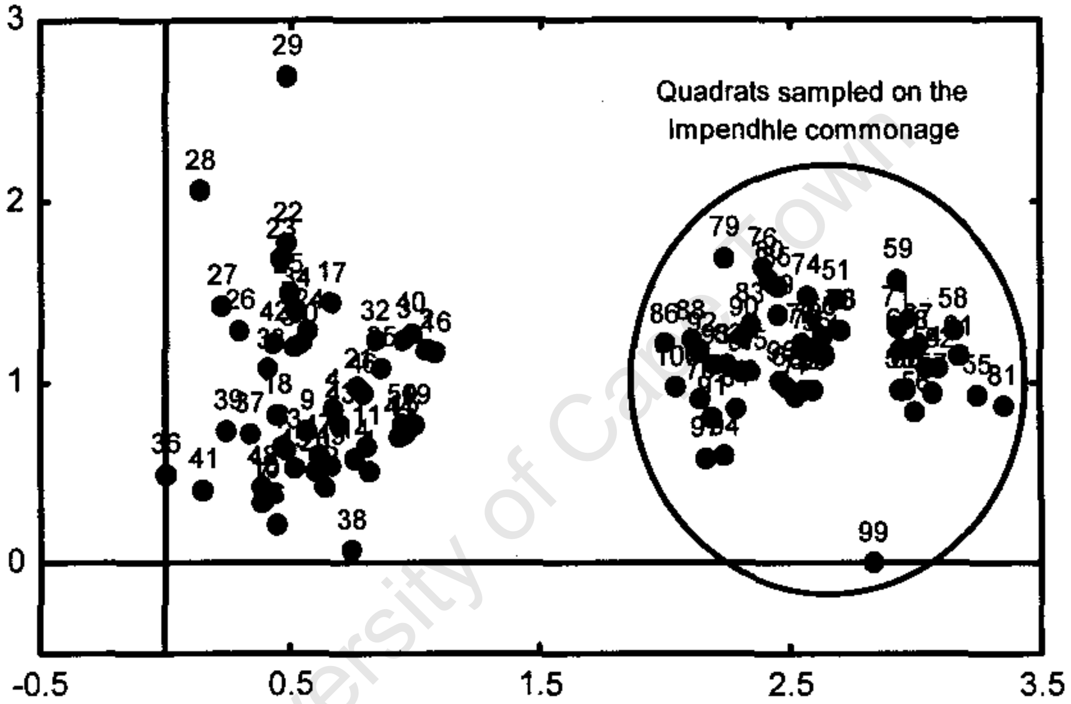


Figure 7.6 Detrended correspondence analysis of the 50 paired 10 m^2 quadrats (5 m x 2 m) sampled under light grazing by native herbivores inside Impendle Nature Reserve (quadrats 1 - 50) and heavy cattle grazing (— 1 AU / 2.5 ha) outside the reserve on the adjacent Impendhle Commonage (quadrats 51 - 100), based on the species presence-absence data recorded for each quadrat.

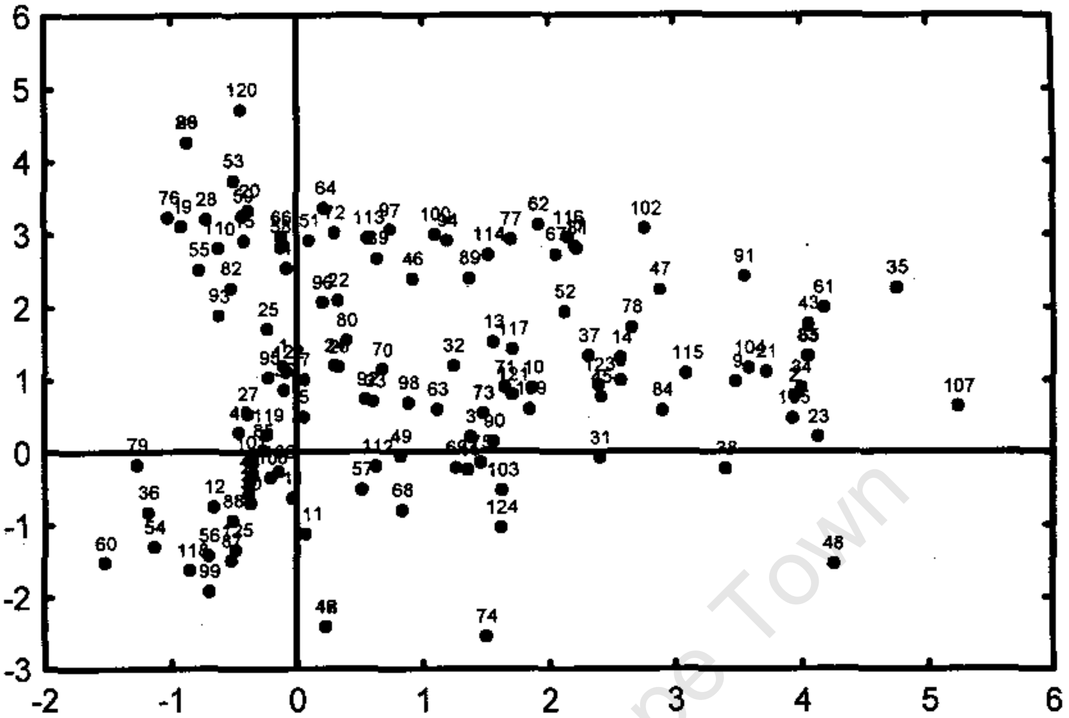


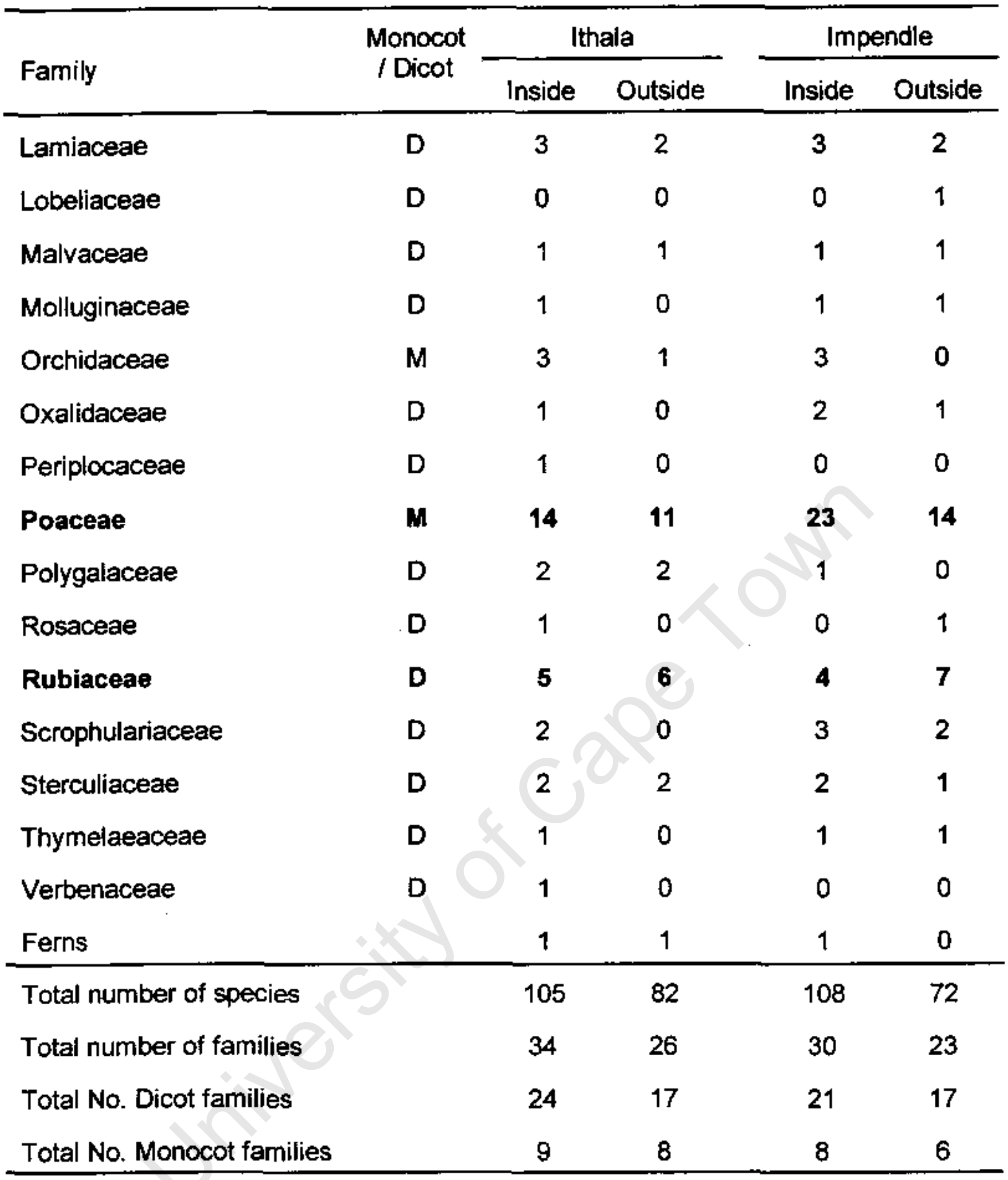
Figure 7.7 Detrended correspondence analysis of the species recorded as present or absent in the 50 paired 10 m^2 quadrats (5 m x 2 m) sampled under light grazing by native herbivores inside Impendle Nature Reserve and heavy cattle grazing (- 1 AU / 2.5 ha) outside the reserve on the adjacent Impendhle Commonage. See Appendix 7.2 for a key to the species.

7.4.3 Family richness

Across both sites, the numbers of species representing each family were greater under light grazing by native herbivores inside the reserves than heavy cattle grazing on the commonages (Table 7.1). Dicots consistently formed around 70 % of the families encountered across both sites. Dicot families also showed the greatest decline under heavy cattle grazing at both sites. Soft-leaved monocot families that showed the greatest difference between treatments included: Hyacinthaceae, Hypoxidaceae and Orchidaceae. The other soft-leaved monocot families (Amaryllidaceae, Asphodelaceae, Commelinaceae and Eriospermaceae) were too poorly represented to claim marked differences, although they generally also showed declines.

Table 7.1 Species richness of the plant families encountered across the fence line contrasts of light grazing by native herbivores inside to heavy cattle grazing on the communal lands outside of Ithala Game Reserve (34 families, 118 species, encountered in 40 paired 10m^2 quadrats [5 m x 2 m]) and Impendle Nature Reserve (33 families, 125 species, encountered in 50 paired 10 m^2 quadrats [5 m x 2 m]); including whether the angiosperm families were monocots or divots. Dominant families in bold.

Family	Monocot / Dicot	Ithala		Impendle	
		Inside	Outside	Inside	Outside
Acanthaceae	D	2	2	0	0
Amaryllidaceae	M	1	0	0	0
Apiaceae	D	1	1	0	1
Asclepiadaceae	D	2	2	2	2
Asphodelaceae	M	1	1	0	0
Asteraceae	**D**	**25**	**25**	**25**	**23**
Campanulaceae	D	1	1	1	0
Chenopodiaceae	D	0	0	1	0
Clusiaceae	D	1	1	1	0
Commelinaceae	M	2	1	1	1
Convolvulaceae	D	1	1	0	0
Crassulaceae	D	0	0	1	0
Cucurbitaceae	D	1	1	1	0
Cyperaceae	M	1	1	5	1
Dipsacaceae	D	1	1	1	0
Eriospermaceae	M	0	0	1	0
Euphorbiaceae	D	3	2	3	2
Fabaceae	**D**	**12**	**10**	**6**	**3**
Gentianaceae	D	1	1	1	1
Geraniaceae	D	0	0	1	1
Hyacinthaceae	M	3	2	5	1
Hypoxidaceae	M	3	1	3	1
Iridaceae	M	4	2	4	3



Family	Monocot / Dicot	Ithala		Impendle	
		Inside	Outside	Inside	Outside
Lamiaceae	D	3	2	3	2
Lobeliaceae	D	0	0	0	1
Malvaceae	D	1	1	1	1
Molluginaceae	D	1	0	1	1
Orchidaceae	M	3	1	3	0
Oxalidaceae	D	1	0	2	1
Periplocaceae	D	1	0	0	0
Poaceae	**M**	**14**	**11**	**23**	**14**
Polygalaceae	D	2	2	1	0
Rosaceae	D	1	0	0	1
Rubiaceae	**D**	**5**	**6**	**4**	**7**
Scrophulariaceae	D	2	0	3	2
Sterculiaceae	D	2	2	2	1
Thymelaeaceae	D	1	0	1	1
Verbenaceae	D	1	0	0	0
Ferns		1	1	1	0
Total number of species		105	82	108	72
Total number of families		34	26	30	23
Total No. Dicot families		24	17	21	17
Total No. Monocot families		9	8	8	6

7.4.4 Plant functional type richness

As seen with the plant families, divots dominated the flora inside and outside of both the reserves (Figure 7.8). Mimicking the species richness in the 10 m^2 quadrats (Figure 7.3), dicot richness was significantly higher (df = 78, t = -4.08, p < 0.001) outside of Ithala Game Reserve (IGR), but significantly lower (df = 98,t = 4.23, *p* < 0.001) outside of Impendle Nature Reserve (INR) [Figure 7.8, Table 7.2]. Monocot richness was consistently lower outside the reserves at both the 10 m^2 quadrat scale (IGR: df = 78, t = 3.29, p < 0.01; INR: df = 98, t = 4.40, *p* < 0.001) and for the total richness at each site (Figure 7.8; Table 7.2). Of the 89 forb species (excluding grasses and sedges) recorded inside Ithala Game Reserve (sampled with 40 pairs of 10 m^2 quadrats), 17 were monocots (19 %) while only eight of the 69 (11.6 %) forb species recorded outside of the reserve were monocots (Table 7.1). At Impendle Nature Reserve (sampled with 50 pairs of 10 m^2 quadrats), monocots were represented by 17 of the 79 (21.5 %) forb species encountered inside the reserve, while there were only six monocots amongst the 57 (10.5 %) forb species recorded outside of the reserve (Table 7.1).

Long-lived forbs dominated the vegetation along the two fencelines sampled, with very few short-lived species recorded (Figure 7.9). The few short-lived forbs that I did encounter were mostly in the communal lands outside of the reserves. Their richness, although on average only approximately one species per 10 m^2 quadrat, was significantly higher outside of the reserve (IGR: df = 78, t = -8.51, $p < 0.01$; INR: df = 98, t = -8.67, $p < 0.001$) [Figure 7.9; Table 7.2]. Species richness does not, however, do this pattern justice, as I observed the numbers of annual plants to be considerably higher outside of the reserves, although this was not captured by my presence-absence sampling strategy.

Sprouting forb species dominated the floras inside both reserves, while non-sprouting forbs showed significant increases (IGR: df = 78, t = -5.74, $p < 0.01$; INR: df = 98, t = -4.84, $p < 0.001$) on the commonages (Figure 7.10; Table 7.2). Of the 89 forb species recorded inside the fence-line of Ithala Game Reserve, 24 (27 %) were non-sprouters. The same number (24) of non-sprouting forb species were encountered outside of the fence, but out of a total of 69 species this raised their proportional representation to 35 %. A similar pattern was recorded at Impendle Nature Reserve, where 23 of the 79 forb species (29 %) inside the reserve were non-sprouters, against 21 of the 57 forb species (35 %) outside.

Other than the radical-erect taxa (which were not abundant), none of the growth forms recorded showed consistent trends across the fence-line contrasts of the two reserves (Figure 7.11). As expected, cauline-erect forbs dominated the quadrats, with the generally low proportions of radical growth forms corresponding to the paucity of monocots.

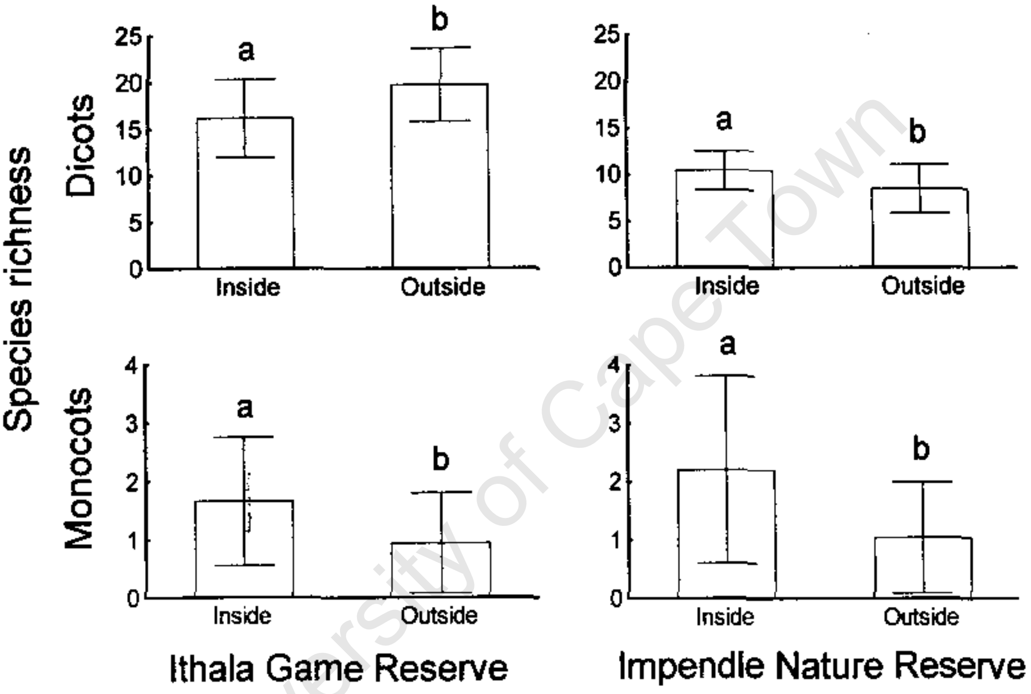


Figure 7.8 Mean species richness of dicot and monocot forbs sampled under light grazing by native herbivores inside, and heavy cattle grazing outside, of Ithala Game Reserve (40 pairs of 10 m^2 quadrats [5 m x 2 m]) and Impendle Nature Reserve (50 pairs of 10 m^2 quadrats [5 m x 2 m]). Symbols denote statistically different (a:b) levels of species richness based on paired t-tests (Table 7.2).

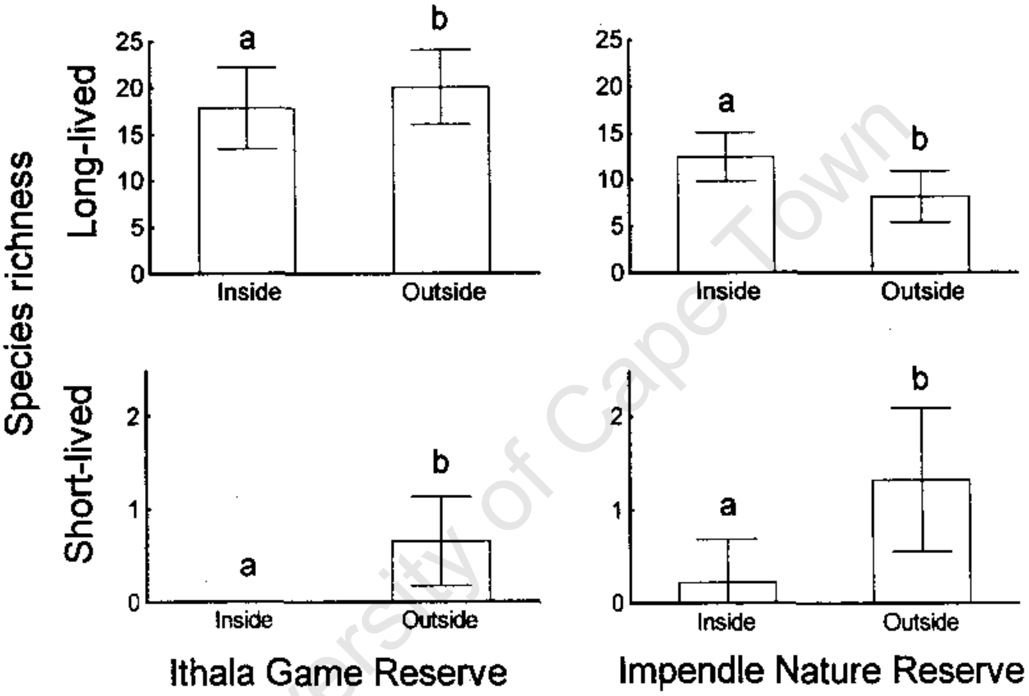


Figure 7.9 Mean species richness of long-lived (perennial) and short-lived (annual and biennial) (orbs sampled under light grazing by native herbivores inside, and heavy cattle grazing outside, of Ithala Game Reserve (40 pairs of 10 m2 quadrats [5 m x 2 m]) and Impendle Nature Reserve (50 pairs of 10 m^2 quadrats [5 m x 2 m]). Symbols denote statistically different (a:b) levels of species richness based on paired t-tests (Table 7.2).

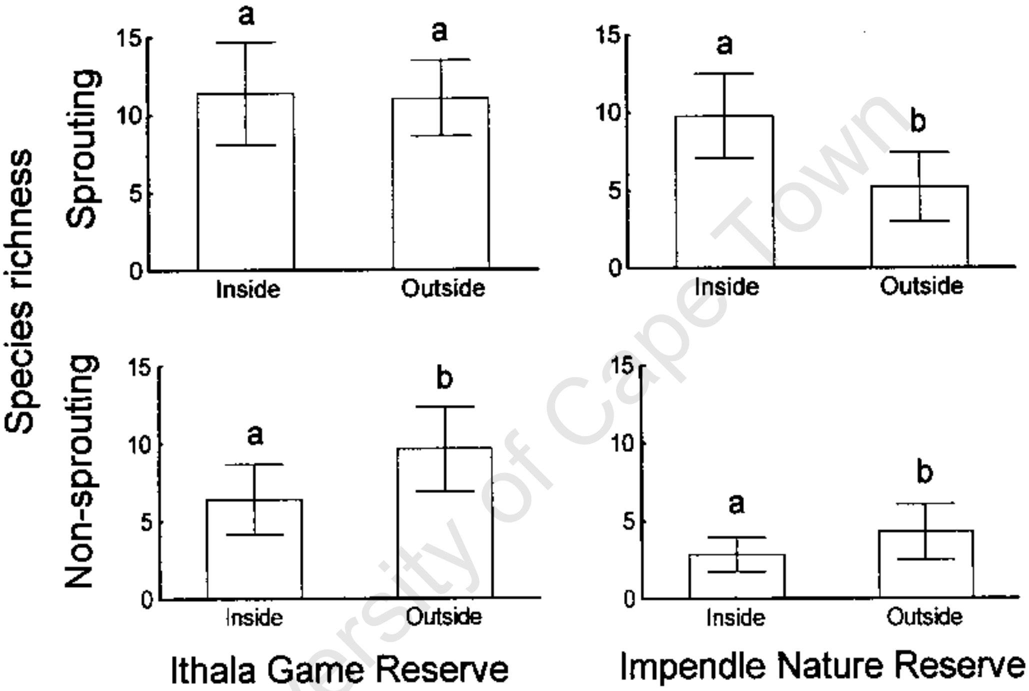


Figure 7.10 Mean species richness of sprouting and non-sprouting forbs sampled under light grazing by native herbivores inside, and heavy cattle grazing outside, of Ithala Game Reserve (40 pairs of 10 m^2 quadrats [5 m x 2 m]) and Impendle Nature Reserve (50 pairs of 10 m^2 quadrats [5 m x 2 m]). Symbols denote statistically different (a:b) levels of species richness based on paired t-tests (Table 7.2).

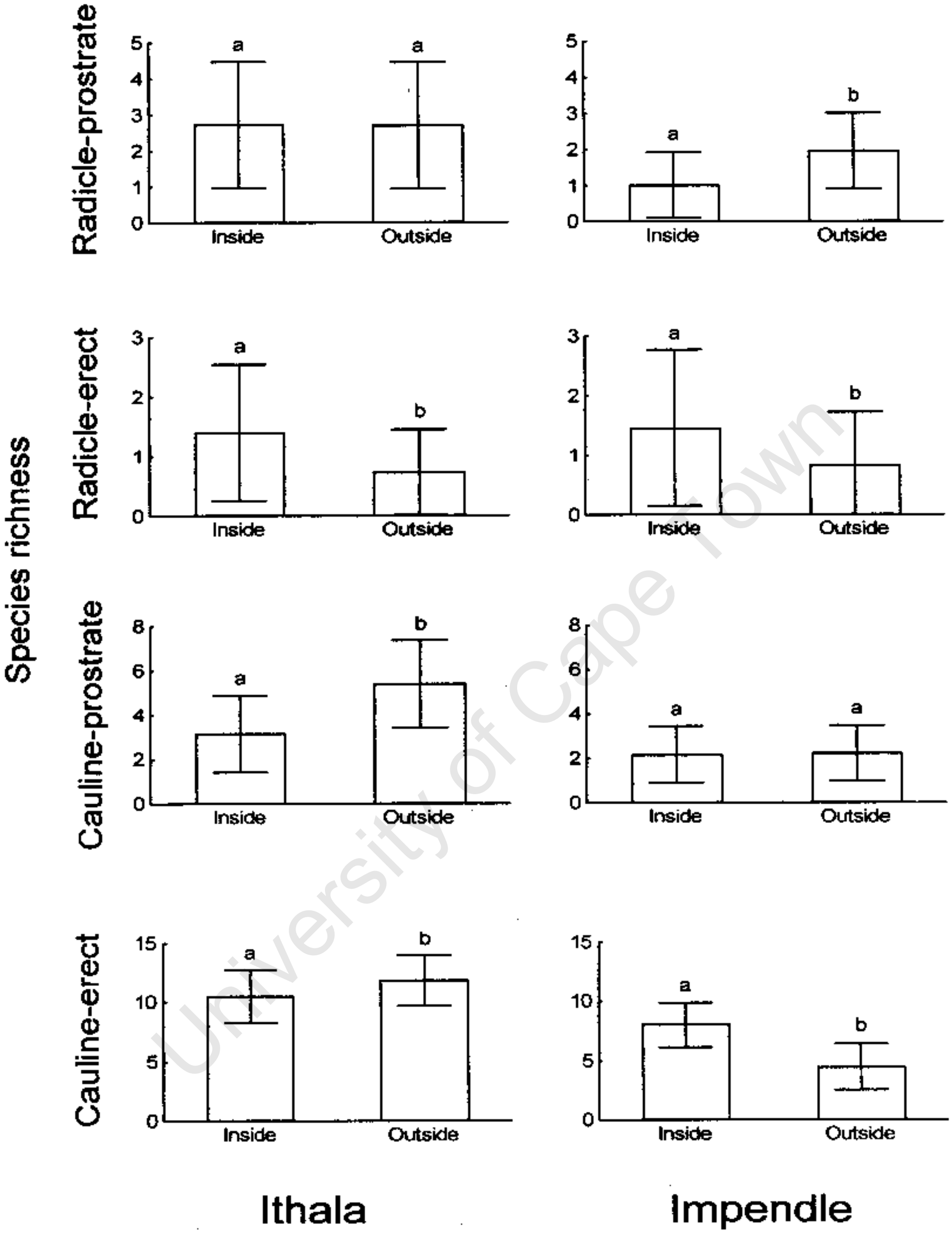


Figure 7.11 Mean species richness of above-ground forb growth forms sampled under light grazing by native herbivores inside, and heavy cattle grazing outside, of Ithala Game Reserve (40 pairs of 10 m^2 quadrats [5 m x 2 m]) and Impendle Nature Reserve (50 pairs of 10 m^2 quadrats [5 m x 2 m]). Symbols denote statistically different (a:b) levels of species richness based on paired t-tests (Table 7.2).

7.5 Discussion

There has been considerable debate as to whether communal grazing is resulting in the degradation of southern African rangelands. However, to date little understanding has emerged beyond the effects that such intense grazing is having on the dominant grass species (Everson and Hatch, 1999). As with my previous study of grazing effects (Chapter 6), scale had a strong influence on the interpretation of grazing impacts. At the 10 m^2 plot scale species richness did not respond uniformly across both reserves. When the total species richness was compared for each site, however, fewer species were found outside of both reserves. There was also a different suite of taxa encountered in these intensely grazed rangelands, to the species encountered in the lightly grazed, yet frequently burnt, reserves. Similar results have been recorded in fence-line contrasts across southern Africa, from the Namaqualand succulent shrublands on the west coast (Todd *et al.,* 1998; Todd and Hoffman, 1999), to the grassland and spinescent thickets in the Eastern Cape (Fabricius and Burger, 1997), and to the savannas (Venter *et al,* 1986; Shackleton, 1993, 1998).

The most noticeable compositional shifts in the grasslands studied (other than that of the grass composition) were that soft-leaved monocot forbs were largely absent outside of the reserve, while short-lived divot taxa increased under heavy grazing. The clearest example of this was that I observed six ground orchid species inside of Ithala Game Reserve, but did not find a single orchid plant outside of the reserve, despite an exhaustive search. Opinions as to why this might have been the case vary from selective grazing, to trampling, to compaction, to plant collecting for traditional use. Game are known to browse on some orchid species (Pooley, 1998), but soft-leaved monocot forbs displayed themselves as characteristic of Seme, the heavily grazed lawn-grass site in Hluhluwe Game Reserve (Chapter 7). There was also little preventing people from collecting plants within the reserve, as they were already herding their cattle through holes cut in the fence to illegally graze within the reserve. It was interesting to note that many of the soft-leaved monocot forbs that were recorded in the reserve, but not on the commonage, were observed in a small fenced graveyard in the centre of the Louwsburg Commonage outside of Ithala.

Regarding the greater abundance of short-lived forts outside of the reserves, it should be remembered that such species were found to be characteristically absent from the mesic grasslands (Chapter 4). Thus, the absence of soft-leaved monocots and the presence of short-lived dicots outside the reserve would appear to be a result of the intense cattle disturbance. Grazing and trampling damage undoubtedly play a role, but I suspect that the shorter grass sward with little leaf litter was resulting in greater soil dessication. Remembering that monocot forbs displayed a proportional increase with precipitation (Chapter 4), I postulate that the soft-leaved monocots were, in part, absent outside of the reserve due to the altered soil moisture status. This, however, remains to be quantified.

Besides the soft-leaved monocot forbs, the O_4 grasses also displayed clear patterns according to grazing intensity. Inside of both reserves, the sward was dominated by palatable grasses, such as *Themeda triandra* and *Tristachya leucothrix.* In contrast, the adjacent commonages were dominated by less palatable species, recognized by stock owners as being characteristic of overutilization (namely: *Aristide junciformis, Eragrostis curvula, E. plane* and *Sporobolus africanus)* [Tainton, 1999]. Although not quantified, grass height was also blatantly different, swards inside of the reserves being, on average, 30 cm tall, while outside on the commonages the sward was cropped to 10 cm and less. Observations suggest that such short grass will not carry a fire any distance except under unusual circumstances (Bond, *unpublished).* Thus, while there was lithe grazing inside of the reserve, there was correspondingly little fire outside of the reserve. Although grazing was the controlled variable across the fencelines, the ultimate disturbance effects represented a comparison between intense grazing by cattle on the commonage and intense burning of the fire-break just inside of the reserve.

7.6 Conclusions

Based on the predominance of long-lived sprouting forb species, these mesic rangelands appear well suited to moderately frequent disturbance, but not overly intense defoliation. Short-lived species do not appear as a common feature of such mesic rangelands under moderate disturbance regimes (Chapter4), suggesting that these ecosystems have no history of intense grazing. Their presence on the commonages was therefore directly due to the intense utilization. This concurred with my observations from the North American tallgrass prairie, where short-lived fort species also increased under intense bison grazing (Chapter 8). Communal grazlng is thus seen to promote a different suite of species to those found under 'natural' disturbance regimes. This results in greater community heterogeneity at the landscape scale where such land-use strategies are interspersed with less intense disturbance regimes. However, we need to question whether we should be promoting such ruderal forbs which are not a natural feature of these ecosystems when well managed (Chapter 4). Heavy livestock grazing clearly results in a decline in species richness at the landscape scale and is therefore not ideally sulted to support conservation objectives for these rangelands. Nevertheless, as opposed to the urbanisation, and till and plantatign farming that are destroying these rangelands, livestock grazing does retain diversity, many ecosystem processes and therefore maintains a place in the conservation landscape.

8 Comparison of a North American tallgrass prairie, Konza, to the southern African rangelands

Abstract

I compared the plant taxonomic richness, functional type composition, and fire and grazing responses of Konza Prairie in the North American tallgrass prairies, to my observations from the rangelands east of the escarpment in southern Africa. Taxonomic richness and functional type composition in 1000 m^2 plots at Konza were more similar to the semi-arid rangelands in southern Africa than its mesic analogue. Species richness decreased with increasing fire frequency and increased with moderate grazing in the tallgrass prairie, but no such consistent patterns could be found for southern Africa's rangelands. The increased richness was, however, attributed to the invasion of short-lived taxa, the southern African equivalent of which occurs with heavy grazing in mesic rangelands. Consequently, management practices for southern Africa's rangelands cannot be extrapolated from studies in the tallgrass prairies.

8.1 Introduction

Disturbance effects on rangeland plant diversity have received considerable attention in North America and Australia in particular, but have only recently begun to be explored for southern African ecosystems. While there is a temptation to apply the results of disturbance studies from these and similar rangelands around the world to the management of southern Africa's rangelands, preliminary results suggest that this may not be appropriate. Fire studies in the North American tallgrass prairie have shown a distinct, linear decline in species richness with increasing fire frequency (Collins *et al.,* 1995). Yet, similar studies in Australia and South Africa did not agree, finding no clear, consistent relationship between either frequency or season of fire and plant species richness under frequent burns five year fire intervals) [Lunt and Morgan, 2002; Fynn *et al.,* 2004; Uys *et al.,* 2004]. Grazing results presented for southern Africa above (Chapter 6) also do not agree with those from the North American prairie that showed an increase in species richness in grazed over ungrazed tallgrass prairie (Hartnett *et al.,* 1996; Collins *et al.,* 1998). In addition to the studies mentioned above, the effects of both fire and grazing have received considerable attention in rangelands around the world, but there have been few cross continental comparisons.

Notable exceptions to the paucity of cross continental comparisons of disturbance effects are the grazing models of Milchunas *at al.* (1988) and Olff and Ritchie (1998). These authors used a broad range of studies to develop testable predictions of grazing effects under different moisture versus evolutionary history of grazing, and moisture versus soil fertility conditions respectively (see Chapter 6 for a discussion of these models). The North American tallgrass prairies fit into the Milchunas *et al.* (1988) model, as subhumid grasslands with a short evolutionary history of grazing. Accordingly, such rangelands are predicted to display their highest diversity at low grazing intensities, with a sharp decline under grazing protection and increasing grazing pressure. According to the Olff and Ritchie (1998) model, the North American tallgrass prairies would be classified as occurring on infertile soils in an environment where precipitation is non-limiting. Such conditions are then predicted to support net increases in rangeland plant diversity under grazing. According to the grazing models, southern Africa's mesic rangelands differ from the tallgrass prairies in that they represent a long evolutionary history of grazing and occur on fertile soils. One might expect distinctly different grazing responses based on these models. Thus, the Milchunas *et al.* (1988) model predicts a hump-backed diversity response to grazing intensity, while the Olff and Ritchie (1998) model suggests that diversity may either increase or decrease depending on the herbivores present These two models, nevertheless, failed to predict the diversity response of the southern African rangelands studied (Chapter 6). It is therefore interesting to see whether the predictions of these models would hold up for the tallgrass prairies.

In addition to cross continental comparisons of disturbance effects, numerous attempts have been made to identify global plant response groupings according to life-form and life-history characteristics (Grime, 1977; Noble and Slatyer, 1980;

Lavorel *et al,* 1997; Westoby, 1998; McIntyre et *at,* 1999; Weiher *et at,* 1999; Lavorel and Gamier, 2002; Cornelissen *et al.,* 2003). Much of this work has been conducted in rangelands around the world, but none in classifying and comparing the southern African rangeland flora to other floras around the world (Comelissen *et* at, 2003). Little attention has also been paid to cross continental comparisons of rangeland plant species and family diversity (but see Knapp *et al,* 2004), although there have been some within continental comparisons (Australia - Rice and Westoby, 1983; Tremont and McIntyre, 1994; southern Africa - Cowling *et aL* 1989; Cowling and Hilton-Taylor, 1994). Patterns of taxonomic richness across the southern African rangelands that I studied showed a distinct linear increase with mean annual precipitation, only limited by altitude above - 2000 m a.s.l. (Chapter 3). If similar environmental drivers are operating to determine patterns of richness across the tallgrass prairies, I would expect the rangelands of the Konza Prairie Research Natural Area to display similar levels of taxonomic richness and forb functional type composition to Konza's southern African analogue, my Midmar Dam site. I therefore predicted that the rangelands of Konza Prairie should support - 75 plant species and - 25 plant families per 1000 m^2, including a forb flora of 55 species (- 75 % of total species richness), dominated by - 70 % long-lived, sprouting dicots, with approximately 22 % of the forbs (- 12 spp.) being monocots, and no more than five percent of short-lived forb species (- three spp.).

8.2 Study sites

8.2.1 Konza prairie

Konza Prairie Research Natural Area is located in the Flint Hills of northeastern Kansas, United States of America (93°05'N, 96°35'W). At - 400 m a.s.l. the region receives most (75 %) of its 835 mm mean annual precipitation (MAP) over the growing season (April - September). The frost-free season lasts - 180 days and there is a mean annual temperature of 13 °C, with an average winter (January) minimum of - 3 °C and a summer (July) maximum of 27 °C (Towne, 2002). The conversion of the site from a cattle ranch to a conservation and research facility began with an initial purchase of 371 ha in 1971, with the remaining 3116 ha purchased in 1977 to bring Konza Prairie to its current 3487 ha. With most of the North American prairies having been transformed through ploughing, this conservation area (managed by the Division of Biology at Kansas State University) represents one of the largest intact remnants of native taligrass prairie in the United States of America.

Botanically, the biomass of the grasslands at Konza Prairie is dominated by a few C_4 grass species: *Andropogon geradii, A. scoparius, Sorghastrum nutans* and *Panicum virgatum.* Unlike most of southern Africa's rangelands, however, there was also a substantial C_3 grass component to the prairies, characterised by: *Bouteloua curtipendula, B. gracilis,* Elymus canadensis, *Koeleria cristata* and *Poa pratensis* (Freeman, 1998). This is important for graziers as the C_3 grasses provide good quality winter forage which is not available in the sourveld rangelands east of the escarpment in southern Africa (Ode and Tieszen, 1980; Tainton, 1999). Including the grasses, Konza Prairie (3487 ha) supports 576 species of vascular plants (Towne, 2002). These are predominantly represented by the following families in descending order of species richness: Asteraceae, Poaceae, Fabaceae, Brassicaceae, Euphorbiaceae, Cyperaceae, Lamiaceae, Scrophulariaceae, Polygonaceae and Rosaceae (Freeman, 1998). Of these 576 species, 180 species (31.3 %) are listed as annuals, 24 species (4.2 %) as biennials, 316 species (54.9 %) as herbaceous perennials, and 56 species (9.7 %) as woody perennials (Towne, 2002).

Konza Prairie was divided into 52 watershed areas that had been treated with different frequencies and seasons of burn for - 25 years at the time of sampling. In addition to these fire treatments, ten of the watersheds had been grazed by the native bison *(Bison bison)* for 10 - 15 years at the time of sampling. Bison were reintroduced in 1987 to a 469 ha enclosure which was subsequently expanded to 949 ha in 1992 (Towne, 1992). The herd is maintained at - 210 animals (Konza Prairie Research Natural Area bison and cattle grazing program fact sheet) which translates to a stocking rate of - 1 AU / 5 ha. The bison, however, tend to congregate on the flatter uplands and middle lands, especially near the fences, essentially exposing these areas to more intensive stocking rates. In addition to the bison, the only other large mammalian herbivores are domestic cattle run in six watersheds in the southeast of the research natural area and white-tailed deer *(Odocoleus virginianus)* that roam freely throughout Konza Prairie.

I sampled watersheds representing a range of fire frequencies applied in spring (April) and a corresponding set of watersheds that were grazed by native herbivores in addition to being burnt. The burnt and ungrazed watersheds ranged from an annual (SpB), through a biennial (2C), tetraennial (4B), to a decennial (10A) treatment. All these fire treatments, except the ten year fire interval, were mirrored in the burnt and grazed watersheds. I subsequently sampled watersheds with annual (NIB), biennial (N2B) and tetraennial (N48) fire treatments that were continuously grazed. I selected these particular watersheds as these grazed and ungrazed treatments lay adjacent to each other. Furthermore, all of these watersheds had at least part of their area including the upland plateau at the southern end of Konza Prairie. I focussed my sampling on the fairly uniformly shallow silty clay barns, overlying limestone and shale layers of this upland plateau (Towne, 2002) in an attempt to minimise any effect that environmental differences between watersheds may have had on species composition.

8.2.2 South African grasslands studied

Of the 25 sites I surveyed across the mesic to semi-arid and coastal to montane rangelands east of the escarpment in southern Africa, the Midmar Dam site most closely approximated the rangelands of Konza Prairie. Midmar Dam (Chapter 2.5.15; Figure 2.1) had a similar mean annual precipitation (875 mm MAP) and shale substrate as Konza (835 mm MAP), but Midmar Dam sat at a much greater altitude (1100 m a.s.l.) and did not have the extensive limestone outcrops of Konza (400 m a.s.l.). Midmar Dam also represented a local tall grassland type (Southern Tall Grassveld; Acocks, 1988) dominated by *Hyparrhenia hirta, Themeda triandra* and *Tristachya leucothrix.* These grasses, however, seldom approach the - 2.4 m (8 ft) tall swards of the Kansas tallgrass prairies, usually forming grasslands seldom taller than 1.5 m tall in this region.

Grasslands around the dam were burnt on a biennial to triennial rotation between mid winter and early spring (July to September). In contrast to Konza, the game park at Midmar Dam was stocked with a diversity of medium to large herbivores, including: 91 Black Wildebeest *(Connochaetes gnu),* 45 Blesbok *(Damaliscus dorcas phillipsi),* Common duiker *(Sylvicapra grimmia),* Reedbuck *(Redunca arundinurn),* Oribi *(Ourebia ourebi),* 95 Red Hartebeest *(Alcelaphus busclaphus)* and 75 Zebra *(Equus burchell;).*

8.3 Methods

The vegetation of Konza Prairie has been variously surveyed using a range of plot designs, but I used modified Whittaker plots (20 m x 50 m) for comparison to my work in South Africa. This basic plot design has been widely used to quantify diversity in plant communities across the world (Whittaker et *al.,* 1979; Shmida, 1984; Stohlgren *et al.,* 1995, 1997; Schwilk et *al.,* 1997; Barnett and Stohlgren, 2003; Keeley and Fotheringham, 2005), but not (as far as I could tell) at Konza Prairie. It also appeared that most of the plot based vegetation sampling at Konza Prairie had been done at smaller scales than 1000 m^2. Consequently, there were no existing studies for me to compare the results of my surveys across the rangelands east of the escarpment in southern Africa to the tallgrass prairie at Konza, making it necessary that I conduct new surveys.

I used the same method described in Chapter 3 to systematically sample a 20 m x 50 m plot in each of the watersheds selected. In each plot I recorded all the species and families present, identifying the forb life-form and life-history traits according to the same criteria I used for the southern African flora (Chapter **4).** These traits included whether the (orbs were divots or monocots, short-lived (annuals and biennials) or long-lived (perennials) [based on Towne, 2002], sprouters or non-sprouters (based on their underground organs), and their above-ground growth forms. Not knowing the flora, I collected voucher specimens of all taxa that were kindly identified by Mr Gene Towne (see Towne, 2002). Results were analysed in the same manner and compared to the results of my survey across the southern African rangelands (Chapters 3 and 4).

8.4 Results

As with the southern African grassland flora, the herbaceous flora in the quadrats sampled at Konza was dominated by long-lived, sprouting divot forbs displaying the cauline erect growth form (Table 8.1). Approximately three species of forbs were recorded for every non-petaloid monocot (grasses, rushes and sedges) encountered in the seven watersheds sampled (Table 8.1). The mean species richness in 1000 m^2 recorded at Konza Prairie (38.3 spp.) was similar to that of the poorer southern African sites, Bateleur (36 spp.) and Shingwedzi (35 spp.), and was half the mean richness recorded in 1000 m^2 at Midmar Dam (76.5 spp.) that receives a similar amount of MAP (Tables 8.1 and 8.2). The grazed watersheds were richer (x = 43 spp.) than the ungrazed watersheds (v = 34.8 spp.), largely due to an increase in short-lived taxa under grazing (v ungrazed = 1.75 spp. vs x grazed = 6.67 spp.) [Table 8.1].

Twenty-two herbaceous plant families were recorded in the seven 1000 m2 quadrats sampled across the watersheds at Konza Prairie, only eight of which were represented by two or more taxa (Table 8.3; Appendix 8.1). The Acanthaceae, Asteraceae, Euphorbiaceae, Fabaceae, Lamiaceae and Poaceae ranked amongst the most specious families on both continents. Six of the families I encountered at Konza Prairie did not appear in my southern African grassland sites: Cactaceae, Caprifoliaceae, Juncaceae, Linaceae, Onagraceae and Rhamnaceae. Despite this, all of these families are represented in the southern African flora (Gibbs Russell *et al.,* 1990).

No monocot forbs were recorded in this study despite their representing 14.4 % of the forb flora at Konza Prairie (62 spp. out of 430 spp. of forbs) [Towne, 2002]. Non-sprouting forbs were more abundant in the grazed watersheds (2 ungrazed = 6.5 spp. *vs z* grazed = 13.3 spp.), but this merely reflected the increase in short-lived taxa under grazing (Table 8.1). The absence of monocots in the quadrats I sampled was also reflected by the absence of radical growth forms (Table 8.1). Cauline erect growth forms dominated the forb flora, with only two species of cauline prostrate (orbs, *Antennaria neglecta* and *Hymenopappus scabiosaeus* (both in the Asteraceae), recorded from the watersheds sampled (Appendix 8.1).

Table 8.1 Species and forb functional type richness sampled at 1000 m^2 in seven of the watersheds (n = 1) at Konza Prairie Research Natural Area. All of the watersheds sampled were burnt in spring (April) at different fire frequencies, in addition to which, three watersheds were also grazed by Bison (*Bison bison*) at a consistent ~ 1 AU / 5 ha.

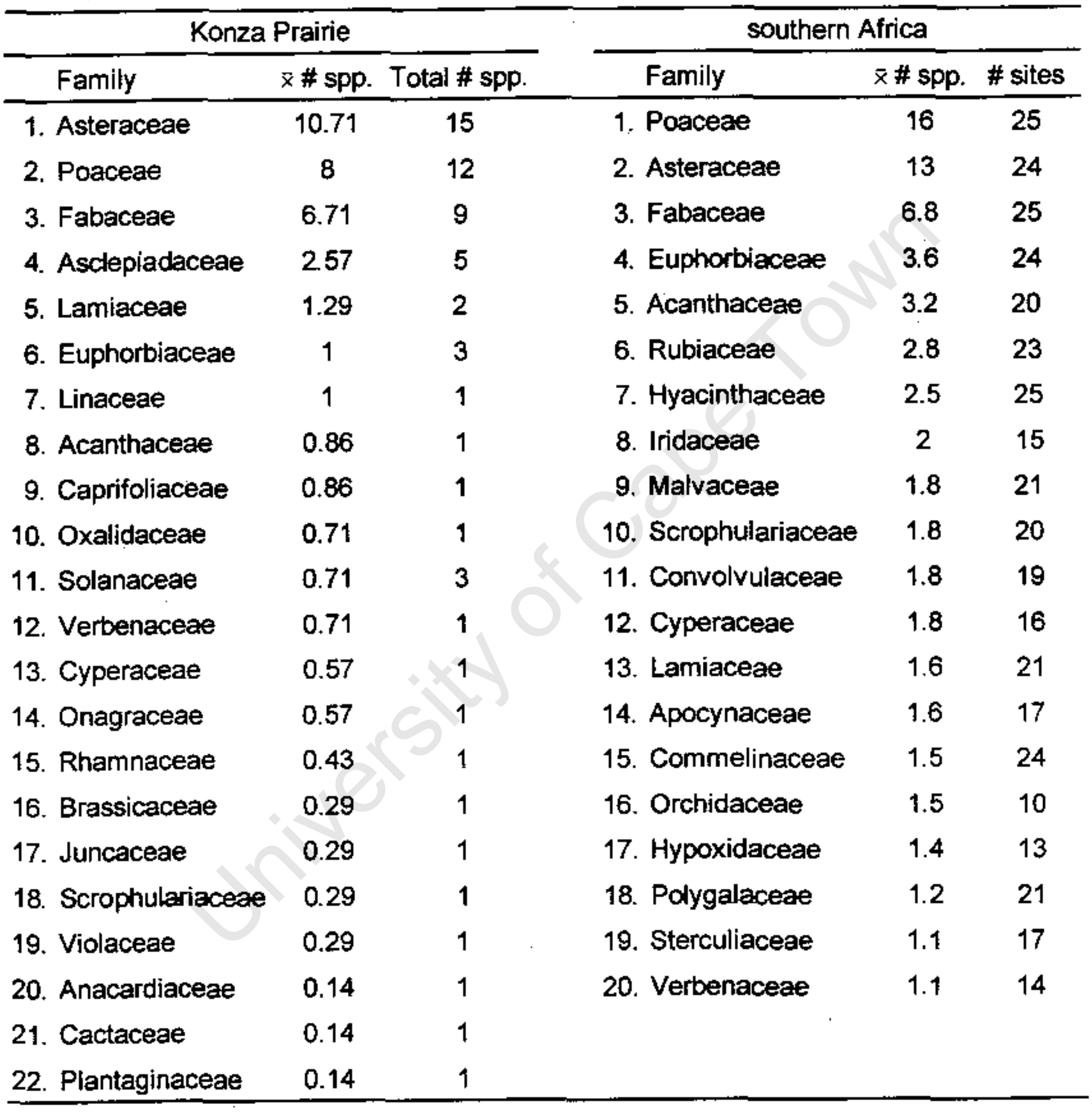
	Fire				Fire and Grazing			Fire		Fire and Grazing		All Watersheds	
	1 yr	2 yr	4 yr	10 yr	1 yr	2 yr	4 yr	Mean	STD	Mean	STD	Mean	STD
Total	31	32	40	36	42	43	44	34.8	3.6	43	0.8	38.3	4.9
Grasses	6	8	9	9	7	6	11	8	1.2	9	2.2	8.86	1.7
Sedges	1	0	2	0	2	0	1	0.75	0.8	1	0.8	0.9	0.8
Forbs	24	24	29	27	33	37	32	26	2.1	34	2.2	29.4	4.5
Dicots	24	24	29	27	33	37	32	26	2.1	34	2.2	29.4	4.5
Monocots	0	0	0	0	0	0	0	0	0	0	0	0	0
Short-lived	2	1	1	3	4	8	8	1.75	0.8	6.67	1.9	3.86	2.8
Long-lived	22	23	28	24	29	29	24	24.3	2.3	27.3	2.4	25.6	2.8
Sprouting	18	19	23	18	22	22	18	19.5	2.1	20.7	1.9	20	2.1
Non-sprouting	6	5	6	9	11	15	14	6.5	1.5	13.3	1.7	9.43	3.7
Cauline Prostrate	0	1	0	0	2	2	2	0.25	0.4	2	0	1	0.9
Cauline Erect	24	23	29	27	31	35	30	25.8	2.4	32	2.2	28.4	3.9
Radical Prostrate	0	0	0	0	0	0	0	0	0	0	0	0	0
Radical Erect	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 8.2 Mean and total species richness and mean family richness from the two 1000 m^2 plots sampled at each site sampled across the rangelands east of the escarpment in southern Africa, with the total numbers of forbs and their various life-form and life-history traits. MAP = mean annual precipitation (mm yr^{-1}), Alt. = altitude (m a.s.l.), short-lived = annual and biennial forbs, long-lived = perennial forbs, Spr. = sprouting forbs, Non-spr. = non-sprouting forbs, CP = cauline prostrate forb growth form, CE = cauline erect forb growth form, RP = radical prostrate forb growth form, RE = radical erect forb growth form. See Chapter 4 for discussion of plant growth forms.

Site	MAP	Alt.	Avg. 0.1 ha	Total 0.2 ha	Avg. # Fam.	Grasses & sedges	Forbs	Monocot	Dicot	Short-lived	Long-lived	Spr.	Non-spr.	Forb growth forms			
														CP	CE	RP	RE
Bateleur	440	340	36	55	19.5	12	43	4	39	6	37	22	21	10	30	2	1
Shingwedzi	460	280	35	45	18.5	9	36	6	30	5	31	20	16	10	23	2	1
Olifants	465	250	22.5	33	16	5	28	3	25	7	21	12	16	7	20	0	1
Satara	490	290	16.5	24	14	3	21	4	18	3	18	12	9	5	14	1	1
Ndumo	520	90	48.5	64	19.5	11	53	6	47	3	50	31	22	14	33	3	3
Skukuza	550	460	39.5	57	22.5	12	45	6	39	6	39	25	20	10	31	1	3
Pongolapoort	650	150	62	77	20	21	56	7	49	14	42	33	23	14	38	3	1
Mkuze (clay)	665	120	51.5	68	18	20	48	7	41	8	40	28	20	12	32	1	3
Mkuze (sand)	670	120	56	72	21	22	50	5	45	7	43	31	19	16	32	2	0
Imfolozi	680	230	47.5	80	21.5	22	58	6	52	11	47	35	23	15	39	1	3
Pretoriuskop	690	570	59.5	80	22	26	54	5	49	4	50	40	14	12	37	2	3
Mooihoek	700	1780	63.5	83	24	15	68	8	60	2	66	47	21	17	35	10	6

			Avg.	Total	Avg.	Grasses				Short-	Long-		Non-	Forb growth forms			
Site	MAP	Alt.	0.1 ha	0.2 ha	# Fam.	& sedges	Forbs	Monocot	Dicot	lived	lived	Spr.	spr.	CP	CE	RP	RE
Hluhluwe	770	245	66.5	119	25	24	95	15	80	11	84	69	26	18	59	8	10
Ithala (savanna)	790	720	64.5	90	23.5	15	75	14	60	5	69	61	13	16	40	10	8
Ithala (tall grass)	790	850	68.5	102	24	22	80	9	71	4	76	65	15	15	49	10	6
Ithala (short grass)	820	1400	79	105	23	19	86	24	62	2	84	70	16	13	45	11	17
Midmar Dam	875	1100	76.5	100	25.5	23	77	17	60	3	74	58	19	14	38	15	10
Chelmsford Dam	1000	1270	79.5	106	26.5	29	77	18	59	2	75	58	19	16	36	13	12
Cobham	1000	1780	68	94	21	24	70	20	50	1	69	51	19	9	37	10	14
QE Park	1070	950	86.5	117	21.5	30	87	20	67	1	86	70	17	14	48	13	12
Impendle	1100	1400	81	99	27	26	73	16	57	3	70	51	22	10	41	11	11
Highmoor	1150	1960	80	104	25	20	84	28	56	1	83	63	21	4	43	23	14
Amatigulu	1170	20	91.5	110	30	18	92	17	75	3	89	65	27	14	58	10	10
Cathedral Peak	1380	1830	57	79	20.5	22	57	14	43	0	57	42	15	10	29	12	6
Sani Pass	1600	2500	57.5	73	18	15	58	9	49	0	58	41	17	3	37	10	8

Table 8.3 Mean and total species richness of the 22 families sampled in 1000 m^2 across the seven quadrats surveyed at Konza Prairie Research Natural Area, and the mean species richness (R # spp.) of the top 20 families recorded from the two 1000 m^2 quadrats sampled at each of the 25 sites surveyed across the rangelands east of the escarpment in southern Africa.



Konza Prairie			southern Africa		
Family	$\bar{x}$ # spp.	Total # spp.	Family	$\bar{x}$ # spp.	# sites
1. Asteraceae	10.71	15	1. Poaceae	16	25
2. Poaceae	8	12	2. Asteraceae	13	24
3. Fabaceae	6.71	9	3. Fabaceae	6.8	25
4. Asclepiadaceae	2.57	5	4. Euphorbiaceae	3.6	24
5. Lamiaceae	1.29	2	5. Acanthaceae	3.2	20
6. Euphorbiaceae	1	3	6. Rubiaceae	2.8	23
7. Linaceae	1	1	7. Hyacinthaceae	2.5	25
8. Acanthaceae	0.86	1	8. Iridaceae	2	15
9. Caprifoliaceae	0.86	1	9. Malvaceae	1.8	21
10. Oxalidaceae	0.71	1	10. Scrophulariaceae	1.8	20
11. Solanaceae	0.71	3	11. Convolvulaceae	1.8	19
12. Verbenaceae	0.71	1	12. Cyperaceae	1.8	16
13. Cyperaceae	0.57	1	13. Lamiaceae	1.6	21
14. Onagraceae	0.57	1	14. Apocynaceae	1.6	17
15. Rhamnaceae	0.43	1	15. Commelinaceae	1.5	24
16. Brassicaceae	0.29	1	16. Orchidaceae	1.5	10
17. Juncaceae	0.29	1	17. Hypoxidaceae	1.4	13
18. Scrophulariaceae	0.29	1	18. Polygalaceae	1.2	21
19. Violaceae	0.29	1	19. Sterculiaceae	1.1	17
20. Anacardiaceae	0.14	1	20. Verbenaceae	1.1	14
21. Cactaceae	0.14	1			
22. Plantaginaceae	0.14	1			

8.5 Discussion

8.5.1 Diversity patterns between continents

Plant life-form and life-history characteristics determine how a community responds to disturbance. In southern Africa, the distribution of life-form and life-history characteristics is strongly related to environmental gradients across the rangelands (Chapter 4). Similarly, both species and family richness display clear linear increases with mean annual precipitation (MAP) across these rangelands, only limited at higher altitudes (> 2000 m a.s.l.) [Chapter 3]. Yet, under the equivalent levels of MAP in the North American tallgrass prairie, the taxonomic richness in Konza Prairie was roughly half that of its southern African analogue, the Midmar Dam site. The species richness of the tallgrass prairies was closer to the semi-arid than mesic rangelands of southern Africa, a comparison further borne out by the plant functional type composition of the sites examined.

As with the southern African rangelands, the prairie flora of Konza was dominated by long-lived, sprouting dicots that displayed cauline erect growth forms. The most startling difference though, was the complete absence of monocot forbs and the abundance of short-lived taxa, especially in the grazing treatments. Such plant functional composition is characteristic of southern Africa's semi-arid rangelands and only encountered in mesic rangelands in this region when they are very heavily grazed. As this was not the case at Konza, it would appear that a different set of environmental drivers are operating to determine the richness and composition of the rangelands on the two continents. It is difficult to place these differences in context though, as regional patterns of richness across the North American rangelands do not seem to have been explored. This may prove challenging because, despite the vast extent of the grassland biome in North America, remarkably little remains untransformed (Samson and Knopf, 1994). Although the richness of native prairies has been sporadically reported, the range of sampling methods and scales used makes it impossible to gain a sense of the environmental determinants of prairie plant diversity across the continent. Richness patterns cannot be explored using the existing literature and require urgent attention if they are to be addressed before the last prairie remnants are transformed.

8.5.2 Comparison of grazing effects

One of the most important discoveries to have been made at Konza was that prairie plant species richness declines with increasing fire frequency, but that this may be avoided if frequently burnt prairies are grazed by bison (Collins, 1987; Collins *et al.,* 1998; Knapp et al., 1999). Increasing the fire frequency is thought to promote denser grass swards and thus suppress the forbs (Collins, 1987). However, retaining moderate bison grazing on a freshly burnt sward (- 1 AU / 5 ha at Konza) prevents this grass accumulation and so maintains species richness. My results from Konza supported these observations, but unlike previous studies, I was also able to show where this additional richness under grazing came from. Grazed plots had an abundance of short-lived forbs not found in the ungrazed plots, that largely accounted for their greater species richness. This increase in short-lived taxa appears to be fairly common and has been widely recorded in grazing lands around the world (e.g. Argentina - Rusch and Oesterheld, 1997; Australia - McIntyre and Lavorel, 2001; China - Zhang, 1998; East Africa - Belsky, 1992; United Kingdom - Bullock *et al.,* 2001; Uruguay - Aletsor *et at,* 1998). Although I found a similar invasion of short-lived taxa in the mesic rangelands of southern Africa, this only occurred under cattle grazing twice the intensity of the utilization on Konza (>1 AU / 2.5 ha) [Chapter 7]. Furthermore, the short-lived species that invaded these rangelands under heavy grazing merely replaced the monocot forbs that had been lost, so retaining similar, if not decreased, levels of species richness. Short-lived taxa are infrequent in moderately disturbed mesic rangelands in southern Africa (Chapter 4), as they also were in the ungrazed treatments at Konza. Such invasions may therefore be viewed as unfavourable in either ecosystem. In addition, if these invading short-lived taxa are exotic weeds, as is often the case in southern Africa's mesic rangelands, they are even less welcome.

The increase in species richness with moderate grazing at Konza Prairie supported the predictions of both the Milchunas et *at* (1988) and Olff and Ritchie (1998) grazing models. It would be interesting to see whether species richness declines under heavy grazing, as predicted by Milchunas *et at* (1988), or whether it is maintained by the introduction of further short-lived taxa. It is important to note that the increase in species richness with moderate grazing of the tallgrass prairie was not replicated under moderate grazing in southern African mesic rangelands. This suggests fundamental differences in the disturbance responses of the two floras, meaning that we should not extrapolate results across the continents.

8.5.3 Comparison of fire effects

In addition to the different grazing responses between the two continents, fire has also been found to have different effects. No clear, consistent responses of plant species richness to fire have been found in the southern African rangelands (Fynn *et al,* 2004; Uys *et al.,* 2004). Species richness, however, has shown a linear decline with increasing fire frequency in the tallgrass prairies (Collins et *aL,* 1995). My survey supported this for the one to four year fire interval treatments, but not for the ten year burn rotation. This may, nevertheless, have been due to the ten year treatment not having been burnt for five years at the time of sampling. One possible explanation for the difference in the fire response between the two continents is the abundance of short-lived taxa in the tallgrass prairies (35.5 % of the Konza fort flora; Towne, 2002), compared with their scarcity in the mesic southern African rangelands (< 10 % of the forb flora in the two 1000 m^2 quadrats sampled at each site; Chapter 4). The increase in short-lived (orbs under grazing in the tallgrass prairie suggests that these species are not able to tolerate the increased grass biomass that is promoted by frequent fires (Collins, 1987). In contrast, southern Africa's mesic rangelands are dominated by long-lived forts that are able to recover after a burn by resprouting from underground organs (Chapter 4). These underground organs also allow the plants to tolerate several years of shading under moribund swards (Uys *et at,* 2004). Increases in the fire frequency therefore do not appear to influence species richness in southern Africa's mesic rangelands as these ecosystems possess few short-lived taxa and the majority of long-lived taxa appear well suited to a range of fire regimes.

8.5.4 Accounting for the differences between continents

At first glance, the tallgrass prairies look similar to the mesic rangelands in southern Africa, however, several remarkable differences appear upon closer inspection. Pastoralists used to southern Africa's mesic rangelands, that lose their palatability over winter, would undoubtedly be daunted by the prospect of such a tall sward, but equally fascinated to discover the large C3 grass component that provides winter forage. They would most likely find the soils to be foreign, shale occurring widely across the rangelands of both continents, but with such extensive limestone outcrops as occur at Konza Prairie being unknown in southern Africa. They would also be challenged by the severity of the winters that are only rivalled by those of the high mountains of Lesotho in the south. The latitude effect that generates these harsh winters (northern hemisphere rangelands occurring at higher latitudes than in the south) also has an evolutionary context that may explain some of the fundamental differences between these floras. Due to its high latitude, North America was more severely affected by the last glacial period (ending - 12000 B.P.) than southern Africa. This is particularly true of the prairies, whose current distribution was either covered in ice (in the north) or is believed to have been forest or woodland (further south) until 15000 - 12000 B.P. (Wells, 1970; Davis, 1976; Stebbins, 1981; Axelrod, 1985; Jacobs *et al.,* 1999). Consequently, the prairie flora has only attained its current extent in post-glacial times. While many genera have speciated widely in the adjoining savannas and woodlands, they have not done so in the prairies that contain few endemic taxa (Axelrod, 1985). In contrast, the southern African rangelands, not having been as severely affected by the last glaciation, represent a wealth of endemic taxa. These rangelands also support a range of genera that have speciated as, or more widely than their savanna and forest counterparts (Gibbs Russell, 1987; Cowling *et al.,* 1989; Garbutt and Edwards, 2004). Consequently, although the tallgrass prairies and southern African rangelands bear passing similarities, their evolutionary histories and environmental differences appear to have resulted in significantly different rangeland floras on each continent.

8.6 Conclusions

Studies of rangeland biodiversity have been fairly localised around the world and there is a temptation to extrapolate results of disturbance studies between continents. The results presented here, however, indicate that the wealth of prairie literature from North America does not easily extrapolate to the southern African rangelands. Although they may appear superficially similar, my results suggest that these ecosystems are fundamentally different. Floristically, the taxonomic richness and plant functional type composition of the prairie was more similar to that of the semi-arid rangelands of southern Africa. It is therefore not surprising that marked differences occur in the fire and grazing effects between the two continents. I ascribe the differences in these floras to the differences in their evolutionary histories and environmental conditions. As similarly large differences occur between the southern African rangelands and other rangelands around the world, we cannot rely on the results of disturbance studies from other continents to improve our rangeland management. Cross continental comparisons, however, provide a means by which to challenge our understanding of the composition and functioning of our own ecosystems and should therefore be urgently pursued while sufficient rangelands exist for them to be conducted.

9 Conclusions

Southern Africa's rangeland flora has received considerable attention, but little of this research has addressed the forb species that constitute most of the plant diversity of these ecosystems. Consequently, we still know very little about the basic biology of many of our rangeland plant species or how the diversity of these ecosystems should be managed. The work presented here attempted to improve this situation by exploring regional patterns of diversity and some of the main processes (grazing and recruitment) responsible for maintaining them.

9.1 Patterns of diversity and disturbance response

Cross cutting this work is the idea that the climatic surrogates, altitude and MAP, serve as primary correlates for patterns of plant diversity. Both species and family richness displayed clear linear increases with MAP that overrode both local environmental differences (Chapter 3) and disturbance effects (Chapter 6). This relationship, however, broke down at higher altitudes (> 2000 m a.s.I.), where cold temperatures appeared to account for a decline in richness irrespective of increasing rainfall. In the absence of attitudinal effects, casual observations by fellow researchers suggest that richness should maintain its linear increase with MAP up to at least 1300 mm MAP. Subsequently, in re-examining the various theoretical predictions of diversity patterns, conflicts were accounted for by the differentially dominating effects of altitude and MAP.

It is interesting to note that the patterns of taxonomic richness observed in this study correspond to similar patterns in the grass sward. As with taxonomic richness, available moisture appears to be the primary factor determining the rate at which biomass accumulates across these rangelands (O'Connor and Bredenkamp, 1997; Rutherford, 1980). Furthermore, the influences of altitude and MAP on taxonomic richness correspond to the gradient from moisture to temperature limitation that controls the onset of grass production across these same semi-arid to mesic rangelands (O'Connor and Everson, 1998).

Patterns of forb functional type diversity were also best accounted for by the MAP gradient across these rangelands. I related the distribution of plant functional traits to disturbance responses and these to the shift in the predominant disturbance types. Grass fires usually do not heat the soil to any depth, favouring plants able to recover their destroyed aboveground parts by resprouting from underground organs. In contrast, severe droughts result in the total death of most plants, favouring species that survive through seed. As biomass accumulates more rapidly in mesic rangelands, resulting in more frequent fires, I predicted that these ecosystems should favour resprouting taxa. Similarly, as severe drought conditions are increasingly experienced into the semi-arid rangelands I predicted that these ecosystems should favour reseeders. In support of these hypotheses, forbs with persistent (long-lived, resprouting) functional traits dominated the mesic rangelands, while taxa displaying recruiting traits (short-lived, non-sprouters) increased into the semi-arid areas (Chapter 4). Thus, the mesic and semi-arid rangelands of southern Africa appear to support distinct functional type assemblages that require different management strategies to maintain their diversity.

Pastoralists widely consider semi-arid rangelands more difficult to manage than mesic ecosystems, but the threat to biodiversity through mismanagement may be far greater in mesic rangelands. As it is linked to biomass production, carrying capacity becomes increasingly variable as the coefficient of rainfall variation increases into the semi-arid rangelands (Ellis and Swift, 1988; Illius and O'Connor, 2000). Yet, while these disequilibrium semi-arid rangelands may be more challenging to manage, their relative abundance of recruitment specialists suggests that their forb floras may be better suited to recover from severe unnatural disturbances (Chapter 4). Seed dependence, however, requires disturbances to be sufficiently infrequent for the plants to replenish their seed bank. In contrast, the persistent traits of mesic forbs predispose them to tolerate frequent, albeit low intensity, disturbances such as fire and grazing that generally only remove the aboveground parts. Judging by the rate of old-land recolonization in mesic areas (Roux, 1969; Everson, 1994), it may take well over 500 years to regain the pre-disturbance species composition of these rangelands, if at all. Consequently, although mesic rangelands may be easier to manage for grazing due to their predictable biomass production, it is important that we recognise the threat and long-term consequences that mismanagement poses to their biodiversity.

9.2 The role of forb recruitment

In contrast to the predicted increase in the number of emerging forb seedlings based on the relative shift to obligate seeders with decreasing MAP, patterns of seedling recruitment matched those of species richness. Both the number and richness of seedlings increased with increasing MAP across the six sites studied. Nevertheless, although regional patterns of seedling diversity were determined by MAP, local patterns of recruitment were influenced by disturbance effects. As predicted, recruitment was proportionately higher in the fire treatment at the mesic sites, increasing proportionately in the animal digging and drought treatments as MAP decreased. Marked differences between the species composition of emerging seedlings and the adult swards may account for the slow recovery of pre-disturbance communities in old-lands. Several of the species emerging in the recruitment experiment were "weedy" species characteristic of colonizing disturbed lands *(e.g. Bidens* sp., *Conyza* spp., *Sida* sp. and *Sonchus* sp.). While these species are commonly observed in disturbed areas, such as road verges, they are seldom recorded in well managed rangelands. Their emergence in what was essentially pristine rangeland bears testament to their dispersal abilities and the challenges of recovering pre-disturbance community assemblages.

9.3 Understanding disturbance effects

Grazing impact on species richness, as with fire effects (Uys *at al.,* 2004), appeared to be superceded by both regional and local environmental gradients (Chapter 6). In contrast to their effects on the forb flora, fire and grazing have a dramatic impact on the composition of the dominant grass species (Tainton, 1999). Disturbance impacts on forb species richness may be overlooked due to the generally low evenness of the largely rare and scattered forb flora that constitutes most of the richness in these ecosystems. My observations, however, suggest that intense fire and grazing promote a suite of taxa able to tolerate frequent defoliation, increasing their abundance in the sward. Abundant species are more readily observed in smaller areas (Morrison et *al,* 1995). Consequently, if disturbance-intolerant species are replaced by disturbance-specialists *(i.e.* weeds), small plot studies may not record declines in overall species richness. My observations lead me to suspect that the effects of sampling scale, in conjunction with environmental heterogeneity, are hampering the study of disturbance effects. At larger scales, I predict that frequently disturbed swards should appear more homogeneous, but with fewer species. If this is the case, we need to review the relevance of extrapolating the results of small plot studies to the management of landscapes.

Owing to their fluctuating biomass and subsequent susceptibility to "overgrazing" most of the research into intense stocking rates has focussed on semi-arid rangelands. As discussed above, however, the long-term consequences of mismanagement appear to be more severe for the floral diversity of mesic ecosystems. Based on their functional traits, I predicted that semi-arid rangelands should recover species richness more rapidly following reductions in grazing intensity, while mesic floras should benefit from less intense utilization. The two fence-line contrasts I examined in the mesic rangelands showed an overall decline in richness under intense utilization. Heavy grazing of these communal lands also resulted in a loss of soft-leaved monocots and the invasion of dicot weeds (Chapter 7). These trends for mesic rangelands are supported in the southern Africa's grazing literature, with stocking rates being shown to have a greater impact on sward composition than grazing regimes (continuous versus rotational grazing) [Tainton, 1985; O'Reagain and Turner, 19921 Further studies are nevertheless required to firmly establish these differences between mesic and semi-arid rangelands and to understand how grazing effects might differ according to local environmental variables.

9.4 Future research

Southern Africa's rangelands are increasingly being lost to agriculture, industrialisation and urbanisation, necessitating the urgent prioritization of conservation targets to ensure habitat representivity. Beyond capturing irreplaceable features in conservation lands, we need to improve our understanding of these ecosystems to ensure that they are not degraded or lost through uninformed management. As my comparison of southern Africa's rangelands to the tallgrass prairies of Konza showed, we cannot rely on understanding gained from seemingly similar ecosystems elsewhere in the world. Instead, we need to improve our knowledge of the basic biology of the forts that constitute most of the floral diversity of southern Africa's rangelands. Particular attention needs to be paid to species of special concern such as the endemic, rare and threatened taxa that form the basis of the Red Data Lists. Such lists find extensive use in conservation planning and environmental impact assessments, but are often based on incomplete records and limited expert opinion. Many of these species also have medicinal or other traditional uses that, as with the horticultural potential of this flora, remain largely untapped.

Functional traits have been key to understanding how disturbance responses govern the composition of the dominant grasses, yet similar patterns remain to be explored for the forbs. Although untested, my observations support those of West (1951), suggesting that many forbs appear to avoid grass competition by emerging from enlarged underground organs early in the growing season (vernal aspect species), before the grass sward bulks up. Forbs that initiate growth and flowering later in the season (autumnal aspect species), often display cauline prostrate growth forms that force a gap in the sward, so overcoming competition for light (e.g. *Haplocarpha scaposa).* Autumnal species typically include a number of tall woody taxa that are not easily overshadowed by the grasses, but require fire protection *(e.g. Leonotis* spp.). Other taxa are known to rely on fire, only emerging after a burn *(e.g. Cyrtanthus* spp. [Fire Lilies]) and observations suggest that there may even be a suite of species that only emerge in response to droughts. Consequently, understanding forb growth patterns and allocation tradeoffs (storage vs recruitment) may provide insights into how they respond to the timing of disturbances.

Conservation agencies are increasingly being called upon to prioritize land towards conservation targets, yet often lack the information to do so. In the absence of extensive floristic surveys, meeting this challenge requires a better understanding of local patterns of diversity and the processes that maintain them. Thus, for example, shallow rocky soils are often seen to support greater levels of species richness, but it is not known whether the deeper soils of the lowlands, which are usually the first to fall to the plough, contain distinct species assemblages. We also need to quantify the contribution of old-lands and the costs of afforestation to meeting conservation targets. By identifying plant functional types recruiting into these disturbed sites, we may be able to target taxa for the revegetation of transformed areas. This is especially relevant for recovering eroded areas and areas cleared of alien vegetation; a threat which, along with the impacts of bush encroachment / bush thickening, urgently requires attention. Improved rehabilitation approaches are also required for rangelands that have been degraded through poor management. To tackle these and other disturbance related questions we need to maintain the existing long-term ecological research sites in the region and look to initiate additional trials, especially at the landscape scale.

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11 Appendices

Appendix 3.1 Species richness at the various scales sampled across the study sites, ordered according to MAP. The mean and standard deviation (STD) of the richness in 1 m^2 at each site was calculated from two sets of 5 x 1 m^2 quadrats.

	MAP	Altitude	1 m^2		10 m^2		100 m^2		1000 m^2	
Site	(mm yr^{-1})	(m a.s.l.)	Mean	STD	Site 1	Site 2	Site 1	Site 2	Site 1	Site 2
Bateleur	440	340	3.5	1.7	17	8	32	14	44	28
Shingwedzi	460	280	2.6	0.7	11	9	19	14	39	31
Olifants	465	250	4.2	1	12	12	17	16	21	24
Satara	490	290	1.5	0.7	3	5	7	10	14	19
Ndumo	520	90	4.6	1.3	19	13	31	32	47	50
Skukuza	550	460	4.4	1.3	11	14	18	25	37	42
Pongolapoort	650	150	8.8	2	27	21	41	35	67	57
Mkuze (clay)	665	120	7.6	2.2	20	20	35	28	53	50
Mkuze (sand)	670	120	10.1	1.7	18	29	24	38	54	58
Imfolozi	680	230	6.3	2.4	15	10	30	21	50	45
Pretoriuskop	690	570	4.7	2	22	10	37	25	66	53
Mooihoek	700	1780	9.5	1.8	28	23	40	40	60	67
Hluhluwe	770	245	9	2.3	14	25	26	42	60	73
Ithala (savanna)	790	720	7	1.6	20	23	35	37	64	65
Ithala (tall grass)	790	850	10	2.4	25	35	34	51	52	85
Ithala (short grass)	820	1400	10.3	2.4	30	30	46	47	74	84
Midmar Dam	875	1100	16.9	3.2	34	34	48	52	75	78
Chelmsford Dam	1000	1270	10.3	2.9	27	27	43	44	73	86
Cobham	1000	1780	12.6	1.7	24	30	37	46	67	69
QE Park	1070	950	12.5	2.6	28	33	51	58	86	87
Impendle	1100	1400	17.4	3.8	45	34	58	60	74	88
Highmoor	1150	1960	15	1.6	26	36	47	55	73	87
Amatigulu	1170	20	15.6	3.7	30	43	50	62	87	96
Cathedral Peak	1380	1830	15.6	1.3	30	31	34	37	48	66
Sani Pass	1600	2500	11.8	4.5	20	35	35	41	56	59

Appendix 3.2 Numbers of herbaceous species recorded from the 67 families encountered across the 25 sites, sampled across two 1000 m^2 quadrats at each site including the number of sites each family was recorded at. Nomenclature according to Arnold and De Wet (1993).

	Bateleur	Shingwedzi	Olifants	Satara	Ndumo	Skukuza	Pongolapoort	Mkuze (clay)	Mkuze (sand)	Imfolozi	Pretoriuskop	Mooihoek	Hluhluwe	Ithala (savanna)	Ithala (tall grass)	Ithala (short grass)	Midmar Dam	Chelmsford Dam	Cobham	Q E Park	Impendle	Highmoor	Amatigulu	Cathedral Peak	Sani Pass	No. of spp.		No. of sites
MAP (mm yr^{-1})	440	460	465	490	520	550	650	665	670	680	690	700	770	790	790	820	875	1000	1000	1070	1100	1150	1170	1380	1600	Total	Avg.	
Acanthaceae	1	1	1	0	11	2	7	7	5	6	2	2	7	4	5	1	5	3	0	2	0	0	6	1	0	79	3.2	20
Alliaceae	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Amaranthaceae	1	0	1	1	1	1	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	8	0.3	8
Amaryllidaceae	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	0	1	1	0	1	0	0	8	0.3	8
Anthericaceae	0	0	0	0	0	0	1	1	1	0	0	1	1	2	1	1	0	0	0	0	0	0	1	0	0	10	0.4	9
Apiaceae	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	0	4	9	0.4	5
Araceae	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	0	0	6	0.2	6
Asclepiadaceae	1	0	0	0	0	0	2	2	0	1	0	5	3	2	2	1	5	2	3	2	2	2	2	4	0	41	1.6	17
Asparagaceae	1	2	1	1	0	1	1	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	12	0.5	11
Asphodelaceae	0	0	0	1	0	1	0	0	0	0	0	0	2	3	1	2	2	1	0	3	1	0	2	0	0	19	0.8	11
Asteraceae	4	0	3	2	5	1	6	5	3	7	6	25	18	18	21	21	14	21	16	28	21	23	20	15	22	325	13	24
Boraginaceae	1	1	1	1	1	1	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	12	0.5	12
Brassicaceae	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Campanulaceae	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	2	0	1	2	1	4	1	1	2	17	0.7	10
Capperaceae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Caryophyllaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	2	3	0.1	2
Chenopodiaceae	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0.1	3

Clusiaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	5	0.2	5
Colchicaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
Commelinaceae	1	1	1	1	1	1	2	2	2	1	2	2	3	2	2	2	1	2	2	1	1	1	3	1	0	38	1.5	24
Convolvulaceae	3	2	2	2	3	4	3	3	5	3	2	3	3	1	1	1	1	1	0	0	0	0	1	0	0	44	1.8	19
Crassulaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	0	1	0	4	0.2	4
Curcubitaceae	1	1	0	0	2	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	2	0	1	0	0	11	0.4	9
Cyperaceae	2	0	0	0	0	1	0	1	3	0	2	0	0	2	1	0	4	2	3	4	3	3	6	6	2	45	1.8	16
Dipsacaceae	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	1	1	2	0	0	1	0	1	0	0	9	0.4	8
Droseraceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1
Ebenaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0	2
Ericaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	2	5	0.2	4
Eriospermaceae	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0	0	0	2	0	7	0.3	5
Euphorbiaceae	6	6	4	1	3	3	5	3	3	3	5	2	7	6	6	1	4	2	3	5	2	2	6	2	0	90	3.6	24
Fabaceae	3	5	3	1	4	6	8	7	7	9	11	4	12	8	11	7	11	7	6	12	5	2	15	4	3	171	6.8	25
Gentianaceae	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	1	2	2	1	1	2	0	1	1	14	0.6	11
Geraniaceae	0	0	0	0	0	1	1	0	1	0	0	1	1	0	0	0	1	1	0	0	1	2	2	2	0	14	0.6	11
Hyacinthaceae	2	3	1	1	3	1	2	1	1	1	2	2	3	4	2	3	4	5	4	2	4	6	1	3	2	63	2.5	25
Hypoxidaceae	0	0	0	0	0	0	1	0	0	0	0	2	2	1	0	4	4	4	5	2	3	3	3	2	0	36	1.4	13
Illecebraceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1
Iridaceae	0	0	0	0	0	1	0	0	0	0	1	0	3	2	1	5	4	5	4	5	2	8	3	2	4	50	2	15
Lamiaceae	2	1	1	0	1	1	1	1	2	2	2	1	3	2	3	3	1	1	0	4	3	0	3	1	0	39	1.6	21
Lobeliaceae	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	1	1	0	0	0	8	0.3	8
Malvaceae	1	1	2	2	5	2	3	4	3	4	2	2	6	2	0	1	1	1	1	1	1	0	1	0	0	46	1.8	21
Mesembryanthemaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
Molluginaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	3	0.1	3
Myrtaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	0	2
Nyctaginaceae	1	0	1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.2	4
Orchidaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	1	6	3	5	10	1	4	2	38	1.5	10

Oxalidaceae	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	1	2	2	1	1	1	1	1	15	0.6	13
Periplocaceae	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	5	0.2	4
Plantaginaceae	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Poaceae	10	9	5	3	11	11	21	19	19	22	24	15	23	13	20	18	19	27	19	23	22	17	12	16	13	411	16	25
Polygalaceae	0	0	0	0	1	1	1	1	1	2	2	1	3	1	1	1	1	3	1	1	2	1	2	1	1	29	1.2	21
Polygonaceae	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3	0.1	3
Portulacaceae	1	1	1	1	2	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0.4	8
Rosaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1
Rubiaceae	3	2	0	2	1	4	0	2	3	1	3	2	3	3	4	4	3	5	4	5	4	4	3	4	1	70	2.8	23
Santalaceae	0	0	0	0	0	1	0	0	0	2	1	0	1	0	0	0	1	1	2	0	1	1	1	0	1	13	0.5	11
Scrophulariaceae	1	1	0	0	1	1	1	1	1	0	0	1	2	3	3	6	3	1	4	0	3	3	2	2	5	45	1.8	20
Selaginaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	2
Smilacaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1
Solanaceae	1	1	1	1	1	1	3	2	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	19	0.8	16
Sterculiaceae	4	1	2	1	0	3	0	1	2	0	3	1	0	1	2	1	0	1	1	0	1	1	0	1	0	27	1.1	17
Thymelaeaceae	0	1	0	0	1	0	0	0	0	1	0	1	1	1	1	1	0	1	1	1	1	0	2	1	3	18	0.7	15
Tiliaceae	1	1	0	0	0	0	1	0	1	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	7	0.3	7
Velloziaceae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	1
Verbenaceae	1	1	0	0	2	1	3	0	4	4	1	1	3	2	3	1	1	0	0	0	0	0	0	0	0	28	1.1	14
Violaceae	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	6	0.2	6
Vitaceae	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	4	0.2	4
Zygophyllaceae	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.2	4
Total No. of spp.	67	52	42	35	68	69	77	68	72	80	99	83	119	106	103	105	100	106	94	117	99	104	116	79	73			
Mean No. of spp.	36	35	22.5	16.5	48.5	39.5	62	51.5	56	47.5	59.5	63.5	66.5	64.5	68.5	79	76.5	79.5	68	86.5	81	80	91.5	57	57.5			
Total No. of families	25	22	18	17	24	30	24	23	24	27	25	28	30	28	30	36	30	29	23	25	30	28	34	25	20			
Mean No. of families	19.5	18.5	16	14	19.5	22.5	20	18	21	21.5	22	24	25	23.5	24	23	25.5	26.5	21	21.5	27	25	30	20.5	18			

Appendix 4.1 Total species richness and the richness of forbs and their various life-form and life-history traits recorded in 2 x 1000 m^2 quadrats at each site, ordered according to the mean annual precipitation (MAP) [mm yr^{-1}].

Site	MAP	Altitude m a.s.l.	Total	Grasses & sedges	Forb	Monocot	Dicot	Short-lived	Long-lived	Sprouter	Non-sprouter	Cauline Prostrate	Cauline Erect	Radical Prostrate	Radical Erect
Bateleur	440	340	55	12	43	4	39	6	37	22	21	10	30	2	1
Shingwedzi	460	280	45	9	36	6	30	5	31	20	16	10	23	2	1
Olifants	465	250	33	5	28	3	25	7	21	12	16	7	20	0	1
Satara	490	290	24	3	21	4	18	3	18	12	9	5	14	1	1
Ndumo	520	90	64	11	53	6	47	3	50	31	22	14	33	3	3
Skukuza	550	460	57	12	45	6	39	6	39	25	20	10	31	1	3
Pongolapoort	650	150	77	21	56	7	49	14	42	33	23	14	38	3	1
Mkuze (clay)	665	120	68	20	48	7	41	8	40	28	20	12	32	1	3
Mkuze (sand)	670	120	72	22	50	5	45	7	43	31	19	16	32	2	0
Imfolozi	680	230	80	22	58	6	52	11	47	35	23	15	39	1	3
Pretoriuskop	690	570	80	26	54	5	49	4	50	40	14	12	37	2	3
Mooihoek	700	1780	83	15	68	8	60	2	66	47	21	17	35	10	6
Hluhluwe	770	245	119	24	95	15	80	11	84	69	26	18	59	8	10
Ithala (savanna)	790	720	90	15	75	14	60	5	69	61	13	16	40	10	8
Ithala (tall grass)	790	850	102	22	80	9	71	4	76	65	15	15	49	10	6
Ithala (short grass)	820	1400	105	19	86	24	62	2	84	70	16	13	45	11	17
Midmar Dam	875	1100	100	23	77	17	60	3	74	58	19	14	38	15	10
Chelmsford Dam	1000	1270	106	29	77	18	59	2	75	58	19	16	36	13	12

Site	MAP	Altitude m a.s.l.	Total	Grasses & sedges	Forb	Monocot	Dicot	Short-lived	Long-lived	Sprouter	Non-sprouter	Cauline Prostrate	Cauline Erect	Radical Prostrate	Radical Erect
Cobham	1000	1780	94	24	70	20	50	1	69	51	19	9	37	10	14
QE Park	1070	950	117	30	87	20	67	1	86	70	17	14	48	13	12
Impendle	1100	1400	99	26	73	16	57	3	70	51	22	10	41	11	11
Highmoor	1150	1960	104	20	84	28	56	1	83	63	21	4	43	23	14
Amatigulu	1170	20	110	18	92	17	75	3	89	65	27	14	58	10	10
Cathedral Peak	1380	1830	79	22	57	14	43	0	57	42	15	10	29	12	6
Sani Pass	1600	2500	73	15	58	9	49	0	58	41	17	3	37	10	8

Appendix 5.1 Number of plots (out of 60) that adult forb species were recorded in before the application of disturbance treatments and the number of plots that seedling species were recorded in as a total (out of 60 plots) and per-treatment (out of 20 plots each) in the first and second season after the application of the fire, drought and animal diggings treatments in the seedling recruitment trial at Pongolapoort. Nomenclature according to Arnold and De Wet (1993).

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Aloe sp.	1								
Alysicarpus rugosus		3		1	2	2			2
Bidens sp.		15	2	6	7	10	3	1	6
Blepharis integrifolia		11	4	2	5	2	1	1	
Chaetacanthus burchellii	13	2			2	3	1	1	1
Chamaechrista sp.		17	1	6	9	4	2	1	1
Chascanum headeraceum	15	11	3	6	2	2	1		1
Chorchorus asplenifolius		1		1					
Commelina africana	17	4	2	2		1		1	
Conyza sp.	8								
Crabbea hirsuta	4								
Cucumis sp.	1								
Cyphostemma schlechteri	13								
Eriospermum sp.	1	8	3	2	3				
Heliotropium steudneri	1	2	1		1				
Hibiscus pusillus	13	4	1		3				
Indigofera sp.	1	6		2	4	8	4	4	
Ipomoea sp.	7	1		1					
Justicia flava	2	2		1	1				
Ledebouria apertiflora	14								
Lobelia erinus	6								

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Orthosiphon serratus						1		1	
Phylanthus meyerianus		9		2	7				
Phyllanthus maderaspatensis		5		4	1				
Polygala sp.	5								
Portulaca oleracea						3		2	1
Pyctolobium plicatum						7	1	3	3
Rhyncosia sp.		2			2				
Sida sp.		8	1	3	4	1			1
Sp. ? (Hyacinthaceae)	2								
Tagetes minuta	16								
Talinum caffrum	18								
Thesium sp.	1								
Thunbergia atripicifolia	8								
Zornia capensis	14								
Unidentified seedlings		16	2	6	8	2			2
Seedling sp. 1		2		1	1				

Appendix 5.2 Number of plots (out of 60) that adult forb species were recorded in before the application of disturbance treatments and the number of plots that seedling species were recorded in as a total (out of 60 plots) and per-treatment (out of 20 plots each) in the first and second season after the application of the fire, drought and animal diggings treatments in the seedling recruitment trial at Mkuze. Nomenclature according to Arnold and De Wet (1993).

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Abutilon angulatum	15	4	1	3		8	1	3	4
Alysicarphus rugosus	1								
Anthericum cooperi	2								
Azoon galinoides						3		1	2
Becium obovatum	1								
Blepharis integrifolia		1	1						
Chaetacanthus burchellii	6								
Chamaecrista sp.	10								
Chascanum headeraceum	6	1			1	2			2
Commelina africana	21	1		1					
Conyza sp.		1		1					
Crabbea hirsuta	6	1			1				
Cucumis hirsutus	2								
Dicliptera clinopodia		3	1	2					
Evolvulus alsinoides	4								
Gomphocarpus physocarpus	3								
Heliotropium steudneri						1			1
Hibiscus pusillus	16	5	1	2	2	4	1	2	1
Indigofera costatum	2					2			2
Indigofera rhytidocarpa	5								
Indigofera schimperi	1								

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Ipomoea obscura	2								
Justicia flava	9								
Kohautia caespitosa	4								
Lobelia erinus	1								
Melhania didyma		1		1		2		1	1
Phylanthus meyerianus	14					10		2	8
Phyllanthus maderaspatensis	4	1	1			2		1	1
Portulaca oleracea						6		4	2
Rhyncosia totta	1								
Sida cordifolia	24	1	1			1			1
Solanum panduriforme	47	10	1	4	5	3		2	1
Sp. ?	17								
Tephrosia polystachya	2					1		1	
Thunbergia dregeana	1								
Vernonia oligocephala	1	1			1	1			1
Unidentified seedlings		4	2	1	1				
Seedling sp. 1		2			2				
Seedling sp. 2						4		1	3

Appendix 5.3 Number of plots (out of 60) that adult forb species were recorded in before the application of disturbance treatments and the number of plots that seedling species were recorded in as a total (out of 60 plots) and per-treatment (out of 20 plots each) in the first and second season after the application of the fire, drought and animal diggings treatments in the seedling recruitment trial at Imfolozi. Nomenclature according to Arnold and De Wet (1993).

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Bulbostylus sp.	2								
Chaschanum hederaceum	17	7	4	3		16	1	8	7
Commelina africana	16					3	3		
Convolvulus natalensis	2								
Conyza sp.						1		1	
Corchorus asplenifolius	3								
Crotalaria sp.	2	3		2	1				
Cyphostemma schlechteri	2	3		2	1				
Dicliptera clinopodia						2		1	1
Helichrysum oxyphyllum	1	1		1		1		1	
Heliotropium steudneri						2		1	1
Hibiscus pusillus	27	5	1	1	3	9	4	2	3
Ipomoea obscura	2								
Melhania didyma		1		1					
Orthosiphon serratus		1	1						
Phyllanthus maderaspatensis		7	5	1	1	18	5	7	6
Phyllanthus meyerianus		6	4	2		18	8	6	4
Polygala sp.	2	4		1	3	1	1		
Pseudarthria hookeri	1								
Rhyncosia hirsuta	1								
Rhyncosia sp.		1			1	1			1

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Ruellia cordata	7								
Sp. ?	52								
Sp. ?	3								
Thesium sp.	7								
Thunbergia atripicifolia	7	2		1	1				
Vernonia oligocephala		14	5	6	3	6	4		2
Zornia capensis	40	15	4	6	5	7	3	4	
Unidentified seedlings						8	4	1	3
Seedling sp. 1		1	1						
Seedling sp. 2						3	1	1	1

Appendix 5.4 Number of plots (out of 60) that adult forb species were recorded in before the application of disturbance treatments and the number of plots that seedling species were recorded in as a total (out of 60 plots) and per-treatment (out of 20 plots each) in the first and second season after the application of the fire, drought and animal diggings treatments in the seedling recruitment trial at Hluhluwe. Nomenclature according to Arnold and De Wet (1993).

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Alepidea longifolia	3	1		1					
Alysicarpus rugosus	2	1			1				
Argyrolobium rotundifolium	17								
Aster bakerianus	20								
Berkeyha speciosa	2								
Bidens sp.		1		1					
Centella asiatica	4	9	4	1	4	9	3		6
Chaetacanthus burchellii	13								
Chamaecrista plumosa	1								
Chaschanum hederaceum		1	1						
Chromolaena odorata		13	1	12		1			1
Commelina africana	38	6	4	2		2	2		
Crabbea hirsuta	21	1		1		1	1		
Datura stramonium		1		1					
Eriosema cordatum	15	2			2				
Evolvulus alsinoides						2	1	1	
Gerbera ambigua	22								
Gerbera piloselloides	8								
Helichrysum oreophilum	4								
Hibiscus pusillus	3								
Hypoxis angustifolia	4								

Indigofera hedyantha	1								
Oxalis smithiana	7	18	13		5	3	2		1
Pelargonium luridum	22	3			3				
Pentanisia prunelloides	10								
Phyllanthus maderaspatensis		2		1	1	1			1
Pollygala sp.	9	4		2	2				
Pseudarthria hookeri	16	3		1	2				
Rhus sp.	2								
Rhyncosia hirsuta		4	2	1	1				
Rhyncosia hirsuta	9								
Ruellia cordata	43	2	1	1		8	4		4
Scabiosa columbaria	7								
Senecio bupleuroides	4	1	1						
Senecio erubescence	8								
Senecio sp.	12								
Sida sp.	1	26	2	6	18	24	4	9	11
Solanum panduriforme	1								
Sonchus sp.	1					1		1	
Sp. ?	6								
Sp. ? (Orchidaceae)	2								
Spermacoce natalensis						1		1	
Tephrosia pollystachya	15								
Tephrosia sp.		2			2	4	2	2	
Thunbergia atripicifolia	44	6		4	2				
Watsonia sp.	1								
Zornia capensis	6	7	2	1	4	4		2	2
Unidentified seedlings		17	7	3	7	11	6	1	4
Seedling sp. 1		3		2	1				
Seedling sp. 2		1	1						
Seedling sp. 3		6	2	2	2				
Seedling sp. 4		2			2				
Seedling sp. 5		7	5	1	1				
Seedling sp. 6						2	1		1

Appendix 5.5 Number of plots (out of 60) that adult forb species were recorded in before the application of disturbance treatments and the number of plots that seedling species were recorded in as a total (out of 60 plots) and per-treatment (out of 20 plots each) in the first and second season after the application of the fire, drought and animal diggings treatments in the seedling recruitment trial at Midmar Dam. Nomenclature according to Arnold and De Wet (1993).

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Aster bakerianus	7	2			2	1		1	
Becium obovatum	49	6	1	3	2	4	4		
Berkheya sp.		1	1						
Bidens pilosa		2		1	1				
Commelina africana	3								
Conyza sp.		11	1	10	2		2		
Eriosema salignum		2	1		1				
Eucomis autumnalis	4								
Euphorbia striata	5								
Gladiolus sp.	3								
Graderia scabra	31								
Helichrysum aureonitens	1								
Helichrysum oreophilum	1								
Helichrysum pilosellum	2	1		1					
Hibiscus pusillus	2	5	4		1				
Hypoxis acuminata		5	2	3					
Hypoxis rigidula	7	1		1					
Kohautia amatymbica		11	3	4	4	1			1
Ledebouria cooperi	4	2	1		1	1			1
Oxalis latifolia	20	23	9	7	7				
Pentanisia prunelloides	8	1		1					

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Polygala hottentotta	2								
Ruellia cordata	5								
Scabiosa columbaria	2	1	1						
Sebeae sp.	5	6	2	4		2	1	1	
Senecio barbatus	1	1		1					
Sonchus sp.	7	2		1	1	1			1
Sp. ? (Asclepiadaceae)	2								
Sp. ? (Asteraceae)	10								
Spermacoce natalensis		44	19	19	6	19	14	3	2
Tephrosia elongata	2								
Thesium sp.	22								
Thunbergia alata	41	2	1		1				
Vernonia natalensis		18	4	9	5				
Zornia capensis	17	29	13	12	4				
Unidentifiable seedlings		19	12	5	2	8	6		2
Seedling sp. 1		10	4	2	4				
Seedling sp. 2		4	2		2				
Seedling sp. 3		2	2						
Seedling sp. 4		6	4	1	1				
Seedling sp. 5		3	1	2					
Seedling sp. 6		2	1	1					
Seedling sp. 7		2	1		1				
Seedling sp. 8		4		4					
Seedling sp. 9						5	1	1	3
Seedling sp. 10						5	2		3
Seedling sp. 11						1			1
Seedling sp. 12						1		1	

Appendix 5.6 Number of plots (out of 60) that adult forb species were recorded in before the application of disturbance treatments and the number of plots that seedling species were recorded in as a total (out of 60 plots) and per-treatment (out of 20 plots each) in the first and second season after the application of the fire, drought and animal diggings treatments in the seedling recruitment trial at Highmoor. Nomenclature according to Arnold and De Wet (1993).

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Argyrolobium rupestre	1								
Commelina africana	2	2			2	1	1		
Conyza sp.		3	1	2		4	1	3	
Dierama sp.	3								
Gerbera ambigua	1								
Gladiolus sp.	4								
Haplocarpha scaposa	7					2	2		
Hebenstretia comosa	11								
Helichrysum aureonitens	4								
Helichrysum glomeratum	32	25	14	6	5	12	9	3	
Helichrysum longifolium	3	1		1					
Helichrysum nudifolium	8	13	4	8	1	5		5	
Helichrysum oreophilum	12					1		1	
Hermannia woodii	9	2	2						
Hesperantha baurii	1								
Hypericum aethiopicum	1								
Hypoxis acuminata	18	2	1	1		3		3	
Kohautia amatymbica	3								
Ledebouria cooperi	1	2	1		1				
Lobelia erinus		1	1						
Monsonia attenuata	4	9	3	2	4	2	1		1

Species	Sward Spp. frequency	First season seedling frequency				Second season seedling frequency			
		Total	Fire	Drought	Diggings	Total	Fire	Drought	Diggings
Oxalis obliquifolia	37	47	15	17	15	42	15	13	14
Polygala rehmannii	4	2	1	1					
Sebeae sp.		3	3						
Senecio bupleuroides	3	7	4	2	1	2	2		
Senecio paucicalyculatus	1								
Sp. ? (Asclepiadaceae)	1	2			2	1			1
Sp. ? (Asteraceae)	1								
Tephrosia sp.	3								
Vernonia oligocephala						1	1		
Wahlenbergia fasiculata	15	14	8	4	2				
Watsonia sp.	2								
Unidentifiable seedlings		20	12	6	2	12	10	1	1
Seedling sp. 1		4	1	3					
Seedling sp. 2		1			1				
Seedling sp. 3		4		1	3				
Seedling sp. 4		1			1				
Seedling sp. 5		1		1					
Seedling sp. 6		2	2						
Seedling sp. 7		3		1	2				
Seedling sp. 8		2		1	1				
Seedling sp. 9						3	3		
Seedling sp. 10						2	1	1	

Appendix 6.1 Key to the species, their families, and life-form and life-history traits encountered in the grazing exclusion trials across Hluhluwe and Imfolozi.

Nomenclature according to Arnold and De Wet (1993).

1. = sampling year in which the species was recorded: - only in unburnt year (22 spp.), + only in burnt year (51 spp.), t both years (101 spp.). 2. = species that emerged in the ordination (Figure 7.5) in group 1 (g1) or as characterising mesic (me) [55 taxa] and semi-arid (s-a) [45 taxa] rangelands. Plant life-form and history characters: M/D = monocot (m) or dicot (d), NP = short-lived annual / biennial (a) or long-lived perennial (p), UGO = underground growth forms: b = bulb, c = corm, f = fibrous root, r = rhizome, rp = root parasite, *d* = root tubers, st = stem tubers, tr = tap root, wtr = woody tap root, we = woody caudex, wc+rt = woody caudex with root tubers, GF = above ground growth form: 1 = cauline-prostrate, 2 = radical-flat, 3 = radical-erect, 4 = cauline-erect. Exotic species have been marked in bold.

Sp. #	1.	2.	Species	Family	M/D	A/P	UGO	GF
1	‡	s-a	*Abutilon angulatum*	Malvaceae	d	p	tr	4
2	‡	me	*Acalypha villicaulis*	Euphorbiaceae	d	p	wc+rt	1
3	‡		*Achyropsis leptostachya*	Amaranthaceae	d	a	tr	4
4	+	s-a	*Acrotome hispida*	Lamiaceae	d	p	tr	4
5	+	me	*Aeschynomene micrantha*	Fabaceae	d	p	wtr	1
6	‡	me	*Agathisanthemum bojeri*	Rubiaceae	d	p	tr	4
7	+	s-a	*Aizoon glinoides*	Aizoaceae	d	p	tr	1
8	‡	s-a	***Alternanthera pungens***	Amaranthaceae	d	p	tr	1
9	‡		*Alysicarphus rugosus*	Fabaceae	d	p	st	4
10	+	g1	*Anthericum cooperi*	Asphodelaceae	m	p	b	2
11	-	g1	*Anthericum fasiculatum*	Anthericaceae	m	p	c	2
12	‡	g1	*Argyrolobium molle*	Fabaceae	d	p	tr	4
13	‡	me	*Aristea cognata*	Iridaceae	m	p	f	2
14	-	g1	*Asclepiad sp1*	Asclepiadaceae	d	p	st	4
15	‡		*Asclepiad sp2*	Asclepiadaceae	d	p	st	4
16	+		*Asclepiad sp3*	Asclepiadaceae	d	p	st	4
17	+		*Asclepiad sp4*	Asclepiadaceae	d	p	st	4
18	‡	s-a	*Asparagus sp1*	Asparagaceae	m	p	rt	1
19	‡		*Asparagus sp2*	Asparagaceae	m	p	rt	1
20	+	s-a	*Asparagus sp3*	Asparagaceae	m	p	rt	4
21	+	s-a	*Asparagus sp4*	Asparagaceae	m	p	rt	4
22	+	s-a	*Asphodelaceae sp.*	Asphodelaceae	m	p	b	2
23	‡	me	*Aster bakerianus*	Asteraceae	d	p	rt	4
24	-	s-a	*Athrixia phylicoides*	Asteraceae	d	p	wtr	4
25	‡		*Barleria elegans*	Acanthaceae	d	p	wtr	4
26	‡		*Becium obovatum*	Lamiaceae	d	p	wtr	4
27	‡	g1	*Berkheya speciosa*	Asteraceae	d	p	wc	4
28	‡	s-a	***Bidens pilosa***	Asteraceae	d	a	tr	4
29	‡		*Blepharis integrifolius*	Acanthaceae	d	p	wtr	4
30	‡	s-a	***Boerhavia diffusa***	Nyctaginaceae	d	p	wtr	4
31	+	g1	*Bulbine capitata*	Asphodelaceae	m	p	f	2
32	+	me	*Callilepis Laureola*	Asteraceae	d	p	wc	4

Sp. #	1.	2.	Species	Family	M/D	A/P	UGO	GF
33	‡		*Chaetacanthus burchellii*	Acanthaceae	d	p	rt	4
34	‡		*Chamaechrista mimosoides*	Fabaceae	d	a	tr	4
35	‡	s-a	*Chaschanum hederaceum*	Verbenaceae	d	p	wtr	4
36	‡	s-a	*Chenopodium carinatum*	Chenopodiaceae	d	a	tr	4
37	‡	s-a	*Chenopodium mucronatum*	Chenopodiaceae	d	a	tr	4
38	-		***Chromolaena odorata***	Asteraceae	d	p	tr	4
39	‡		*Commelina africana*	Commelinaceae	m	p	rt	1
40	‡		*Commelina erecta*	Commelinaceae	m	p	rt	1
41	-	me	*Convolvulus natalensis*	Convolvulaceae	d	p	wtr	1
42	+	me	*Convolvulus sagittatus*	Convolvulaceae	d	p	wtr	1
43	‡		*Conyza sp.*	Asteraceae	d	a	tr	4
44	‡		*Corchorus asplenifolius*	Tiliaceae	d	p	wtr	4
45	‡		*Crabbea hirsuta*	Acanthaceae	d	p	rt	1
46	+		*Crinum delagoense*	Amaryllidaceae	m	p	b	3
47	-		*Cucumis zeyheri*	Curcubitaceae	d	p	wtr	1
48	+		*Curcubit sp.*	Curcubitaceae	d	p	wtr	1
49	‡	g1	*Cyanotis speciosa*	Commelinaceae	m	p	c	1
50	+	me	*Cycnium adonense*	Scrophulariaceae	d	p	rp	4
51	‡	me	*Cyphostemma natalitium*	Vitaceae	d	p	wc	1
52	‡	s-a	*Cyphostemma schlecteri*	Vitaceae	d	p	wc	1
53	+		***Datura stramonium***	Solanaceae	d	a	tr	4
54	+	s-a	*Delosperma smytheae*	Mesembryanthemaceae	d	p	tr	4
55	‡	me	*Desmodium gangeticum*	Fabaceae	d	p	tr	1
56	‡		*Dicliptera clinopodia*	Acanthaceae	d	p	wtr	4
57	+	g1	*Dicoma argyrophylla*	Asteraceae	d	p	wtr	1
58	+	s-a	*Dicoma macrocephala*	Asteraceae	d	p	tr	4
59	+	g1	*Dipcadi viride*	Hyacinthaceae	m	p	b	2
60	‡	me	*Eriosema salignum*	Fabaceae	d	p	wc	4
61	+	s-a	*Eriospermum cooperi*	Eriospermaceae	m	p	st	3
62	‡	me	*Eriospermum sp.*	Eriospermaceae	m	p	st	3
63	+		*Euphorbia tirucalli*	Euphorbiaceae	d	p	wtr	4
64	‡	g1	*Euphorbia trichadenia*	Euphorbiaceae	d	p	st	4
65	‡	s-a	*Evolvulus alsinoides*	Convolvulaceae	d	p	tr	1
66	‡		*Felicia mossamedensis*	Asteraceae	d	p	tr	4
67	‡	me	*Freesia laxa*	Iridaceae	m	a	c	2
68	‡	me	*Gerbera ambigua*	Asteraceae	d	p	rt	3
69	+	me	*Gerbera piloselloides*	Asteraceae	d	p	rt	3
70	-	me	*Gerbera viridifolia*	Asteraceae	d	p	rt	3
71	+	me	*Gladiolus sp.*	Iridaceae	m	p	c	2
72	‡	g1	*Gnidia capitata*	Thymelaeaceae	d	p	wtr	4
73	‡		*Gomphocarphus physocarpus*	Asclepiadaceae	d	a	tr	4
74	‡	s-a	***Gomphrena celosioides***	Amaranthaceae	d	p	st	4
75	‡	me	*Helichrysum oxyphyllum*	Asteraceae	d	p	wc+rt	4
76	+	me	*Helichrysum pilosellum*	Asteraceae	d	p	wc+rt	3
77	‡		*Helichrysum rugulosum*	Asteraceae	d	p	tr	4
78	-	s-a	*Heliotropium strigosum*	Boraginaceae	d	p	tr	4
79	‡	s-a	*Heliotropium studneri*	Boraginaceae	d	p	wtr	4
80	‡		*Hibiscus pusillus*	Malvaceae	d	p	tr	4
81	‡		*Hibiscus trionum*	Malvaceae	d	p	tr	4

Sp. #	1.	2.	Species	Family	M/D	A/P	UGO	GF
82	‡	me	*Hoslundia opositifolia*	Lamiaceae	d	p	wtr	4
83	‡	s-a	*Hybanthus enneaspermus*	Violaceae	d	p	tr	4
84	‡	me	*Hypericum aethiopicum*	Clusiaceae	d	p	rt	4
85	+		*Hypoxis argentea*	Hypoxidaceae	m	p	c	2
86	‡	me	*Hypoxis hemerocallidea*	Hypoxidaceae	m	p	c	2
87	‡		*Indigastrum costatum*	Fabaceae	d	p	tr	4
88	-		*Indigofera confusa*	Fabaceae	d	p	wtr	4
89	+	s-a	*Indigofera filipes*	Fabaceae	d	p	tr	4
90	‡	me	*Indigofera hilaris*	Fabaceae	d	p	wtr	4
91	+		*Indigofera velutiana*	Fabaceae	d	p	tr	1
92	‡		*Ipomoea crassipes*	Convolvulaceae	d	p	wtr	1
93	‡	s-a	*Ipomoea obscura*	Convolvulaceae	d	p	wtr	1
94	-	me	*Ipomoea pellita*	Convolvulaceae	d	p	wc	1
95	‡	g1	*Ipomoea simplex*	Convolvulaceae	d	p	st	1
96	‡		*Justicia betonica*	Acanthaceae	d	p	tr	4
97	‡	s-a	*Justicia flava*	Acanthaceae	d	p	tr	4
98	‡		*Justicia protracta*	Acanthaceae	d	p	rt	4
99	+	me	*Kohautia amatymbica*	Rubiaceae	d	p	wtr	4
100	‡	s-a	*Kohautia caespitosa*	Rubiaceae	d	p	tr	4
101	+		*Lactuca inermis*	Asteraceae	d	a	tr	4
102	+		***Lantana camara***	Verbenaceae	d	p	wtr	4
103	‡		*Lantana rugosa*	Verbenaceae	d	p	wtr	4
104	‡	s-a	*Ledebouria cooperi*	Hyacinthaceae	m	p	b	3
105	+	me	*Ledebouria stenophylla*	Hyacinthaceae	m	p	b	2
106	-	me	*Leonotis intermedia*	Lamiaceae	d	p	wtr	4
107	‡	s-a	*Lepidium africanum*	Brassicaceae	d	a	tr	4
108	-	s-a	*Leucas glabrata*	Lamiaceae	d	p	wtr	4
109	‡	me	*Lippia javanica*	Verbenaceae	d	p	wtr	4
110	‡	me	*Lobelia erinus*	Lobeliaceae	d	a	tr	4
111	+	me	*Macrotyloma axillare*	Fabaceae	d	p	tr	1
112	‡	me	*Melanthera scandens*	Asteraceae	d	p	tr	1
113	‡	s-a	*Melhania didyma*	Malvaceae	d	p	tr	4
114	-	s-a	*Monsonia angustifolia*	Geraniaceae	d	p	tr	4
115	-	s-a	*Mukia maderaspatana*	Curcubitaceae	d	p	tr	1
116	‡	s-a	*Nidorella anomala*	Asteraceae	d	p	tr	4
117	-	me	*Oldenlandia affinis*	Acanthaceae	d	a	tr	4
118	‡		*Orthosiphon serratus*	Lamiaceae	d	p	wtr	4
119	+		***Oxalis corniculata***	Oxalidaceae	d	p	st	4
120	‡	me	*Oxalis smithiana*	Oxalidaceae	d	p	st	4
121	‡	me	*Pachycarphus appendiculatus*	Asclepiadaceae	d	p	wc	4
122	+	me	*Pelargonium luridum*	Geraniaceae	d	p	wc	4
123	‡	me	*Pentanisia prunelloides*	Rubiaceae	d	p	wc	4
124	‡	s-a	*Phyllanthus maderaspatensis*	Euphorbiaceae	d	a	tr	4
125	‡		*Phyllanthus meyerianus*	Euphorbiaceae	d	a	tr	4
126	+		*Polycarpon tetraphyllum*	Caryophyllaceae	d	a	tr	4
127	‡		*Polygala amatymbica*	Polygalaceae	d	p	tr	1
128	‡	me	*Polygala hottentotta*	Polygalaceae	d	p	wtr	4
129	‡		*Polygala rehmannii*	Polygalaceae	d	p	wtr	1
130	‡		***Portulaca oleracea***	Portulacaceae	d	a	tr	4

Sp. #	1.	2.	Species	Family	M/D	A/P	UGO	GF
131	‡	s-a	*Priva cordifolia*	Verbenaceae	d	p	wc+rt	4
132	‡	me	*Pseudarthria hookerii*	Fabaceae	d	p	wtr	4
133	‡	s-a	*Ptycholobium plicatum*	Fabaceae	d	p	tr	4
134	‡		*Rhyncosia hirsuta*	Fabaceae	d	p	tr	1
135	-	me	*Rhyncosia nervosa*	Fabaceae	d	p	rt	1
136	+	me	*Rhyncosia sordida*	Fabaceae	d	p	wc	4
137	+		*Rhyncosia totta*	Fabaceae	d	p	rt	1
138	‡		*Ruellia cordata*	Acanthaceae	d	p	rt	4
139	‡	me	*Scabiosa columbaria*	Dipsacaceae	d	p	tr	3
140	+	s-a	*Scadoxus multiflorus*	Hyacinthaceae	m	p	b	3
141	+	g1	*Schizobasis sp.*	Hyacinthaceae	m	p	b	4
142	+		*Schizoglossum sp.*	Asclepiadaceae	d	p	st	4
143	‡	s-a	***Schkuhria pinnata***	Asteraceae	d	a	tr	4
144	-	s-a	*Seddera capensis*	Convolvulaceae	d	p	wtr	1
145	‡	me	*Senecio bupleuroides*	Asteraceae	d	p	rt	4
146	‡	me	*Senecio latifolius*	Asteraceae	d	p	rt	4
147	-	me	*Senecio pterophorus*	Asteraceae	d	p	rt	4
148	‡		*Sida cordifolia*	Malvaceae	d	p	tr	4
149	‡		*Sida dregi*	Malvaceae	d	p	tr	4
150	‡		*Solanum incanum*	Solanaceae	d	p	tr	4
151	‡		*Solanum panduriforme*	Solanaceae	d	p	tr	4
152	+		*Sonchus nanus*	Asteraceae	d	p	tr	3
153	-		*Spermacoce natalensis*	Rubiaceae	d	p	tr	4
154	+		*Sphenostylis angustifolia*	Fabaceae	d	p	wtr	4
155	+	me	*Sphenostylis marginata*	Fabaceae	d	p	wtr	4
156	‡		*Stachys natalensis*	Lamiaceae	d	p	tr	4
157	‡	me	*Stylochiton natalensis*	Araceae	m	p	r	4
158	‡	s-a	***Tagetes minuta***	Asteraceae	d	a	tr	4
159	+	g1	*Tephrosia forbesii*	Fabaceae	d	p	tr	1
160	-		*Tephrosia polystachya*	Fabaceae	d	p	tr	1
161	‡	s-a	*Thesium sp.*	Santalaceae	d	p	rp	4
162	‡	me	*Thunbergia atripicifolia*	Acanthaceae	d	p	wc+rt	4
163	+	me	*Trachyandra asperata or margaretae*	Asphodelaceae	m	p	f	2
164	‡	s-a	*Tragia meyeriana*	Euphorbiaceae	d	p	tr	1
165	‡	s-a	*Tribulus terrestris*	Zygophyllaceae	d	a	tr	1
166	+	me	*Turbina oblongata*	Fabaceae	d	p	wtr	1
167	-		*Vernonia capensis*	Asteraceae	d	p	wtr	4
168	+	me	*Vernonia dregeana*	Asteraceae	d	p	rt	4
169	+	me	*Vernonia natalensis*	Asteraceae	d	p	wtr	4
170	‡		*Vernonia oligocephala*	Asteraceae	d	p	wtr	4
171	+	me	*Vigna vexillata*	Fabaceae	d	p	wtr	1
172	-	me	*Wahlenbergia undulata*	Campanulaceae	d	p	tr	4
173	+	s-a	***Zinnia peruviana***	Asteraceae	d	a	tr	4
174	‡	me	*Zornia capensis*	Fabaceae	d	p	tr	1

Appendix 6.2 Average frequency of the (71 out of 174) forb species constituting 90% of the individuals recorded in the plots (1500 x 1 m^2 quadrats in each reserve) sampled at Hluhluwe and Imfolozi, the average (Avg. Diss.) and standard deviation (Diss. SD) Bray Curtis dissimilarity in the proportional representation of these species between the two reserves, and the percentage that each species contributed (% Contrib.) to the total numbers of forbs encountered in the plots sampled across the park, with the cumulative total thereof (Cum. %). Nomenclature according to Arnold and De Wet (1993).

	Avg. frequency					
Species	Hluhluwe	Imfolozi	Avg. Diss.	Diss. SD	% Contrib.	Cum. %
Chaschanum hederaceum	13.33	49.00	3.15	1.24	4.21	4.21
Chaetacanthus burchellii	44.27	3.13	2.82	1.47	3.76	7.97
Justicia flava	7.60	43.20	2.41	1.22	3.21	11.18
Blepharis integrifolius	35.33	37.00	2.40	1.29	3.21	14.39
Hibiscus pusillus	58.67	64.47	2.40	1.24	3.20	17.59
Orthosiphon serratus	26.67	8.53	1.72	1.15	2.30	19.89
Phyllanthus meyerianus	10.80	33.53	1.70	1.33	2.27	22.16
Solanum panduriforme	27.87	9.80	1.68	1.00	2.24	24.40
Ruellia cordata	29.67	15.73	1.68	1.30	2.24	26.64
Dicliptera clinopodia	21.07	3.40	1.67	0.78	2.23	28.87
Thesium sp.	7.80	28.07	1.66	1.25	2.21	31.08
Tephrosia polystachya	6.53	30.07	1.64	1.33	2.19	33.27
Bidens pilosa	1.20	26.93	1.53	1.02	2.04	35.31
Heliotropium studneri	0.07	22.40	1.53	0.90	2.04	37.35
Rhyncosia hirsuta	21.33	5.40	1.50	0.89	2.01	39.36
Justicia betonica	17.33	9.67	1.40	0.71	1.87	41.23
Helichrysum rugulosum	19.80	2.73	1.36	0.75	1.82	43.05
Thunbergia atripicifolia	18.13	6.47	1.19	0.99	1.58	44.63
Commelina erecta	9.80	12.07	1.13	0.79	1.51	46.14
Ledebouria cooperi	8.47	18.13	1.12	1.06	1.50	47.64
Aizoon glinoides	3.67	17.33	1.11	0.71	1.48	49.12
Commelina africana	12.40	22.60	1.11	0.98	1.48	50.60
Chenopodium mucronatum	0.00	18.07	1.08	0.51	1.45	52.05
Polygala amatymbica	15.47	5.13	1.07	0.87	1.43	53.48
Justicia protracta	18.13	0.00	1.05	0.77	1.40	54.88
Phyllanthus maderaspatensis	5.40	20.27	1.03	1.44	1.38	56.26

	Avg. frequency					
Species	Hluhluwe	Imfolozi	Avg. Diss.	Diss. SD	% Contrib.	Cum. %
Stachys natalensis	15.40	0.00	1.02	0.86	1.36	57.62
Crabbea hirsuta	15.13	1.13	0.97	0.89	1.29	58.91
Portulaca oleracea	9.87	10.53	0.94	1.03	1.26	60.17
Abutilon angulatum	6.87	10.47	0.93	0.60	1.24	61.41
Ipomoea obscura	2.47	15.93	0.89	1.52	1.19	62.60
Sida cordifolia	11.53	12.80	0.89	0.86	1.19	63.79
Tagetes minuta	1.40	14.80	0.88	0.76	1.18	64.97
Seddera capensis	0.00	12.40	0.84	0.79	1.13	66.10
Schkuhria pinnata	0.00	14.47	0.84	0.66	1.12	67.22
Evolvulus alsinoides	4.27	12.53	0.84	1.09	1.12	68.34
Rhyncosia nervosa	14.20	0.07	0.83	0.71	1.11	69.45
Becium obovatum	3.20	13.53	0.82	0.87	1.09	70.54
Priva cordifolia	0.47	13.73	0.80	0.68	1.07	71.61
Hybanthus enneaspermus	0.13	13.13	0.76	0.59	1.02	72.63
Tragia meyeriana	1.73	12.53	0.76	0.74	1.01	73.64
Helichrysum oxyphyllum	13.20	0.00	0.72	0.53	0.96	74.60
Senecio bupleuroides	13.47	0.00	0.72	0.50	0.96	75.56
Indigofera velutiana	2.27	11.73	0.71	0.97	0.95	76.51
Vigna vexillata	10.40	0.00	0.64	0.84	0.86	77.37
Acalypha villicaulis	11.87	0.00	0.64	0.42	0.86	78.23
Zornia capensis	7.13	5.07	0.64	0.68	0.85	79.08
Melhania didyma	3.73	8.53	0.61	0.75	0.81	79.89
Ipomoea simplex	8.53	0.00	0.55	0.52	0.73	80.62
Barleria elegans	6.67	0.20	0.46	0.34	0.61	81.23
Indigastrum costatum	1.53	6.07	0.42	0.90	0.57	81.80
Lippia javanica	7.80	0.00	0.42	0.43	0.56	82.36
Lantana rugosa	2.40	6.00	0.40	0.85	0.54	82.90
Chenopodium carinatum	0.13	6.87	0.40	0.41	0.53	83.43
Boerhavia diffusa	0.00	7.27	0.39	0.46	0.52	83.95
No specimen	0.00	6.93	0.38	0.43	0.51	84.46
Gomphrena celosioides	1.33	5.60	0.37	0.45	0.49	84.95
Melanthera scandens	7.13	0.00	0.37	0.39	0.49	85.44
Lepidium africanum	0.47	4.73	0.32	0.31	0.42	85.86
Ptycholobium plicatum	0.00	4.93	0.31	0.61	0.41	86.27
Alternanthera pungens	1.00	4.13	0.30	0.41	0.40	86.67
Leucas glabrata	0.07	5.47	0.30	0.38	0.40	87.07

	Avg. frequency					
Species	Hluhluwe	Imfolozi	Avg. Diss.	Diss. SD	% Contrib.	Cum. %
Achyropsis leptostachya	3.80	0.53	0.29	0.45	0.39	87.46
Chamaechrista mimosoides	3.53	2.93	0.28	0.93	0.37	87.83
Indigofera hilaris	5.07	0.00	0.28	0.51	0.37	88.20
Cyanotis speciosa	4.33	0.00	0.27	0.49	0.36	88.56
Stylochiton natalensis	4.13	0.53	0.26	0.95	0.35	88.91
Lactuca inermis	3.47	0.73	0.25	0.57	0.34	89.25
Hypoxis hemerocallidea	4.13	0.00	0.25	0.80	0.34	89.59
Aster bakerianus	4.80	0.00	0.25	0.34	0.33	89.92
Gerbera ambigua	3.73	0.00	0.22	0.62	0.30	90.22

Appendix 7.1 Key to the species, their families, and the life-form and life-history traits of the (orbs encountered in the comparison between the light conservation grazing inside and heavy communal grazing outside of Ithala Game Reserve. Nomenclature according to Arnold and De Wet (1993). Sampled from 40 pairs of quadrats (5 x 2 m), spaced at 25 m intervals along the reserve / Louwsburg Commonage fence line. Plant life-form and history characters: MID = monocot (m) or dicot (d), A/P = short-lived annual / biennial (a) or long-lived perennial (p), UGO = underground growth forms: b = bulb, c = corm, f = fibrous root, r = rhizome, rp = root parasite, rt = root tubers, st = stem tubers, tr = tap root, wtr = woody tap root, we = woody caudex, wc+rt = woody caudex with root tubers, GF = above ground growth form: 1 = cauline-prostrate, 2 = radical-flat, 3 = radical-erect, 4 = cadne-erect. Exotic species have been marked in bold.

Spp.#	Species	Family	M/D	A/P	UGO	GF
Grasses						
1	*Alloteropsis semialata*	Poaceae				
2	*Aristida junciformis*	Poaceae				
3	*Cymbopogon excavatus*	Poaceae				
4	*Diheteropogon amplectense*	Poaceae				
5	*Eragrostis capensis*	Poaceae				
6	*Eragrostis curvula*	Poaceae				
7	*Eragrostis plana*	Poaceae				
8	*Eragrostis racemosa*	Poaceae				
9	*Heteropogon contortus*	Poaceae				
10	*Hyparrhenia sp.*	Poaceae				
11	*Melinis nerviglumis*	Poaceae				
12	*Microchloa caffra*	Poaceae				
13	*Rendlia altera*	Poaceae				
14	*Setaria paladifusca*	Poaceae				
15	*Sporobolus nitens*	Poaceae				
16	*Themeda triandra*	Poaceae				
17	*Tristachya leucothrix*	Poaceae				
Sedge						
18	*Bulbostylus sp.*	Cyperaceae				
Forbs						
19	*Acalypha punctata*	Euphorbiaceae	d	p	wc	4
20	*Acalypha schinzii*	Euphorbiaceae	d	p	wc	4
21	*Anthospermum herbaceum*	Rubiaceae	d	p	tr	1

Spp.#	Species	Family	M/D	A/P	UGO	GF
22	*Anthospermum hispidulum*	Rubiaceae	d	p	tr	4
23	*Aristea cognata*	Iridaceae	m	p	f	2
24	*Aster perfoliatus*	Asteraceae	d	p	rt	4
25	*Athrixia gerradii*	Asteraceae	d	p	wtr	4
26	*Athrixia phylicoides*	Asteraceae	d	p	wtr	4
27	*Becium obovatum*	Lamiaceae	d	p	wtr	4
28	*Berkheya echinaceae*	Asteraceae	d	p	rt	4
29	*Berkheya setifera*	Asteraceae	d	p	wc	4
30	***Centella asiatica***	Apiaceae	d	p	tr	4
31	*Chaetacanthus burchellii*	Acanthaceae	d	p	tr	4
32	*Chascanum latifolium*	Verbenaceae	d	p	wtr	4
33	*Cliffortia nitidula*	Rosaceae	d	p	wtr	4
34	*Commelina africana*	Commelinaceae	m	p	rt	1
35	*Conyza sp.*	Asteraceae	d	a	tr	4
36	*Crabbea aucaulis*	Acanthaceae	d	p	tr	3
37	*Craterocapsa tarsoides*	Campanulaceae	d	p	tr	3
38	*Cucumis myriocarpus*	Curcubitaceae	d	p	wc	1
39	*Cyanotis speciosa*	Commelinaceae	m	p	r	1
40	*Dicoma anomala*	Asteraceae	d	p	r	1
41	*Dipcadi viride*	Hyacinthaceae	m	p	b	2
42	*Eriosema cordatum*	Fabaceae	d	p	wc	1
43	*Eriosema salignum*	Fabaceae	d	p	wc	4
44	*Eulophia sp.*	Orchidaceae	m	p	c	2
45	*Euphorbia striata*	Euphorbiaceae	d	p	wtr	4
46	*Euryops sp.*	Asteraceae	d	p	wc+rt	4
47	*Felicia muricata*	Asteraceae	d	p	tr	4
48	*Gazania krebsiana*	Asteraceae	d	p	wtr	3
49	*Gerbera ambigua*	Asteraceae	d	p	rt	3
50	*Gladiolus ecklonii*	Iridaceae	m	p	c	2
51	*Gladiolus sp.*	Iridaceae	m	p	c	2
52	*Gnidia capitata*	Thymelaeaceae	d	p	wc+rt	4
53	*Graderia scabra*	Scrophulariaceae	d	p	wtr	4
54	*Haemanthus sp.*	Amaryllidaceae	m	p	b	3
55	*Haplocarpha scaposa*	Asteraceae	d	p	rt	3
56	*Helichrysum adenocarpum*	Asteraceae	d	p	tr	3

Spp.#	Species	Family	M/D	A/P	UGO	GF
57	*Helichrysum aureonitens*	Asteraceae	d	p	tr	4
58	*Helichrysum glomeratum*	Asteraceae	d	p	tr	4
59	*Helichrysum miconiifolium*	Asteraceae	d	p	wc+rt	3
60	*Helichrysum oxyphyllum*	Asteraceae	d	p	wc+rt	4
61	*Helichrysum pallidum*	Asteraceae	d	p	wc+rt	3
62	*Helichrysum pilosellum*	Asteraceae	d	p	wc+rt	3
63	*Helichrysum subfalcatum*	Asteraceae	d	p	tr	1
64	*Hermannia grandistipula*	Sterculiaceae	d	p	tr	4
65	*Hermannia woodii*	Sterculiaceae	d	p	rt	1
66	*Hibiscus aethiopicus*	Malvaceae	d	p	wtr	4
67	*Hypericum aethiopicum*	Clusiaceae	d	p	rt	4
68	*Hypoxis acuminata*	Hypoxidaceae	m	p	c	2
69	*Hypoxis multiceps*	Hypoxidaceae	m	p	c	2
70	*Hypoxis rigidula*	Hypoxidaceae	m	p	c	2
71	*Indigofera hedyantha*	Fabaceae	d	p	tr	4
72	*Indigofera hilaris*	Fabaceae	d	p	wtr	4
73	*Indigofera pondoensis*	Fabaceae	d	p	wtr	4
74	*Ipomoea oblongata*	Convolvulaceae	d	p	wtr	1
75	*Kohautia amatymbica*	Rubiaceae	d	p	tr	4
76	*Ledebouria cooperi*	Hyacinthaceae	m	p	b	2
77	*Ledebouria ovalifolia*	Hyacinthaceae	m	p	b	3
78	*Limnosella minor*	Scrophulariaceae	d	p	tr	4
79	*Lotononis corymbosa*	Fabaceae	d	p	wtr	4
80	*Lotononis lotonoides*	Fabaceae	d	p	tr	4
81	*Lotononis mucronata*	Fabaceae	d	p	wtr	4
82	*Lotononis procumbens*	Fabaceae	d	p	wtr	4
83	*Moreae sp.*	Iridaceae	m	p	c	2
84	*Orchid sp.*	Orchidaceae	m	p	c	2
85	*Oxalis smithiana*	Oxalidaceae	d	p	st	4
86	*Pentanisia prunelloides*	Rubiaceae	d	p	wc	4
87	*Pergularia daemia*	Asclepiadaceae	d	p	st	1
88	*Polygyla amatymbica*	Polygalaceae	d	p	wtr	1
89	*Polygyla rhinostigma*	Polygalaceae	d	p	wtr	1
90	*Psammotropha mucronata*	Molluginaceae	d	p	tr	2
91	*Pygmaeothamnus chamaeodendrum*	Rubiaceae	d	p	st	3

Spp.#	Species	Family	M/D	A/P	UGO	GF
92	*Raphionacme hirsuta*	Periplocaceae	d	p	st	4
93	*Rhyncosia adenodes*	Fabaceae	d	p	wtr	1
94	*Rhyncosia confusa*	Fabaceae	d	p	tr	1
95	*Rhyncosia totta*	Fabaceae	d	p	rt	1
96	*Satyrium sp.*	Orchidaceae	m	p	c	4
97	*Scabiosa columbaria*	Dipsacaceae	d	p	tr	3
98	*Scilla nervosa*	Hyacinthaceae	m	p	b	2
99	*Sebeae sp.*	Gentianaceae	d	p	tr	4
100	*Senecio bupleuroides*	Asteraceae	d	p	rt	4
101	*Senecio conrathii*	Asteraceae	d	p	rt	4
102	*Senecio rhomboideus*	Asteraceae	d	p	rt	3
103	*Senecio variabilis*	Asteraceae	d	p	rt	3
104	*Sonchus nanus*	Asteraceae	d	p	st	3
105	*Spermacoce natalense*	Rubiaceae	d	p	tr	4
106	*Stachys nigricans*	Lamiaceae	d	p	tr	4
107	*Syncolostemon parvifolius*	Lamiaceae	d	p	wtr	4
108	*Tephrosia natalensis*	Fabaceae	d	p	tr	1
109	*Trachyandra asperata*	Asphodelaceae	m	p	r	2
110	*Ursinia nana*	Asteraceae	d	p	tr	4
111	*Ursinia tenuiloba*	Asteraceae	d	p	wtr	4
112	*Vernonia dregeana*	Asteraceae	d	p	rt	4
113	*Vernonia natalensis*	Asteraceae	d	p	wtr	4
114	*Vernonia oligocephala*	Asteraceae	d	p	wtr	4
115	*Vernonia thodii*	Asteraceae	d	p	tr	3
116	*Xysmalobium parviflorum*	Asclepiadaceae	d	p	st	1
117	*Zornia capensis*	Fabaceae	d	p	tr	1
Fern						
118	*Pteridium aquilinum*	Dennstaedtiaceae				

Appendix 7.2 Key to the species, their families, and the life-form and life-history traits of the forbs encountered in the comparison between the light conservation grazing inside and heavy communal grazing outside of Impendle Nature Reserve. Nomenclature according to Arnold and De Wet (1993). Sampled from 50 pairs of quadrats (5 x 2 m), spaced at 25 m intervals along the reserve / Impendhle Commonage fence line. Plant life-form and history characters: M/D = monocot (m) or divot (d), NP = short-lived annual / biennial (a) or long-lived perennial (p), UGO = underground growth forms: b = bulb, c = corm, f = fibrous root, r = rhizome, rp = root parasite, rt = root tubers, st = stem tubers, tr = tap root, Mr = woody tap root, we = woody caudex, wc+rt = woody caudez with root tubers, GF = above ground growth form: 1 = cauline-prostrate, 2 = radical-flat, 3 = radical-erect, 4 = cauline-erect. Exotic species have been marked in bold.

Spp.#	Species	Family	M/D	A/P	UGO	GF
Grasses						
1	*Alloteropsis semi-alata*	Poaceae				
2	*Aristida junciformis*	Poaceae				
3	*Bracaeria serrata*	Poaceae				
4	*Digitaria sp.*	Poaceae				
5	*Diheteropogon amplectense*	Poaceae				
6	*Diheteropogon fillifolius*	Poaceae				
7	*Eragrostis capensis*	Poaceae				
8	*Eragrostis curvula*	Poaceae				
9	*Eragrostis plana*	Poaceae				
10	*Eragrostis racemosa*	Poaceae				
11	*Grass sp1*	Poaceae				
12	*Harpochloa falx*	Poaceae				
13	*Heteropogon contortus*	Poaceae				
14	*Hyparrhenia sp.*	Poaceae				
15	*Koeleria capensis*	Poaceae				
16	*Loudetia simplex*	Poaceae				
17	*Michrochloa caffra*	Poaceae				
18	*Monocymbium cereesiforme*	Poaceae				
19	*Panicum ecklonii*	Poaceae				
20	*Panicum natalense*	Poaceae				
21	*Paspalum sp.*	Poaceae				
22	*Setaria paladifusca*	Poaceae				
23	*Sporobolus africanus*	Poaceae				

Spp.#	Species	Family	M/D	A/P	UGO	GF
24	*Themeda triandra*	Poaceae				
25	*Trachypogon spicatus*	Poaceae				
26	*Tristachya leucothrix*	Poaceae				
Sedges						
27	*Bulbostylus sp1*	Cyperaceae				
28	*Bulbostylus sp2*	Cyperaceae				
29	*Bulbostylus sp3*	Cyperaceae				
30	*Sedge sp1*	Cyperaceae				
31	*Sedge sp2*	Cyperaceae				
Forbs						
32	*Acalypha punctata*	Euphorbiaceae	d	p	wc	4
33	*Acalypha schinzii*	Euphorbiaceae	d	p	wc	4
34	*Acanthospermum australe*	Asteraceae	d	p	tr	1
35	*Agathisanthemum bojeri*	Rubiaceae	d	p	wtr	4
36	*Ajuga ophrydis*	Lamiaceae	d	p	tr	4
37	*Anthospermum pumilum*	Rubiaceae	d	p	wtr	4
38	*Aristea cognata*	Iridaceae	m	p	f	2
39	*Asclepias sp.*	Asclepiadaceae	d	p	st	4
40	*Aster bakerianus*	Asteraceae	d	p	rt	4
41	*Becium obovatum*	Lamiaceae	d	p	wtr	4
42	*Berkheya speciosa*	Asteraceae	d	p	wtr	3
43	**Centella asiatica**	Apiaceae	d	p	tr	1
44	*Clutia sp.*	Euphorbiaceae	d	p	wtr	4
45	*Commelina africana*	Commelinaceae	m	p	rt	1
46	*Conyza pinnata*	Asteraceae	d	a	tr	1
47	*Conyza sp1*	Asteraceae	d	a	tr	4
48	*Conyza sp2*	Asteraceae	d	a	tr	4
49	*Corycium nigrescence*	Orchidaceae	m	p	c	4
50	*Crassula alba*	Crassulaceae	d	p	tr	4
51	*Cucumis hirsutus*	Curcubitaceae	d	p	wtr	1
52	*Diascia purpurea*	Scrophulariaceae	d	p	tr	1
53	*Dicoma anomala*	Asteraceae	d	p	r	1
54	*Dierama sp.*	Iridaceae	m	p	c	2
55	*Dipcadi marlothi*	Hyacinthaceae	m	p	b	2
56	*Eriosema distinctum*	Fabaceae	d	p	wtr	1

Spp.#	Species	Family	M/D	A/P	UGO	GF
57	*Eriosema salignum*	Fabaceae	d	p	wc	4
58	*Eriospermum cooperi*	Eriospermaceae	m	p	rt	3
59	*Eucomus autumnalis*	Hyacinthaceae	m	p	b	3
60	*Eulophia sp.*	Orchidaceae	m	p	c	2
61	*Euryops sp.*	Asteraceae	d	p	rt	4
62	*Euryops transvaalensis*	Asteraceae	d	p	tr	4
63	*Gazania krebsiana*	Asteraceae	d	p	wtr	3
64	*Gerbera ambigua*	Asteraceae	d	p	rt	3
65	*Gerbera piloselloides*	Asteraceae	d	p	rt	3
66	*Gladiolus ecklonii*	Iridaceae	m	p	c	2
67	*Gladiolus sp1*	Iridaceae	m	p	c	2
68	*Gladiolus sp2*	Iridaceae	m	p	c	2
69	*Gnidia kraussiana*	Thymelaeaceae	d	p	wtr	4
70	*Graderia scabra*	Scrophulariaceae	d	p	wtr	4
71	*Helichrysum aureonitens*	Asteraceae	d	p	tr	4
72	*Helichrysum cephaloideum*	Asteraceae	d	p	tr	4
73	*Helichrysum glomeratum*	Asteraceae	d	p	tr	4
74	*Helichrysum herbaceum*	Asteraceae	d	p	tr	4
75	*Helichrysum miconiifolium*	Asteraceae	d	p	wc+rt	3
76	*Helichrysum pallidum*	Asteraceae	d	p	wc+rt	3
77	*Helichrysum pilosellum*	Asteraceae	d	p	wc+rt	3
78	*Helichrysum rugulosum*	Asteraceae	d	p	tr	4
79	*Hermania gerradii*	Sterculiaceae	d	p	rt	1
80	*Hermania woodii*	Sterculiaceae	d	p	rt	1
81	*Hibiscus aethiopicus*	Malvaceae	d	p	wtr	4
82	*Hypericum aethiopicum*	Clusiaceae	d	p	rt	4
83	*Hypochoeris radicata*	Asteraceae	d	p	tr	3
84	*Hypoxis acuminata*	Hypoxidaceae	m	p	c	2
85	*Hypoxis argentea*	Hypoxidaceae	m	p	c	2
86	*Hypoxis costata*	Hypoxidaceae	m	p	c	2
87	*Indigofera rostrata*	Fabaceae	d	p	wtr	4
88	*Knipofia gracilis*	Hyacinthaceae	m	p	f	2
89	*Kohautia amatymbica*	Rubiaceae	d	p	wtr	4
90	*Ledebouria sp.*	Hyacinthaceae	m	p	b	2
91	*Lobelia erinus*	Lobeliaceae	d	a	tr	4

Spp.#	Species	Family	M/D	A/P	UGO	GF
92	*Lopiocarpus latifolius*	Chenopodiaceae	d	a	tr	4
93	*Orchid sp.*	Orchidaceae	m	p	c	3
94	*Oxalis obliquifolia*	Oxalidaceae	d	p	st	4
95	*Oxalis smithiana*	Oxalidaceae	d	p	st	4
96	*Pachycarphus sp.*	Asclepiadaceae	d	p	wc	4
97	*Pelargonium luridum*	Geraniaceae	d	p	wc	3
98	*Pentanisia prunelloides*	Rubiaceae	d	p	wc	4
99	*Polygyla rehmanii*	Polygalaceae	d	p	wtr	4
100	*Psamotropha mucronata*	Molluginaceae	d	p	tr	3
101	*Pyctolobium plicatum*	Fabaceae	d	p	wtr	4
102	*Pygmaeothamnus chamaedendrum*	Rubiaceae	d	p	st	3
103	*Rhyncosia totta*	Fabaceae	d	p	rt	1
104	***Richardia brasiliensis***	Rubiaceae	d	p	st	1
105	***Rubus cuneifolius***	Rosaceae	d	p	wtr	4
106	*Scabiosa columbaria*	Dipsacaceae	d	p	tr	3
107	*Schizoglossum sp.*	Asclepiadaceae	d	p	wc	4
108	*Scilla nervosa*	Hyacinthaceae	m	p	b	3
109	*Sebeae sedoides*	Gentinaceae	d	p	tr	4
110	*Senecio bupleuroides*	Asteraceae	d	p	rt	4
111	*Senecio erubescence*	Asteraceae	d	p	rt	3
112	*Senecio sandersonii*	Asteraceae	d	p	rt	4
113	*Senecio variabilis*	Asteraceae	d	p	rt	4
114	*Senecio sp.*	Asteraceae	d	p	rt	4
115	*Sonchus nanus*	Asteraceae	d	a	tr	3
116	*Spermacoce natalense*	Rubiaceae	d	p	tr	4
117	*Stachys sessilis*	Lamiaceae	d	p	tr	4
118	*Striga bilabiata*	Scrophulariaceae	d	p	rp	4
119	*Vernonia natalensis*	Asteraceae	d	p	wtr	4
120	*Vernonia oligocephala*	Asteraceae	d	p	wtr	4
121	*Vernonia thodii*	Asteraceae	d	p	tr	3
122	*Wahlenbergia cuspidata*	Campanulaceae	d	p	tr	4
123	*Zornia capensis*	Fabaceae	d	p	tr	1
124	Specimen misplaced		d	p	tr	4
Fern						
125	*Pteridium aquilinum*	Dennstaedtiaceae				

Appendix 8.1 Species encountered in 1000 m^2 in the various burnt and burnt and grazed watersheds at Konza Prairie Research Natural Area, along with their families, and forb life-form and history characteristics. M / D = monocot (m) or dicot (d); S / L = short-lived (annuals [a] and biennials [b]) or long-lived (perennials [p]); UGO = underground organs (r = rhizome, rt = root tuber, st = stem tuber, tr = tap root, wtr = woody tap root, wc = woody caudex, wc +rt = woody caudex with root tubers); Spr / N-Spr = sprouter (Spr) or nonsprouter (N-Spr); GF = growth form (CE = cauline erect, CP = cauline prostrate); C_3 / C_4 = C_3 photosynthetic pathway (3) or C_4 photosynthetic pathway (4).

					Spr /		C_3 /	Fire				Fire & Grazing		
Species	Family	M / D	S / L	UGO	N-Spr	GF	C_4	SpB	2C	4B	10A	N1B	N2B	N4B
Grasses														
Andropogon gerardii	Poaceae	m	p				4	1	1	1	1	1	0	1
Bouteloua curtipendula	Poaceae	m	p				4	1	1	1	1	1	1	1
Bouteloua gracilis	Poaceae	m	p				4	0	0	0	0	1	1	1
Bromus japonicus	Poaceae	m	a				3	0	0	0	0	0	0	1
Dichanthelium oligosanthes	Poaceae	m	p				3	1	1	1	1	1	1	1
Elymus canadensis	Poaceae	m	p				3	0	0	1	1	1	1	1
Eragrostis Spectabilis	Poaceae	m	p				4	1	0	1	1	1	1	1
Koeleria macrantha	Poaceae	m	p				3	0	1	0	1	0	1	1
Muhlenbergia schreberi	Poaceae	m	p				4	0	1	1	0	0	0	1
Schizachyrium scoparium	Poaceae	m	p				4	1	1	1	1	0	0	0
Sorghastrum nutans	Poaceae	m	p				4	1	1	1	1	1	0	1
Sphenopholis obtusata	Poaceae	m	p				3	0	1	1	1	0	0	1

					Spr /		C_3 /	Fire				Fire & Grazing		
Species	Family	M / D	S / L	UGO	N-Spr	GF	C_4	SpB	2C	4B	10A	N1B	N2B	N4B
Sedges														
Carex brevior	Cyperaceae	m	p				3	1	0	1	0	1	0	1
Juncus interior	Juncaceae	m	p				3	0	0	1	0	1	0	0
Forbs														
Achillea millefolium	Asteraceae	d	p	st	Spr	CE	3	1	1	1	1	1	1	1
Ambrosia psilostachya	Asteraceae	d	p	tr	N-Spr	CE	3	1	1	1	1	1	1	1
Amorpha canescens	Fabaceae	d	p	wtr	Spr	CE	3	1	1	1	1	1	1	1
Antennaria neglecta	Asteraceae	d	p	rt	Spr	CP	3	0	1	0	0	1	1	1
Artemisia ludoviciana	Asteraceae	d	p	tr	N-Spr	CE	3	0	1	1	1	1	1	1
Asclepias stenophylla	Asclepiadaceae	d	p	st	Spr	CE	3	1	1	1	1	0	0	0
Asclepias tuberosa	Asclepiadaceae	d	p	wtr	Spr	CE	3	0	1	1	0	0	0	0
Asclepias verticillata	Asclepiadaceae	d	p	rt	Spr	CE	3	1	1	1	1	0	0	0
Asclepias viridiflora	Asclepiadaceae	d	p	wtr	Spr	CE	3	0	1	1	0	1	1	0
Asclepias viridis	Asclepiadaceae	d	p	wc	Spr	CE	3	1	0	0	1	1	0	1
Baptisia australis	Fabaceae	d	p	wtr	Spr	CE	3	1	1	1	1	1	1	1
Brickellia eupatoroides	Asteraceae	d	p	st	Spr	CE	3	1	1	1	1	1	1	1
Ceanothus herbaceus	Rhamnaceae	d	p	wtr	Spr	CE	3	0	0	0	0	1	1	1
Chamaesyce nutans	Euphorbiaceae	d	a	tr	N-Spr	CE	3	1	0	0	1	0	0	1
Cirsium vulgare	Asteraceae	d	b	tr	N-Spr	CE	3	0	0	0	0	1	1	0
Dalea candida	Fabaceae	d	p	st	Spr	CE	3	1	1	1	1	1	1	1

					Spr /		C_3 /	Fire				Fire & Grazing		
Species	Family	M / D	S / L	UGO	N-Spr	GF	C_4	SpB	2C	4B	10A	N1B	N2B	N4B
Dalea multiflora	Fabaceae	d	p	wtr	Spr	CE	3	0	0	0	0	1	1	1
Dalea purpurea	Fabaceae	d	p	wtr	Spr	CE	3	1	1	1	0	1	1	1
Desmodium illinoense	Fabaceae	d	p	r	Spr	CE	3	0	1	1	1	0	0	0
Eupatorium altissimum	Asteraceae	d	p	rt	Spr	CE	3	0	0	0	1	0	0	0
Euphorbia marginata	Euphorbiaceae	d	a	tr	N-Spr	CE	3	0	0	0	0	0	1	1
Gaura mollis	Onagraceae	d	a	tr	N-Spr	CE	3	0	0	0	1	0	1	0
Hedeoma hispida	Lamiaceae	d	a	tr	N-Spr	CE	3	0	0	0	0	0	1	1
Hymenopappus scabiosaeus	Asteraceae	d	b	tr	N-Spr	CP	3	0	0	0	0	1	1	1
Lepidium densiflorum	Brassicaceae	d	a	tr	N-Spr	CE	3	0	0	0	0	0	1	1
Lespedeza capitata	Fabaceae	d	p	wtr	Spr	CE	3	0	1	1	0	1	1	0
Liatris punctata	Asteraceae	d	p	wc	Spr	CE	3	0	0	1	0	1	1	0
Linum sulcatum	Linaceae	d	a	tr	N-Spr	CE	3	1	1	1	1	1	1	1
Mimosa nuttallii	Fabaceae	d	p	r	Spr	CE	3	1	1	1	1	1	1	1
Oligoneuron rigidum	Asteraceae	d	p	rt	Spr	CE	3	1	0	1	1	0	0	1
Opuntia macrorhiza	Cactaceae	d	p	tr	N-Spr	CE	3	0	0	0	0	0	0	1
Oxalis stricta	Oxalidaceae	d	p	tr	N-Spr	CE	3	1	0	0	1	1	1	1
Penstemon cobaea	Scrophulariaceae	d	p	wc+rt	Spr	CE	3	0	0	0	0	1	1	0
Physalis pumila	Solanaceae	d	p	r	Spr	CE	3	0	0	0	0	1	1	0
Physalis pumila	Solanaceae	d	p	wc	Spr	CE	3	1	0	1	0	0	0	0
Plantago patagonica	Plantaginaceae	d	a	tr	N-Spr	CE	3	0	0	0	0	0	0	1
Psoralidium tenuiflorum	Fabaceae	d	p	st	Spr	CE	3	1	0	1	0	0	1	0

					Spr /		C_3 /	Fire				Fire & Grazing		
Species	Family	M / D	S / L	UGO	N-Spr	GF	C_4	SpB	2C	4B	10A	N1B	N2B	N4B
Rhus glabra	Anacardiaceae	d	p	tr	N-Spr	CE	3	0	0	0	0	0	1	0
Ruellia humilis	Acanthaceae	d	p	wc+rt	Spr	CE	3	1	1	1	1	0	1	1
Salvia azurea	Lamiaceae	d	p	wc+rt	Spr	CE	3	1	1	1	1	1	1	1
Solanum rostratum	Solanaceae	d	a	tr	N-Spr	CE	3	0	0	0	0	0	0	1
Solidago missouriensis	Asteraceae	d	p	tr	N-Spr	CE	3	1	1	1	1	1	1	1
Stenosiphon linifolius	Onagraceae	d	b	tr	N-Spr	CE	3	0	0	0	0	1	1	0
Symphoricarpos orbiculatus	Caprifoliaceae	d	p	wtr	Spr	CE	3	1	0	1	1	1	1	1
Symphyotrichum ericoides	Asteraceae	d	p	r	Spr	CE	3	1	1	1	1	1	1	1
Symphyotrichum oblongifolium	Asteraceae	d	p	tr	N-Spr	CE	3	1	1	1	1	1	0	0
Symphyotrichum sericeum	Asteraceae	d	p	wc+rt	Spr	CE	3	0	1	1	1	1	1	1
Tragia betonicifolia or ramosa	Euphorbiaceae	d	p	tr	N-Spr	CE	3	0	0	0	0	1	1	0
Verbena stricta	Verbenaceae	d	p	tr	N-Spr	CE	3	0	0	1	1	1	1	1
Vernonia baldwinii	Asteraceae	d	p	wc+rt	Spr	CE	3	1	1	0	1	1	1	1
Viola pedatifida	Violaceae	d	p	rt	Spr	CE	3	0	0	1	0	1	0	0