Above ground perennial plant biomass across an altitudinal and land-use gradient in Namaqualand, South Africa

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Abstract

This study set out to generate estimates of the standing perennial biomass for six different vegetation types, and associated upland and lowland habitats, across the altitudinal gradient presented by the Kamiesberg mountain range in the Namaqualand region of the Northern Cape Province of South Africa. Volume-biomass regressions, established for 94 perennial species accounting for 70–80% of the plant cover, were used to generate these estimations. Comparisons to other studies give similar findings, corroborating the method adopted. Biomass was found to vary significantly in relation to the altitudinal, and associated rainfall, gradient, as well as by habitat type where the rocky uplands have considerably more biomass that the sandy lowland habitats. An examination of the impact of sustained heavy grazing associated with a communal rangeland on this standing perennial biomass, showed a significant decrease in on the lowland habitats. This loss in biomass is principally of palatable species, with no evidence of a response in terms of perennial biomass. These findings point to degradation on the lowland habitats of the communal rangeland, with negative consequences for livestock farmers in the region.
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Keywords: Above ground biomass; Communal land use; Grazing impacts; Volume-biomass regressions

1. Introduction

South Africa's land tenure systems still reflect the historical legacy of the apartheid era. Within a rangeland context, private land tenure farmers, who are predominantly white, received generous support from the previous government during the apartheid era, and stocked their farms according to the recommended government stocking rate. Stocking rates in communal areas in South Africa well exceed those recommended by government. In the western arid regions of South Africa these continue to be on average 1.85 times those of the government recommended rates (Todd and Hoffman, 2000). As a result stark fence line contrasts can frequently be seen defining the boundary between communally- and privately-owned rangelands in these arid regions.

Anderson and Hoffman (2007) document plant community change in response to sustained heavy grazing pressure on these arid communal rangelands where they demonstrate a significant shift towards a more ephemeral community on the communal rangeland. This current study aims to take this understanding of the impacts of sustained heavy grazing further, by contrasting perennial standing biomass between these two management types.

A detailed understanding of standing plant biomass as a resource is important; both from a livelihood and a conservation standpoint. An understanding of perennial biomass tells us of the *status quo* of a system, the effects of past impacts, and can elucidate ecological responses and dynamics, all of which in turn feed in to livelihood and conservation management considerations, as they emerge within a democratic setting.

There is considerable scope for expanding our knowledge of plant biomass in different vegetation types, and for improving measurement techniques (Navar et al., 2004). The accurate assessment of plant biomass is difficult, where the area to be

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covered, the nature of the vegetation, the question to be addressed, and inevitable time and financial constraints, all influence the method to be adopted and the degree of accuracy achieved (Catchpole and Wheeler, 1992). Accuracy in measuring biomass is described as paramount where a detailed understanding of available forage is vital for rangeland management decisions and environmental sustainability (Le Houerou et al., 1988). Methodologies based on extensive destructive sampling are increasingly hard to justify, as well as being expensive and time consuming (Navar et al., 2004).

This study examined standing plant biomass cross both natural and human-induced gradients through a combined assessment of altitudinal gradient and variable land-use effects. We used a method based on the allometric relationship between plant volume and biomass, to estimate standing biomass in the six different vegetation types across a mountain range in the arid western regions of South Africa, and contrasted communal and private land tenure management systems. This paper addresses the following specific questions:

a) How does standing biomass vary between the different vegetation types across an altitudinal gradient?
b) Has the sustained heavy grazing associated with the communal range, evident in previously recorded impacts in relation to plant community composition, significantly affected standing biomass?
c) Does biomass vary in terms of palatability in response to the sustained heavy grazing on the communal range?
d) Does the method adopted provide an accurate and efficient measure of biomass?

2. Methods

This study was conducted in Namaqualand, in South Africa's Northern Cape Province, across the boundary of the Leliefontein communal area and the immediately adjacent, privately-owned farms. The Leliefontein communal area comprises some 193 000 ha, lying in an east–west band of about 50 km straddling the Kamiesberg mountain range (Fig. 1). The western extreme of the communal area is approximately 15 km from the coast. The Kamiesberg is a large granite-gneiss intrusion surrounded predominantly, and relatively uniformly, by red and yellow weakly-structured apedal soils (Watkeys, 1999). The Kamiesberg mountain range links the lowland coastal plains in the west to the start of the interior plateau to the east. While the region is arid, the mountain receives orographic rainfall, resulting in relatively moist western and upper slopes. The Namaqualand desert falls within the Succulent Karoo biome which is recognised as one of only two biodiversity hotspots within semi-arid areas (Mittermeier et al., 2004). The Kamiesberg is host to a number of different vegetation types and is itself an area of noted biodiversity and conservation concern (Lombard et al., 1999).
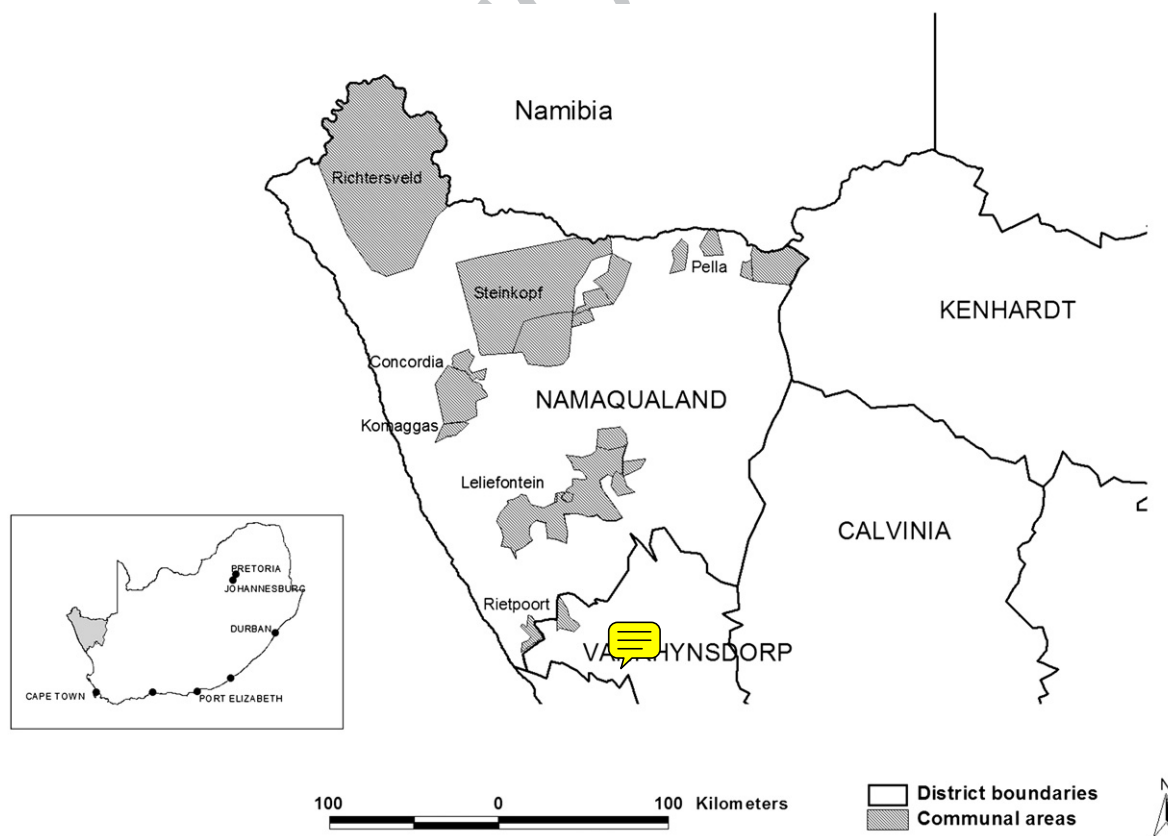

Q1 Fig. 1. Namaqualand with the communal areas shown as 'islands' surrounded by privately-owned farms. The study was conducted in and around the Leliefontein communal area.

The study area covers a diverse range of vegetation types. West of the Kamiesberg, on the inner margins of the coastal plain of Namaqualand, at an elevation of about 200 m is Heuweltjieveld (Mucina and Rutherford, 2006). The Heuweltjieveld is characteristically a low shrubland, dominated by succulent shrubs of the Mesembryanthemaceae family such as *Drosanthemum oculatum* and *Ruschia lerouxiae*. While predominantly a succulent vegetation, the few woody shrubs in this vegetation type are low in architecture and include species such as *Zygophyllum cordifolium* and an unknown species of Salsola. An increase in elevation at the foothills of the Kamiesberg, at elevations between 300 m and 800 m with the presence of rocky granite hills (klipkoppe) sees a change to Namaqualand klipkoppe shrubland (Mucina and Rutherford, 2006). This vegetation is more varied in height with a mix of succulent and woody shrubs. Dominant succulent species here include *Ruschia viridifolia* and *Leipoldtia laxa* while woody shrubs include *Zygophyllum morgsana* and *Lycium ferocissimum*. The lowland areas of this vegetation type are referred to as Blomveld, but are not viewed as a separate vegetation type in this study (Mucina and Rutherford, 2006). On the western slopes of the Kamiesberg between 800 m and 1300 m is Kamiesberg mountain shrubland (Mucina and Rutherford, 2006). Mountain shrubland is dominated by larger woody shrubs such as *Didelta spinosa* with other woody shrub species such as *Lebeckia multiflora* and *Euryops laterifolius*. A grassy element becomes evident in this vegetation type with the presence of *Ehrharta barbinodis*. Once on the plateau, with a height of 1500 m, there are isolated patches of Namaqualand granite renosterveld (Mucina and Rutherford, 2006), characterised by large stands of the woody shrub *Dicerothamnus rhinocerotis* and the grass species *Merxmuellera stricta*. With the gentle decline onto the escarpment to the east of the Kamiesberg, there is the re-emergence of the Namaqualand klipkoppe shrubland at about 1000 m. For the sake of this study, the klipkoppe vegetation is divided into what are termed Western klipkoppe and Eastern klipkoppe. The Eastern klipkoppe are characterised by a similar mix of succulent and woody shrubs, with characteristic dominants on this eastern side in the form of the woody shrubs *Hirpicium alienatum*, *Chrysochoma cilliata* and *Zygophyllum retrofractum* and the succulents *Leipoldtia schultzei*, *Ruschia robusta* and *Cheiridopsis denticulate*. The extreme eastern boundary of the Leliefontein communal area falls within the ecotone between the Eastern klipkoppe and Bushmanland arid grassland vegetation types (Mucina and Rutherford, 2006). This ecotone signifies the start of the shift from the winter rainfall region of the Succulent Karoo to the thunderstorm-dominated, summer rainfall region of the Nama Karoo. This final vegetation type included in this study is termed the Bushmanland ecotone, which sees the start of the shift into the Nama Karoo at around 900 m. This Bushmanland ecotone is dominated by the grass *Stipagrostis brevifolia* interspersed with succulent species such as *Conicosia elongata*. The Kamiesberg mountain range is characterised by rocky upland and sandy lowland habitats and each vegetation type (with the exception of Mountain Shrubland which has only the rocky upland component) can be divided into these two habitat types. As these two habitats are used variably for grazing, with the sandy lowlands being more heavily utilized

(Samuels et al., 2007), these habitats were viewed independently in this study. End points of sample sites in each of the six vegetation types sampled ranged from 5 km to 20 km apart.

This east–west gradient follows both an altitudinal and a rainfall gradient, with a rapid decrease in rainfall to the east of the Kamiesberg. Rainfall ranges from about 140 mm per annum in the Heuweltjieveld, to 320 mm at the top of the Kamiesberg, to 200 mm east of the mountain top at the start of the escarpment, and to 125 mm at Vaalputs to the immediate east of the study area (Desmet and Cowling, 1999). The winter rainfall is typically predictable, while the summer rainfall to the eastern extreme of the study area is less so.

A subjective grazing score was generated to substantiate broad level grazing scores for the region. This grazing score was set on a scale of one (heavily grazed) to five (no evidence of grazing). This was based on a relative assessment of grazing evidence where the amount of dung, grazing-damaged shrubs, and extent of livestock footpaths was recorded.

Species cover data were collected for all species in 66 modified Whittaker plots (Stohlgren et al., 1997; Stohlgren et al., 1998) across the communal-private land tenure boundary in the Kamiesberg mountain range. Half of these were on communal land and half on private land, with 12 plots in the Heuweltjieveld, 12 in the Western klipkoppe, 12 in the Renosterveld, 12 in the Eastern klipkoppe and 12 in the Bushmanland ecotone vegetation types. These plots were spread evenly between upland and lowland habitats (i.e. three in each habitat). The Mountain shrubland vegetation type is restricted to slopes, and in this vegetation type no lowland component exists, so here only 6 plots were measured. Sites in each vegetation type were selected so as to minimise variability in slope and aspect, as well as for accessibility. A minimum avoidance distance of 50 m was given to known stock posts and water points to avoid the 'sacrifice zone' established for the area (Riginos and Hoffman, 2003). Old lands were also avoided.

A list of those species accounting for 80% of the perennial cover was created. A volume-biomass regression curve was generated for each of these species by sampling six individuals of a range of sizes (Catchpole and Wheeler, 1992). A diversity of sizes was used in order to best capture the full range of the volume-biomass relationship for each species. Three individuals of each species was then oven-dried at 60 °C for three days to establish a wet:dry ratio. In order to gain a mean volume for the dominant species at each sample site, height and two diameter measures were taken from ten individuals selected at random of those species dominating cover at that site (Catchpole and Wheeler, 1992). Sampling was carried out in the spring of 2003 and 2004.

Based on the assumption that most shrubs can be represented as an oblate spheroid (Phillips and MacMahon, 1981), the mean circumference of individuals as measured at each site was established. The area was then divided (generated from the percentage area occupied) by the mean circumference to establish mean number of individuals per 1 m^2. This was then multiplied by the mean volume for that specific species at that site. Using this volume, the associated biomass values were then worked out through the relevant regression equation (as generated by a range of species off site) (Flombaum and Sala, 2007). In a few instances data for individual species were log-transformed, improving the

t1.1 Table 1

t1.2 Regression equations, r^2 values and percentage dry weight for the species sampled. Species are grouped according to growth form. Data that were log-transformed are indicated with an asterisk (*).

	Species	Regression equation	r^2	% dry weight
t1.3	Species	Regression equation	r^2	% dry weight
t1.4	**Herbaceous shrub**			
t1.5	*Aizoon canariense* L.	$y=532\,923x+0.6$	0.89	28.2
t1.6	*Asparagus capensis* L.	$y=4395.2x+4.56$	0.74	76.4
t1.7	*Galenia sarcophylla* Fenzl	$y=0.4471x+3.16*$	0.63	59.0
t1.8	*Hypertelis salsoloides* (Burch.) var. salsoloides Adamson	$y=115\,153x+9.7$	0.84	38.6
t1.9	*Manochlamys albicans* (Aiton) Aellen	$y=4487.7x+3.56$	0.79	81.8
t1.10	*Restio cymosus* (Mast.) Pillans	$y=3361.7x+89.51$	0.74	75.4
t1.11	*Tetragonia fruiticosa* L.	$y=4054.2x+2.54$	0.89	23.4
t1.12				
t1.13	**Grass**			
t1.14	*Chaetobromus involucratis* (Schrad.)Nees subsp dregeanus(Nees)Verboom	$y=5280.3x+82.43$	0.76	76.7
t1.15	*Ehrharta barbinodis* Nees ex Trin.	$y=11.32x+32.69$	0.77	69.5
t1.16	*Fingerhuthia africana* Lehm.	$y=12\,272x+20.95$	0.79	73.9
t1.17	*Merxmuellera stricta* (Schrad) Conert	$y=1659x+91.99$	0.77	77.7
t1.18	*Pentaschistis barbata* (Nees) P.H.Linder subsp. Barbata	$y=264\,112x+22.32$	0.81	89.2
t1.19	*Stipagrostis brevifolia* (Nees) DeWinter	$y=15\,500x+27.66$	0.87	73.8
t1.20				
t1.21	**Dwarf shrub**			
t1.22	*Blepharis furcata* (L.f.) Pers.	$y=4871.3x+13.55$	0.92	64.0
t1.23	*Chrysochoma cilliata*	$y=2540.8x+39.34$	0.6	51.1
t1.24	*Hirpicium alienatum* (Thunb.) Druce	$y=1563.9x+34.87$	0.68	51.5
t1.25	*Indigofera heterophylla* Thunb.	$y=11\,706x+12.67$	0.82	78.5
t1.26	*Lobostemon glaucophyllus* (Jacq.) H.Buek.	$y=5704x+182.49$	0.82	57.0
t1.27	*Oftia revoluta* (E.Mey.) Bocq.	$y=5466.9x+228.8$	0.95	32.5
t1.28	*Pentzia incana* (Thunb.) Kuntze	$y=16\,049x+10.6$	0.97	78.9
t1.29	*Phylica montana* Sond.	$y=10\,541x-367.71$	0.91	79.7
t1.30	*Selago multiflora* Hilliard	$y=4782.3x+313.47$	0.94	87.5
t1.31	*Selago scabribracteata* Hilliard	$y=6446.9x-535.65$	0.89	72.8
t1.32	*Senecio cinerascens*	$y=4779.2x-6.8515$	0.79	30.9
t1.33				
t1.34	**Dwarf succulent shrub**			
t1.35	*Antimima compacta* (L.Bolus) H.E.K.Hartmann	$y=140\,469x+24.56$	0.56	34.8
t1.36	*Antimima pusilla*	$y=120\,389x-1.41$	0.71	54.8
t1.37	Antimima spp.	$y=78\,913x-107.63$	0.96	53.3
t1.38	*Cephalophyllum ebracteatum* (Schltr. & Diels) Dinteer & Schwantes	$y=163\,990x+144.63$	0.66	21.8
t1.39	*Cheiridopsis denticulata* (Haw.) N.E.Br.	$y=310\,291x+65.78$	0.89	32.9
t1.40	*Cheiridopsis namaquensis* (Sond.) H.E.K.Hartmann	$y=912\,116x+33.05$	0.65	58.1
t1.41	*Conicosia elongata* (Haw.) N.E.Br.	$y=49\,839x+42.06$	0.73	11.8
t1.42	*Drosanthemum brevifolium* (Aiton) Schwantes	$y=18\,253x+47.24$	0.88	27.6
t1.43	*Drosanthemum hispidum* (L.) Schwantes	$y=823\,515x-19.78$	0.75	21.5
t1.44	*Drosanthemum oculatum* L.Bolus	$y=21\,790x+107.55$	0.94	40.0
t1.45	*Drosanthemum schoenlandianum* (Schltr.) L.Bolus	$y=65\,894x+3.06$	0.97	24.0
t1.46	*Ruschia fugitans* L.Bolus	$y=0.92x+5.18*$	0.73	33.5
t1.47	*Ruschia macownii=Ruschia kheis*	$y=116\,870x+1.94$	0.88	18.8
t1.48	*Ruschia viridifolia* L.Bolus	$y=95\,979x+69.67$	0.97	26.2
t1.49				
t1.50	**Succulent shrub**			
t1.51	*Antimima subtruncata* (L.Bolus) H.E.K.Hartmann	$y=15\,353x+328.71$	0.71	14.1
t1.52	*Aridaria brevicarpa* L.Bolus	$y=15\,528x+262.42$	0.78	45.2
t1.53	*Euphorbia decussata* E.Mey. Ex Boiss.	$y=26\,038x+12.35$	0.69	31.2
t1.54	*Euphorbia mauritanica* L. var. mauritanica	$y=1.01x+4.64*$	0.89	20.4
t1.55	*Kleinia longiflora* DC.	$y=8797.9x+1238$	0.79	29.4
t1.56	*Lampranthus otzenianus* (Dinter) Friedrich	$y=9724.1x+102.72$	0.66	62.9
t1.57	*Leipoldtia laxa* L. Bolus	$y=74\,901x+8.99$	0.96	18.7
t1.58	*Leipoldtia schultzei* (Schltr. & Diels) Friedrich	$y=9781.6x+29.74$	0.89	33.5
t1.59	*Othonna floribunda* Schltr.	$y=1584.3x+776.93$	0.96	71.8
t1.60	*Polymita albiflora* (L.Bolus) L.Bolus	$y=129\,243x+41.2$	0.6	40.5
t1.61	*Ruschia brakdamensis* (L.Bolus) L.Bolus	$y=13\,119x-47.82$	0.84	32.5
t1.62	*Ruschia crassisepala* L.Bolus	$y=23\,391x+449.2$	0.75	43.7
t1.63	*Ruschia goodiae* L.Bolus	$y=0.81x+4.60$	0.85	25.1
t1.64	*Ruschia lerouxiae* (L.Bolus) L.Bolus	$y=17\,717x+26.77$	0.81	26.1
t1.65	*Ruschia robusta* L.Bolus	$y=6331x+17.26$	0.85	43.8
t1.66	*Ruschia stricta* L.Bolus	$y=21\,735x+3.19$	0.99	15.4

t1.67 Table 1 (*continued*)

Species	Regression equation	r^2	% dry weight
Succulent shrub			
Stoeberia beetzii (Dinter) Dinter & Schwantes	$y=9133.3x+1616.5$	0.85	23.5
Zygophyllum cordifolium L.f.	$y=0.79x+3.96*$	0.72	63.1
Zygophyllum morgsana L.	$y=16003x+132.38$	0.96	45.7
Zygophyllum retrofractum Thunb.	$y=45086x+218.77$	0.71	50.6
Woody shrub			
Antizoma miersiana Harv.	$y=2408.4x+578.88$	0.69	66.6
Berkheya spinossisima (L. f.) Druce	$y=2101.1x+38.69$	0.96	38.2
Cadaba aphylla (Thunb.) Wild	$y=9820.9x+429.98$	0.82	73.2
Cliffortia ruscifolia L. var. ruscifolia	$y=2231.4x+77.18$	0.64	82.9
Clutia thunbergii Sond.	$y=8993.9x+379.52$	0.95	87.8
Coleonema juniperinum Sond.	$y=1669.6x+481.68$	0.54	55.1
Dicerothamnus rhinocerotis (L. f.) Koekemoer	$y=1128.5x+787.09$	0.83	78.3
Didelta spinosa (L.f.) Aiton	$y=2633.4x+393.78$	0.87	70.4
Dimorphotheca cuneata (Thunb.) Less.	$y=8933.1x-90.71$	0.84	80.3
Diospyros glabra (L.) De Winter	$y=3523.3x+57.69$	0.85	83.4
Dodonaea viscosa Jacq. var.angustifolia	$y=1110.7x+925.16$	0.88	74.0
Dyerophytum africanum Kuntze	$y=2376.5x+310.38$	0.72	78.4
Eriocephalus ericoides (L. f.) Druce subsp. Ericoides	$y=10434x+0.16$	0.84	74.6
Euryops laterifolius (L.f.) DC.	$y=0.8x+3.8$	0.98	67.9
Galenia africana L.	$y=4249.2x+12.53$	0.93	71.9
Hermannia cuneifolia Jacq. Var. cuneifolia	$y=1603.7x+10.34$	0.81	85.7
Hermannia disermifolia	$y=9422.9x+3.47$	0.97	68.6
Hermannia rigida Harv.	$y=1357.1x+167.04$	0.95	70.8
Hermannia sp. Kheis	$y=3953.5x-23.96$	0.98	54.6
Hermannia trifurca L.	$y=11773x-1.08$	0.99	48.4
Indigofera nigromontana Eckl. & Zeyh.	$y=4363.7x+77.92$	0.86	78.4
Lebeckia cinerea E.Mey.	$y=1.0595x+3.5*$	0.75	56.2
Lebeckia multiflora E.Mey.	$y=5190x+227.51$	0.77	59.1
Lycium ferocissimum Miers	$y=11703x+58.85$	0.92	59.6
Monechma spartioides (T.Anderson) C.B. Clarek	$y=6446.9x-535.65$	0.89	72.8
Montinia caryophyllaceae Thunb.	$y=2273.1x+50.59$	0.89	70.6
Oederoa genistifolia (L.) Anderb. & K.Bremer	$y=2235.5x+124.55$	0.88	74.2
Pteronia incana (Burm.) DC.	$y=8170.7x-337.05$	0.71	72.4
Pteronia inflexa Thunb. Ex L.f.	$y=7733x-98.24$	0.76	90.3
Rhus horrida Eckl. & Zeyh.	$y=4352.1x+7.63$	0.98	83.3
Rhus incisa L. f. var. effusa (C.Presl) R.Fern.	$y=4555.3x+259.03$	0.91	78.6
Rhus undulata Jacq.	$y=5638x+70.12$	0.93	67.9
Salsola grey tight leaves	$y=24201x+9.17$	0.98	68.2
Stachys rugosa Aiton	$y=429.29x+26.27$	0.63	65.4
Struthiola leptantha Bolus	$y=3380x-87.86$	0.86	81.6
Tripteris sinuata DC. Var. sinuata	$y=6638.9x+26.27$	0.92	49.6

219 significance of the volume-biomass regression (marked with
220 asterisk (*) in Table 1). This was in turn converted to dry biomass.
221 After adding all species for a particular site accounting for 80% of
222 the cover, this was extrapolated to dry mass for 1 ha. For general
223 data measures across the Kamiesberg private data are used as a
224 proxy for a 'natural' system, since these lands are less heavily
225 stocked (Todd and Hoffman, 2000; Anderson and Hoffman,
226 2007). Communal data are used for consideration of the grazing
227 impact only.

228 Species were attributed palatability ratings (1 = unpalatable,
229 2 = moderately palatable, 3 = highly palatable) based on available
230 literature and expert knowledge. Expert knowledge was obtained
231 from local herders and botanists who are active in the Kamiesberg
232 area. For each site the biomasses of unpalatable, moderately
233 palatable and highly palatable species was determined.

234 A paired Wilcoxon sign-rank test was used to test for sig-
235 nificant differences in the grazing scores.

236 In examining differences between vegetation types, and
237 between upland and lowland habitats, data were found to be
238 non-normal and the Kruskal–Wallis test was used to test
239 for significant differences. A paired Wilcoxon sign-ranks test
240 was used to test for significant differences in total biomass and
241 biomass graded according to palatability on either side of the
242 fence (Zar, 1996). Multiple comparisons of mean tests were used
243 for a post-hoc comparison in the case of nonparametric tests.

3. Results

244

3.1. Grazing score

245

246 In accordance with the mean stocking rates for the greater
247 Leliefontein reserve (Todd and Hoffman, 2000), the mean
248 grazing score was significantly higher on the communal
249 area.

3.2. Biomass for different vegetation types

A total of 94 species was sampled and volume-biomass regressions, and wet:dry weight ratios, generated (Table 1).

Standing perennial biomass for the lowland areas of the private rangeland ranged from 3292 kg per hectare for a Heuweltjieveld site to 19 780 kg per hectare for a Renosterveld site. Upland equivalents ranged from 3728 kg per hectare for a Western klipkoppe site to 25 645 kg per hectare for a Mountain shrubland site (Fig. 2). Total biomass varied significantly across all sites ($n=32$, $H=19.02$, $p<0.005$). A post-hoc comparison shows a broad grouping of the Western Klipkoppe and Heuweltjieveld vegetation types to the west as having the lowest biomass, the Mountain Shrubland and Renosterveld as having the highest biomass, and the Eastern Klipkoppe and Bushmanland Ecotone vegetation types to the east as being intermediate.

The dwarf succulent shrub *C. elongata* has the highest moisture content at 88% of its total weight and the woody shrub *Pteronia inflexa* had the lowest at 9.7%. The ratio of wet to dry weight varied considerably across the different growth forms. Mean moisture content as a measure of plant weight in herbaceous shrubs is 45% ($\pm$SD$=24$, $n=21$), for grasses is 23% ($\pm$SD$=6.7$, $n=18$), for dwarf shrubs is 38% ($\pm$SD$=19$, $n=33$), for dwarf succulent shrubs is 67% ($\pm$SD$=14$, $n=40$), for succulent shrubs is 63% ($\pm$SD$=16$, $n=60$) and for woody shrubs is 29% ($\pm$SD$=12$, $n=102$).

3.3. Biomass contrasted between lowland and upland sites

Perennial standing biomass as measured on the sandy lowland areas is consistently less that the rocky upland equivalent in each vegetation type (Fig. 3) ($n=32$, $H=7.08$, $p<0.005$). Comparisons within habitat type also vary significantly (lowland: $n=15$, $H=10.4$, $p<0.05$, uplands: $n=17$, $H=12.14$, $p<0.05$). A multiple comparison of means shows this difference in both the lowland and uplands to lie between the Western klipkoppe and Renosterveld vegetation types for the lowlands and the uplands, with the addition of difference between Western klipkoppe and Mountain shrubland for the uplands.
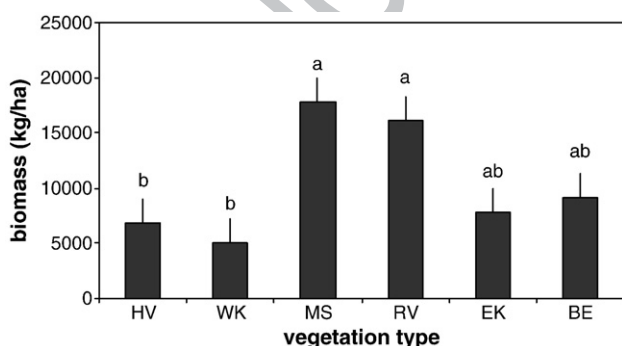

Fig. 2. Mean standing perennial biomass for six vegetation types ($\pm$SE), organised in a west–east direction along the x-axis, across the Kamiesberg Mountain range (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, and BE = Bushmanland ecotone). Post-hoc comparisons, indicated with superscripts, are based on a multiple comparison of means test.
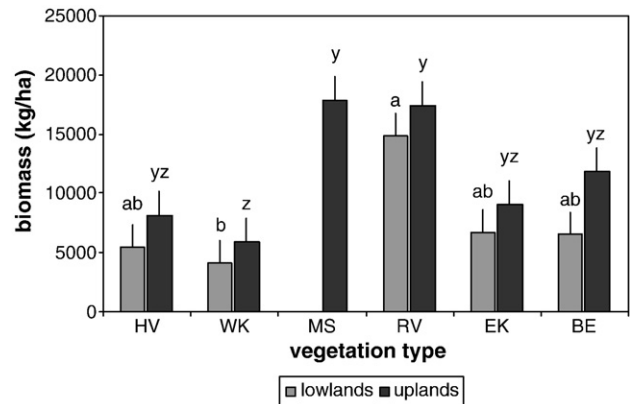

Fig. 3. Mean perennial standing biomass ($\pm$SE), for lowland and upland components of the vegetation different types across the Kamiesberg Mountain range (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, and BE = Bushmanland ecotone). Post-hoc comparisons, indicated with superscripts, are based on a multiple comparison of means test, with a and b indicating significant differences on the lowlands, and y and z indicating significant differences on the uplands.

3.4. Biomass across the communal-private fence line

Biomass was consistently lower on the communal rangeland compared with the private rangeland (Fig. 4a and b). Communal lowland figures range from 459 kg per hectare for an Eastern klipkoppe site to 16 216 kg per hectare for a Renosterveld site. Biomass figures for the communal uplands ranged from 1990 kg for an Eastern klipkoppe site to 22 439 kg per hectare for a Mountain shrubland site. Biomass was significantly lower for all paired communal lowland sites ($n=33$, $T=23.0$, $z=2.101$, $p<0.05$). This was with the exception of the Renosterveld where high variability on the communal range rendered the data nonparametric and no significant difference was found. While the same trend appears to be evident on the uplands, the relationship was not significant.

3.5. Palatability results

Highly palatable biomass was significantly higher on the private rangeland than the communal rangeland ($T=106.00$, $z=2.60$, $p<0.01$) (Fig. 5). Biomass of unpalatable and moderately palatable species did not differ significantly as a function of land use (Fig. 6). Losses in biomass on the communal range include reductions in notable palatable species such as *Hypertelis salsoloides*, *H. alienatum*, *Pentzia incana*, *C. denticulate*, *E. barbinodis*, *Hermannia cuneifolia* and species of Salsola.

4. Discussion

4.1. Perennial standing biomass of the Kamiesberg

The use of linear regressions based on allometric relationships established between biomass and an easily measured variable, in this instance volume, proved effective (Flombaum and Sala, 2007), with our biomass estimates in keeping with other researchers' findings (Table 2; Catchpole and Wheeler,
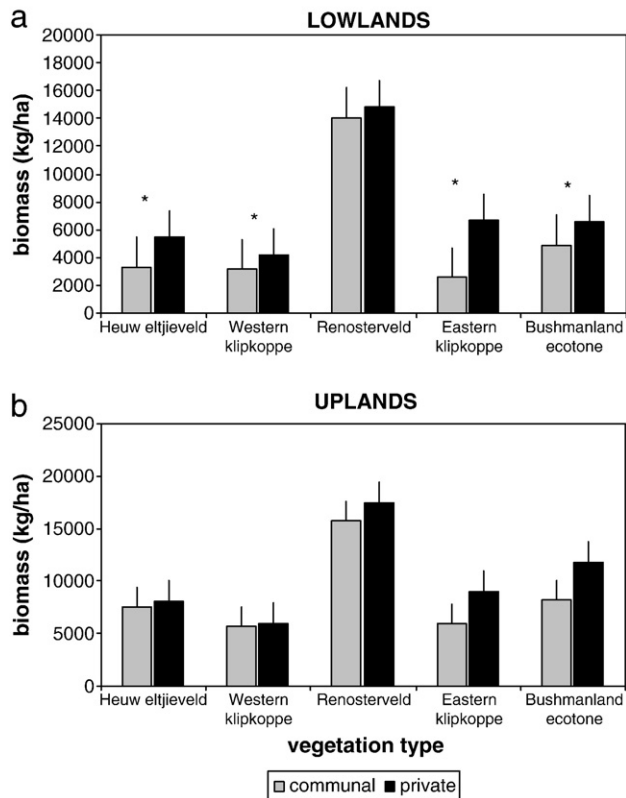
Fig. 6. The distribution of highly palatable biomass (±SE) on the communal and private range according to habitat type. Post-hoc comparisons, indicated with superscripts, are based on a multiple comparisons of means test.

Fig. 4. a and b. Mean standing perennial biomass (±SE), for communal and private rangelands for six different vegetation types across the Kamiesberg Mountain range, for (a) lowland and (b) upland habitats (HV = Heuweltjieveld, WK = Western klipkoppe, MS = Mountain shrubland, RV = Renosterveld, EK = Eastern klipkoppe, and BE = Bushmanland ecotone). Significant differences between paired sites in each vegetation types are indicated with an asterisk (*).

1992). Biomass for the Heuweltjieveld is in agreement with equivalent measures while Mountain shrubland and Renosterveld vegetation types fall in the middle of the range given for Fynbos (Werger and Morris, 1991; Richardson and Cowling, 1992). Measures for the Eastern and Western klipkoppe are in some instances higher, some instances lower, and in the case of a Western klipkoppe measure, exactly the same as, equivalent measures (Werger and Morris, 1991; O'Farrell et al., 2007;
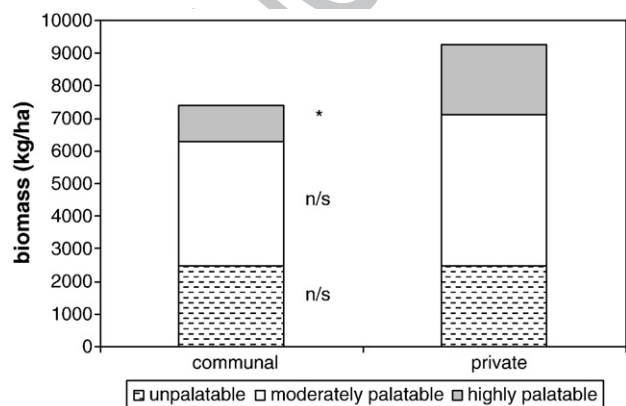

Fig. 5. Cumulative standing perennial biomass of unpalatable, moderately palatable and highly palatable species on communal and private rangeland. Asterisk (*) indicates a significant difference at $p < 0.01$.
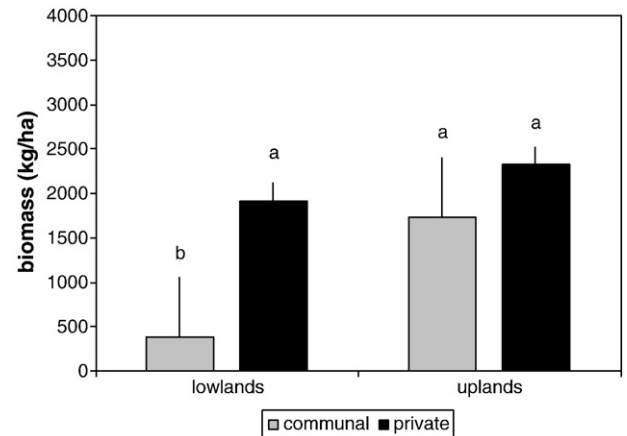
Carrick pers. com.). Biomass measured on the Bushmanland ecotone lowlands is considerably higher than the 'equivalent' measure given here taken from a Nama-karoo grassland site. This may be an inappropriate comparison where the measure of Skowno (2003) is from the Great Karoo and Central Lower Karoo subdivision and characterised as an arid shrubland, while the site in this project falls in the Griqualand West and Bushmanland subdivision of the Nama-karoo biome characterised by arid grasslands (Palmer and Hoffman, 1997; Skowno, 2003). While measures are generally comparable, variability exists between measures in this study and those in the literature. Reasons for this can be explained by the use of different techniques, the heterogeneous nature of the Karoo vegetation and in particular the Kamiesberg vegetation, and the variable and imperfect nature of standing biomass measurements (Beatley, 1969). The range of values in the literature generally is large, and points to both the difficulty of measuring biomass and the high degree of variability in plant biomass. The incorporation of a large number of species was at the expense of greater sample numbers in each instance. Larger sample numbers would serve to refine the values generated.

The vegetation types broadly divide out in terms of their relative biomass into a mountain top, and then western and eastern regions, in accordance with broad-scale rainfall. Interestingly, biomass is greatest not at the wettest part of the Kamiesberg where the Renosterveld grows as perhaps anticipated (Noy-Meir, 1973), but on the western slopes of the mountain, in the Mountain shrubland vegetation. This is likely to be a function of the combination of higher rainfall, warmer temperatures and deeper soils on the lower slopes than on the rocky peaks (Anderson, 2008). In examining primary productivity in semi-arid and arid systems, the role of smaller scale processes has been highlighted. Le Houerou et al. (1988) found that while annual and seasonal productivity was closely tied to rainfall, variability in productivity was 1.5 times higher than variability in rainfall. The relationship between productivity, or in this study standing biomass, and rainfall cannot be assumed to be linear (Le Houerou and Hoste, 1977; Ludwig, 1987; Le Houerou et al., 1988).

It was disappointing not to have been in a position to include annual cover which was negligible as a result of the low rainfall

t2.1 Table 2
t2.2 Biomass values from previous studies for comparative purposes.

Vegetation type	'Equivalent' vegetation type in current study	Biomass (kg/ha^{-1})	Author
Eastern Klipkoppe lowlands	Eastern klipkoppe lowlands	±2500	(Carrick pers.com.)
Nama and Succulent Karoo Biomes	Broadly all vegetation types included in study	500–7600	(Rutherford, 1986)
Nama Karoo	Bushmanland ectone lowlands	3449	(Skowno, 2003)
Tierberg	Eastern klipkoppe lowlands	3268	(Milton, 1990)
Namaqualand coastal belt	Heuweltjieveld	8100	(Werger and Morris, 1991)
Western mountain Karoo	Western klipkoppe	5200	(Werger and Morris, 1991)
Dolerite koppie veld	Eastern and Western klipkoppe uplands	6000	(O'Farrell, 2005)
Mountain fynbos	Renosterveld and Mountain shrubland	15 000–51 000	(Richardson and Cowling, 1992)
Niewoudtville Karoo veld	Eastern and Western klipkoppe lowlands	12 000	(O'Farrell, 2005)

in both years of sampling. However, this is symptomatic of the region, where drought or the timing of rainfall means the production of annual cover is highly variable (Esler, 1999; Samuels et al., 2007). This variability is proliferated through the year as conditions will also affect reproductive allocation where annuals may germinate but have reduced reproductive output due to water stress later in the season (Van Rooyen et al., 1991). Indeed the failure of annuals under certain rainfall conditions is described as a feature of semi-arid systems (e.g. Beatley, 1969; O'Connor and Roux, 1995). The fact that annuals could not be included in this study serves to demonstrate the importance of perennial cover for sustained grazing where annual cover cannot be depended on. This supports the view that compositional shifts in response to grazing couples a system more tightly to rainfall and, potentially places farmers at greater risk (Anderson and Hoffman, 2007).

The moisture content of species sampled is for the most part in keeping with the findings of Milton (1990) who collected and dried a number of species in the southern Karoo. The outer values in this current study were slightly lower, possibly a function of the time of sampling, as Milton sampled in winter. Plant moisture content is an important aspect of forage, influencing how frequently animals will need to access surface water (Owen-Smith, 1999). This is evident where stock keepers move stock posts closer to water points during the dry season and droughts (Hendricks et al., 2005). Succulents are described as making a significant contribution to animal water balance (Owen-Smith, 1999). With intense grazing pressure there may be a reduction in, or complete loss of, species with high moisture content, and this aspect of biomass loss will in turn have implications in how pastoralists use the rangeland.

4.2. Biomass contrasted between lowland and upland sites

Plant composition is different on rocky upland areas as a function of environmental variables such as greater soil moisture due to run-on as a result of higher rock cover and elevated soil nutrient status (Ludwig, 1987; Burke, 2001; Petersen et al., 2004). The rocky upland areas are home to the limited tree species found in Namaqualand, such as several species of Rhus recorded in this study. While the extensive rock cover at each site means plant cover is less on the uplands, biomass is consistently greater. These steep rocky areas are also known to be less heavily grazed than their lowland equivalents due to their frequently

inaccessible nature (Cowling et al., 1994; Riginos and Hoffman, 2003; Petersen et al., 2004; Pienaar et al., 2004; Samuels et al., 2007). The leaves of trees are noted for retaining water through dry periods, making them an appealing forage source for browsers, such as goats, during drought (Owen-Smith, 1999). These areas serve as key resource areas for use in the dry season or times of drought (Illius and O'Connor, 1999; Petersen et al., 2004; Samuels et al., 2007).

The significant difference between the Western Klipkoppe and the Renosterveld for both lowland and upland areas, and the Mountain Shrubland in terms of upland areas, could possibly be attributed to the orographic-induced rainfall. The failure to find a similar result between the Heuweltjieveld, which also sits to the west of the mountain range, and these vegetation types however puts this suggestion in doubt. Contributing factors could be variable community composition, sampling errors, or more intense grazing of the Western Klipkoppe. Of most interest though is the fact that for the majority of the sites, the difference in biomass is between the upland and lowland habitats and less so than between the different vegetation types. This serves to once again highlight the degree of habitat variability in the landscape where this habitat induced mosaic sees excessive exploitation of the lowlands due to accessibility, while the upland areas serve as biomass reserves, or key resource areas.

4.3. Biomass across the communal-private fence line

The sustained heavy grazing associated with the communal range, reported previously in relation to plant community composition for the same area (Anderson and Hoffman, 2007), is once again evident, on the basis of the methods used in this study, in the significant loss of biomass on the communal lowlands. This is also in keeping with findings of losses of plant guilds with shifts from woody perennial dominated cover to smaller more ephemeral species on the communal range, on a smaller scale within the study site (Todd and Hoffman, 1999) and internationally (Fernandez-Gimenez and Allen-Diaz, 1999; Brathen and Oksanen, 2001; Hickman and Hartnett, 2002; Marcelo et al., 2003; Foroughbakhch et al., 2005). This may in turn have implications for those who depend on the natural vegetation for their livelihoods through stock farming (Dube and Pickup, 2001; Foroughbakhch et al., 2005; Reynolds et al., 2007). The lack of a significant difference in the Renosterveld vegetation between the communal and private rangeland is

attributed to the fact that livestock are generally moved out of this area, by both communal and private livestock keepers, in winter (Samuels, per comm. 2009). This would result in a lighter, and more similar, stocking rate on both sides of the fence. In fact, high mobility among private farmers, who tend to have more than one farm between which they will move seasonally (Smith, 1999; Rohde et al., 2006; O'Farrell et al., 2007), would be a contributing factor to the lower experienced stocking rates on the private rangeland. While communal livestock keepers move their stock off the mountain in winter, this large-scale pattern of movement is not expressed elsewhere on the Leliefontein commonage.

The fact that upland biomass on the communal range does not differ significantly from that of the private range corroborates the idea that the upland areas are buffered from the intense grazing pressure associated with the lowland areas, due to their less accessible nature (Petersen et al., 2004; Samuels et al., 2007). While not examined in this study, the lack of any significant difference in the biomass of the communal and private upland areas, which host the few woody species in the region, would suggest that loss of biomass to firewood collection is either ubiquitous across these land tenure types or on a scale that does not register. An examination of fire wood collection would naturally be structured differently, but these current findings point to the fact that, in this study, fire wood collection is not affecting the presented results.

4.4. Standing perennial biomass and palatability

There is considerable literature which demonstrates that sustained heavy grazing results in an increase in unpalatable plants where selective pressure indirectly favours co-occurring species through competitive release (West, 1993; James et al., 1999; Todd and Hoffman, 1999; Hickman and Hartnett, 2002; Riginos and Hoffman, 2003; Foroughbakhch et al., 2005; Diaz et al., 2007). This competitive release can be through reduced reproductive output as flowers or seed pods are grazed, reduced plant size and associated photosynthetic potential, or the complete removal of entire individuals (Hickman and Hartnett, 2002; Marcelo et al., 2003). The findings in this study confirm that the more palatable species are heavily utilized on the communal range, but contrary to what might be anticipated, do not show any evidence of an increase in unpalatable species. There are also reports of increases in the unpalatable species *Galenia africana* on the communal rangeland both anecdotally and in studies in the Eastern klipkoppe vegetation, but this is not evident in this study (Allsopp, 1999). It is possible that this species has a close association with old ploughed lands, which were excluded in this study (Allsopp, 1999). Recent work, also in the Eastern klipkoppe vegetation, shows a close association between *G. africana* and soil depth, perhaps limiting this reported grazing response to areas of deeper soils (Petersen, pers. com.). The findings of this current study suggest a very static or sluggish system where there is the apparent loss of one suite of species with no evident community response.

Previous work in the area, and internationally, has shown that annual plants are favoured by this competitive release and proliferate in the open spaces generated by heavy grazing given good and well-timed rainfall (Todd and Hoffman, 1999; Diaz et al., 2007). While not measured in this study, this is apparently the response to grazing. While annuals present good forage quality, their very short-lived nature means that in attributing their overall grazing value they do not score particularly well (Todd and Hoffman, 2000; Botha et al., 2001). Botha et al. (2001), in establishing grazing index values for a number of karoo plants, incorporate a 'nutritional value during the dormant season,' and 'degree of perenniality' scores, both of which greatly reduce the grazing index value of annual species. Annuals are described as sensitive to disturbance. Studies from the Sahel show a shift from perennial grasslands to annual dominated vegetation in response to heavy grazing. The collapse of the annual 'forage' in response to low rainfall led to a period of famine, and desertification (Van de Koppel et al., 1997). While annuals may present high forage quality, their presence is short-lived and unreliable. Small fluctuations in environmental parameters can lead to relatively large shifts in vegetation states, posing considerable risk to those depending on this resource for their livelihoods (Van de Koppel et al., 1997).

The question remains as to why no perennial unpalatable species are filling the gap created by the heavy grazing on the communal range. It may be that the advantage of a higher and earlier reproductive response of the *r*-selected annual species allows them to out-compete perennial species in colonising available open ground (Grime, 2001). Work on grazing effects in Kansas prairies showed that perennial plants contributed only 3% to the seed bank, giving the annual species a significant competitive advantage (Marcelo et al., 2003). Work in serpentine grasslands in California demonstrated the competitive vigour of annual seedlings where high annual numbers significantly reduced bunchgrass biomass (Hooper, 1998). In this study area the lowland areas are described as heavily utilized during the growing season, in particular on the communal range, further limiting the success of those few perennial seedlings attempting to emerge or establish during this time (Petersen et al., 2004). Or it is possible that the nature of the semi-arid system, where water is the primary limiting factor, means competition is not a driving force. In this instance perennials would only be in a position to germinate and establish in particularly favourable conditions. However, this would be counter to the belief that the proliferation of unpalatable species in response to grazing is in fact more common in arid systems than humid ones (Diaz et al., 2007). Work on grazing by reindeer found the same results as in this study, where the only significant change in biomass was in the loss of highly palatable species (Brathen and Oksanen, 2001). In their study, and indeed in others, researchers attribute responses to the highly individual nature of plant responses to grazing. Plants are allocated to increaser and decreaser categories, described as falling on a continuum from negative to over-compensatory in response, and intraspecifically variable in their direct and indirect responses to grazing (Beatley, 1969; Brathen and Oksanen, 2001; Hickman and Hartnett, 2002; Jauffret and Lavorel, 2003; Marcelo et al., 2003). In addition to palatability, factors such as community composition and associated interspecific variability in architecture, phenology, and local abundance may also vary (Hickman

and Hartnett, 2002). A study looking at grazing by different native ungulates in shrubsteppe communities demonstrates the importance of the grazers in question, where different animals will graze plants variably (Rexroad et al., 2007). The nature of grazing is relevant in determining the type of community response (Fernandez et al., 1993). Evidently plant-herbivore interactions are complex, compounding the scope for ready interpretation and generalisations.

The appearance of unpalatable species is a common indicator of degraded range condition (Owen-Smith, 1999). Whatever the driver, these findings demonstrate that in this system the absence of highly palatable species, rather than the presence of unpalatable species, would make a more effective rangeland condition indicator (Todd, 2006).

5. Conclusions

In comparison to other studies, and in terms of relative measures, this study demonstrates the effective use of linear regressions based on allometric relationships where values for standing perennial biomass were generated for the vegetation types under consideration. The regressions generated here, as well as the broader biomass values, may be effectively used in future modelling or comparative exercises.

Biomass is significantly higher on the mountain top, in association with available moisture. Smaller-scale differences between vegetation types point to the importance of other factors in driving biomass. A key finding of this study is the significant difference between the biomass of the upland and lowland habitats, pointing to the potential importance of the upland areas as key resource areas in times of drought. In terms of variable biomass this mosaic of upland and lowland habitats is a significant overlay on the landscape and a function that must be included in landscape level management and conservation research and plans. On a smaller scale the highly variable moisture content of the different plants sampled suggest that community composition could be of importance in withstanding drought. This is in keeping with previous studies which note the danger of shifts in community composition and associated risk to livestock keepers, and warrants further investigation.

Building on previously reported work examining the impact of sustained heavy grazing on this rangeland, this study shows a significant reduction in biomass on the communal range on the highly accessible sandy lowland areas virtually throughout the Kamiesberg. While there may be an associated increase in annual species on the communal range, this biomass is short-lived and does not compensate for the loss of the more persistent perennial species. Where this difference is absent it is attributed to large-scale mobility patterns, serving to reduce the stocking rate. While this is restricted to one vegetation type on the communal rangeland, it is a common practice on the surrounding privately-owned farms and could be a contributing factor to the lower stocking rates and evident shifts in biomass.

The loss in biomass is principally of highly palatable species, with no evidence of a competitive response from other perennial species to this loss, although the proliferation of annuals on the open ground of communal rangelands is well documented. As an intrinsic response to abiotic and biotic drivers, perennial biomass measured in this study tells us two things. Environmental variability across the Kamiesberg results in highly heterogeneous biomass at a broad scale in response to variable rainfall and more locally in response to habitat variability. Secondly the sustained heavy grazing associated with the communal rangelands is degrading the lowland areas.

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Edited by RI Yeaton