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# Impact of *Prosopis* (mesquite) invasion and clearing on the grazing capacity of semiarid Nama Karoo rangeland, South Africa

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We assessed the impact of *Prosopis* invasion and clearing on the grazing capacity of heavily grazed Nama Karoo rangeland in the Beaufort West district of the Western Cape province of South Africa. Invasion (c. 15% *Prosopis* canopy cover) reduced grazing capacity by 34%, whereas clearing improved it by 110% within six years. Much of the loss in grazing capacity during invasion was due to the displacement of the annual grass *Aristida adscensionis* that dominated herbaceous forage production at the study site. Improvement in rangeland grazing capacity after *Prosopis* clearing was due to increases in abundance of *A. adscensionis*, the perennial grass *Cynodon dactylon* and the establishment of the perennial grasses *Eragrostis obtusa* and *Eragrostis lehmanniana*. Grazing capacity in cleared rangeland was 39% higher than in uninvaded rangeland due to a higher abundance of the annual grasses *A. adscensionis*, *Chloris virgata*, *Setaria verticillata* and *Tragus berteronianus* and the perennial grasses *E. obtusa*, *E. lehmanniana* and *C. dactylon*. Our results indicate that *Prosopis* invasion (>13% mean canopy cover) can lower grazing capacity in Nama Karoo rangeland, whereas clearing *Prosopis* from such rangeland can, even under heavy grazing, substantially improve grazing capacity within 4–6 years.

**Keywords:** exotic invasive plants, management, natural resources, rangeland condition, rehabilitation

## Introduction

There is considerable concern in South Africa over the impact of invasive alien plants (IAPs) on rangeland agricultural productivity (Milton et al. 2003, Macdonald 2004). Over 8% (>10 million ha) of South Africa is covered by IAPs (Binns et al. 2001, van Wilgen et al. 2001) and much of the affected area is natural rangeland (Richardson and van Wilgen 2004). Livestock production on natural rangeland is the most widespread form of land use in South Africa (Milton et al. 2003, Macdonald 2004) and contributes substantially to national employment and gross domestic product. IAPs can drastically reduce livestock production by lowering rangeland grazing capacity through suppressing and displacing important indigenous forage species (Milton et al. 2003, Richardson and van Wilgen 2004).

The Nama Karoo is the largest of the three biomes comprising the Karoo–Namib ecoregion and covers 22.7% of the interior of southern Africa (Palmer and Hoffman 1997). In South Africa, the Nama Karoo stretches from the central to the western parts of the country and supports an important small-stock industry that is based entirely on natural pasture (Palmer and Hoffman 1997). This industry is threatened by a diverse array of IAPs, which include cacti (*Opuntia* species), saltbushes (*Atriplex* species) and several woody shrub and tree species (Richardson and van Wilgen 2004). Most notable among these IAPs are leguminous trees of the genus *Prosopis*, which cover at least 18 000 km<sup>2</sup>

of the low-lying alluvial plains and seasonal watercourses in the Nama Karoo (Richardson and van Wilgen 2004). Some species of *Prosopis*, native to North and Central America, were introduced into the area in the late 1880s to provide shade, fodder and fuel wood (Zimmermann 1991, Zimmermann and Pasiecznik 2005). However, they have had serious negative environmental impacts (Zimmermann and Pasiecznik 2005). One such impact has been the widespread coalescing of infestations into large dense thickets that are thought to have suppressed and displaced indigenous forage species and reduced rangeland grazing capacity (Roberts 2006). Very few studies have attempted to assess and quantify the impact of such invasions on rangeland composition and grazing capacity.

Large areas in the Nama Karoo have been cleared of *Prosopis* trees under a government-led IAP control programme (Zimmermann and Pasiecznik 2005). The programme, called Working for Water (WfW), is principally aimed at securing threatened water resources by clearing IAPs from South Africa's major watersheds (Le Maitre et al. 2000, Binns et al. 2001, Le Maitre et al. 2002). Although the justification for the WfW programme has been explicitly based on its potential to deliver socioeconomic benefits through increased water supply and employment (van Wilgen et al. 1998, Binns et al. 2001, Anon 2006, Hope 2006) there is an implicit assumption that IAP removal will also facilitate

recovery of agricultural productivity in affected areas. This assumption has not, however, been empirically evaluated for *Prosopis* clearing activities in Nama Karoo rangeland.

IAPs are costly to clear and most private and state efforts have proved to be inadequate (Turpie 2004). In the Nama Karoo, where costs of *Prosopis* clearing often exceed the value of land (Zimmermann and Pasiecznik 2005), WfW provides the sole means of adequately tackling the IAP problem. However, the future extent of WfW clearings is uncertain as the WfW programme has to compete with other pressing government initiatives for funding (Turpie 2004). As the competing proposals are mostly developmental rather than environmental, WfW activities have to demonstrate their full socioeconomic worth to compete effectively (Turpie 2004). The benefits of clearing invasive *Prosopis* trees from Nama Karoo rangeland have not been adequately described in financial and economic terms. Ecological studies focused on assessing and quantifying the impact of *Prosopis* invasion and clearing on rangeland grazing capacity could provide a basis (Richardson and van Wilgen 2004, Turpie 2004, Blignaut 2010) for such economic and financial descriptions.

We assessed and quantified the impact of *Prosopis* invasion and clearing on the grazing capacity of heavily grazed and degraded Nama Karoo rangeland on two sheep farms in the Beaufort West district of the Western Cape province of South Africa. Our aims were to: (1) assess and quantify the impact of *Prosopis* invasion and clearance on rangeland grazing capacity, (2) identify and describe the vegetation dynamics that underlay grazing capacity changes following invasion and clearance, and (3) describe and quantify the response of rangeland grazing capacity to increasing *Prosopis* cover. To achieve these aims we addressed the following questions:

- (1) How did *Prosopis* invasion and clearing change the grazing capacity of affected rangeland?
- (2) What changes in plant functional type, species composition and abundance underlay the observed changes in grazing capacity?
- (3) How did grazing capacity respond to increase in *Prosopis* cover?

## Materials and methods

We use the generic term *Prosopis* because of the uncertainty surrounding *Prosopis* classification to species level in South Africa. A number of naturalised *Prosopis* species (notably *Prosopis glandulosa* Torr., *P. juliflora* (Sw.) DC. and *P. velutina* Wooton) have hybridised extensively (Zimmermann 1991) such that most populations in South Africa are composed of overlapping morphotypes that are difficult to classify into distinct species (Roberts 2006). Many South African studies have not attempted to classify *Prosopis* populations further than the general terms *Prosopis* or mesquite (Roberts 2006).

## Study site

The study was located on the farms 'Brandwag' (32°11'36" S, 22°48'19" E) and 'De Hoop' (32°10'13" S, 22°47'5" E). The vegetation is classified as Gamka Karoo with small areas of Southern Karoo Riviere, and Upper

Karoo Hardeveld (Mucina and Rutherford 2006). Gamka Karoo is characteristically dominated by dwarf shrub genera in the families Aizoaceae (*Drosanthemum* and *Ruschia*) and Asteraceae (*Eriocephalus*, *Pentzia* and *Pteronia*) interspersed with grasses (*Aristida*, *Enneapogon*, *Digitaria* and *Stipagrostis*) (Palmer and Hoffman 1997). Taller shrubs and trees (*Acacia karoo* Hayne, *Euclea undulata* Thunb. and *Rhigozum obovatum* Burch.) occur intermittently (Palmer and Hoffman 1997).

Mean annual rainfall is 239 mm (1878–2004, Kraaij and Milton 2006) but annual rainfall has been generally higher than the long-term average for the past eight years (2000–2008, Figure 1). Rainfall is highly seasonal with unimodal peaks occurring from December to March (Palmer and Hoffman 1997).

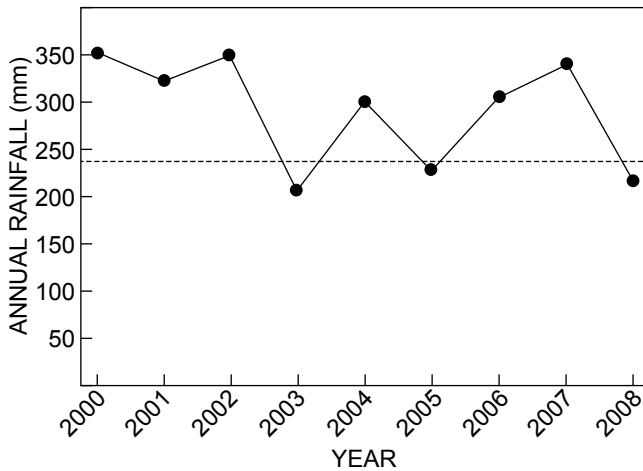
The Western Cape Department of Agriculture (WCDA) ran a five-year (2003–2007) manipulation experiment on Brandwag farm to monitor rangeland recovery after *Prosopis* removal. Six contiguous 50 m × 100 m plots were set up during the WCDA experiment (viz. uninvaded and fenced, uninvaded and unfenced, *Prosopis* infested and fenced, *Prosopis* infested and unfenced, cleared of *Prosopis* in 2003 and fenced, and cleared of *Prosopis* in 2003 and unfenced). Fenced plots excluded grazing and browsing livestock.

*Prosopis* clearing, carried out by a WfW team in March 2003, consisted of felling the trees at 100 mm above the ground and treating the stumps with the herbicide triclopyr ester 480 g a.i. at 4% dilution with diesel. Felled wood and branches were left lying in the field. There was no further intervention to facilitate the recovery of the cleared plots. The plots were monitored for five years for changes in plant density and species composition, soil moisture content, soil nutrients, seed bank composition, infiltration capacity and rate of erosion. When the WCDA experiment was terminated in 2007 the remaining *Prosopis*-infested plots were cleared and sections of the livestock enclosure fencing dismantled.

## Sampling and data collection

Field work was conducted in June and October 2009. Brandwag farm had been successively cleared of *Prosopis* by WfW teams in 2004 and 2005 and was completely cleared of *Prosopis* by the time field work was conducted. The same clearing method used at the WCDA experimental site was used during farm-wide clearings. In contrast, the neighbouring De Hoop farm was invaded by *Prosopis* stands of varying density and age.

Sampling was restricted to rangeland within Brandwag and De Hoop. In addition to two sampling plots (grazed and cleared in 2003 and grazed and uninvaded) from the WCDA experimental site, eight additional 50 m × 100 m plots (grazed and cleared in 2004, grazed and cleared in 2005, four grazed and uninvaded, and two grazed and invaded) were set up on replicate uninvaded, invaded and cleared sites identified on other parts of the farms. The additional sites were selected to match the WCDA experimental site conditions. We pooled data from plots cleared in 2003, 2004 and 2005 in our analyses. Clearing impacts reported in this study therefore relate to conditions 4–6 years after *Prosopis* clearing. All cleared sites ( $n = 3$ ) were located in



**Figure 1:** Annual rainfall for Beaufort West from 2000 to 2008 (South African Weather Service unpublished data). The dashed line represents long-term mean annual rainfall calculated over 126 years (1878–2004, Kraaij and Milton 2006)

Brandwag, whereas invaded sites ( $n = 2$ ) were restricted to De Hoop. The invaded sites had comparable *Prosopis* tree size class distributions and an average cover of 12.93%. Uninvaded sites ( $n = 5$ ) were located on both De Hoop and Brandwag.

Estimates of species cover were obtained using line-point intercepts (Herrick et al. 2005). In each plot, five 100 m transects were laid out at 10 m intervals along a 50 m east–west trending base line. Two 50-point line-point intercept readings were made along each 100 m transect using a 50 m tape. A total of 50, 20 and 30 50-point line point intercepts were set up on uninvaded, invaded and cleared sites, respectively.

### Data analysis

#### Grazing capacity

Grazing capacity values per transect were calculated using the grazing index method (du Toit 1995). This method uses estimates of plant species cover and grazing index values (GIVs) to calculate the current grazing capacity of rangeland in hectares per large stock unit ( $\text{ha LSU}^{-1}$ , du Toit 1995). The GIV of a species indicates its agronomic value in terms of the quality and quantity of its forage, its availability through the year, and the degree to which it protects soil from erosion (du Toit 1995). Species cover estimates per transect were computed from intercept scores by dividing the total number of intercepts of the species in the top or lower canopy layer by 50 and multiplying the product by 100 (Herrick et al. 2005). Species GIVs were collected from published sources (du Toit 2002, Esler et al. 2006). We expressed current grazing capacity as  $\text{LSU } 100 \text{ ha}^{-1}$  for ease of presentation.

#### Range condition scores

The contribution of a species to the transect range condition index (range condition score) was determined by multiplying its cover and GIV (du Toit 1995). The range condition scores of plant functional types were determined by

classifying species occurring along each line-point intercept transect into seven functional types (viz. annual grass, perennial grass, annual forb, perennial forb, succulent shrub, non-succulent shrub, and tree) using descriptions from published sources (Meredith 1955, Le Roux et al. 1994, Shearing and van Heerden 1994, Esler et al. 2006). The range condition scores for species grouped into a given functional type were added to give that functional type's contribution per transect. Range condition indices, which are calculated by adding the range condition scores of all species in a site, indicate the potential of a site to support grazing livestock (du Toit 1995).

### Statistical analyses

The impact of *Prosopis* invasion and clearing on the grazing capacity of rangeland was evaluated by comparing the mean current grazing capacities per transect of uninvaded vs invaded, invaded vs cleared, and uninvaded vs cleared plots. Differences in the mean grazing capacity between the plots were taken to represent the impacts of invasion, clearing and legacy effects respectively. Variation around the means was expressed in standard errors. The significance of the differences was assessed using one-way analysis of variance (ANOVA) and *post hoc* Tukey's pairwise comparisons. Differences were considered significant at  $p \leq 0.05$ . The Shapiro-Wilk test (Shapiro and Wilk 1965) was used to test for normality prior to the significance assessments. All analyses were conducted using the Paleontological Statistics Software Package for Education and Data Analysis (PAST; Hammer et al. 2001).

The vegetation dynamics that underlay grazing capacity changes following invasion and clearing were identified by analysing the significance of the differences in plant functional type and species mean range condition scores between uninvaded vs invaded, invaded vs cleared, and uninvaded vs cleared plots. Significant differences in mean range scores of plant functional groups and species between the plots were taken to be the result (and thus indicative) of the vegetation changes accompanying *Prosopis* invasion and clearing. Plant functional types whose mean range condition score differences tested significant were analysed to species level. The magnitudes and relative importance of the vegetation changes were evaluated by considering the changes in mean range condition scores associated with them. Means and standard errors were calculated using the program PAST, whereas the significance of differences in range condition scores was assessed using the one-way ANOVA via randomisation test in the software package Resampling Procedures 1.3 (David C Howell, University of Vermont, downloaded from <http://www.uvm.edu/dhowell/statPages/Resampling/Resampling.html>). Ten-thousand randomisations were run during each test and differences were considered significant at  $p \leq 0.05$ . Non-parametric randomisation (Manly 1997) was used because the data were non-normal. Normality was tested using the Shapiro-Wilk test (Shapiro and Wilk 1965).

The response of rangeland grazing capacity to increasing *Prosopis* cover was assessed by segmented (piecewise) linear regression using the program SegReg (RJ Oosterbaan, International Institute for Land Reclamation and Improvement; downloaded from

<http://www.waterlog.info/segreg.htm>). Segmented regression applies separate linear regressions to data by introducing one or more breakpoints (Oosterbaan 1994). SegReg selects the best-fitting break-point and linear regression function for a given data set from seven predefined models (Types 0–6; Oosterbaan 1994, 2005). The models are configured as follows: Type 0 is a single horizontal line without a breakpoint (no relationship), Type 1 is a single sloping line without breakpoint (linear regression), Type 2 is a succession of two connected segments with sloping lines, Type 3 is a horizontal segment followed by a sloping line, Type 4 is a sloping segment followed by a horizontal line, Type 5 is a step function with two horizontal segments with significantly different means, and Type 6 consists of two disconnected segments with sloping lines (Oosterbaan 1994, 2005). The selection for best fit in SegReg is based on significance and maximal explanation of variation (Oosterbaan 1994, 2005). Segmented regression was applied because *Prosopis* cover–grazing capacity relationships reportedly have threshold effects (McDaniel et al. 1982, Warren et al. 1996).

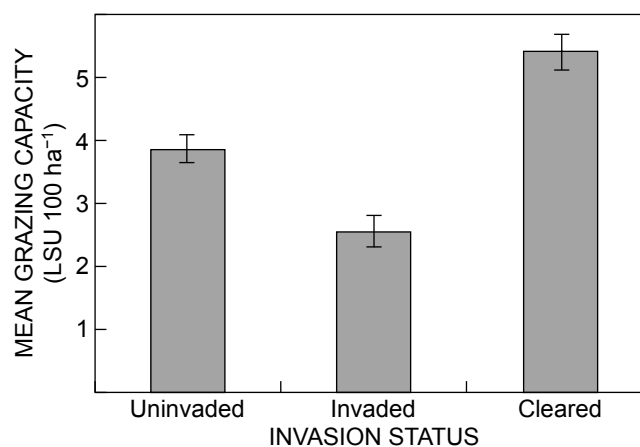
## Results

### Impact of *Prosopis* invasion and clearing on rangeland grazing capacity

Invasion by *Prosopis* (c. 15% canopy cover) reduced rangeland grazing capacity by 34%, whereas clearing, even under heavy grazing, improved it by 110% within four to six years (Figure 2). Average current grazing capacity on invaded sites ( $2.56 \pm 0.25$  LSU 100 ha<sup>-1</sup>) was 34% lower ( $F = 17.68$ ,  $P = 0.013$ ) than on uninvaded sites ( $3.87 \pm 0.21$  LSU 100 ha<sup>-1</sup>). Cleared sites had an average current grazing capacity ( $5.39 \pm 0.30$  LSU 100 ha<sup>-1</sup>) 110% higher ( $F = 17.68$ ,  $P < 0.001$ ) than invaded sites ( $2.56 \pm 0.25$  LSU 100 ha<sup>-1</sup>). Cleared rangeland had a grazing capacity that was significantly higher than uninvaded rangeland (Figure 2). The average grazing capacity in cleared sites ( $5.39 \pm 0.30$  LSU 100 ha<sup>-1</sup>) was 39% higher ( $F = 17.68$ ,  $P = 0.003$ ) than in uninvaded sites ( $3.87 \pm 0.21$  LSU 100 ha<sup>-1</sup>).

### Vegetation dynamics underlying changes in rangeland grazing capacity

Much of the loss in grazing capacity during invasion was caused by the displacement of the annual grass *Aristida adscensionis* L., which dominated herbaceous forage production in the study site. Invading *Prosopis* trees offset about 59% of the forage lost as a result of the displacement of *A. adscensionis*. Apart from *Prosopis* trees ( $F = 58.09$ ,  $P < 0.001$ ) (which contributed positively to grazing capacity during invasion), annual grasses were the only other functional group whose average range condition scores differed significantly ( $F = 10.91$ ,  $P = 0.001$ ) between uninvaded and invaded sites (Table 1). Of the four annual grasses present in the study area, only *A. adscensionis* differed significantly ( $F = 1.57$ ,  $P = 0.001$ ) in its average range condition score in uninvaded and invaded sites. *Aristida adscensionis* accounted for much of the range condition scores of annual grasses in uninvaded and invaded sites and also their greatest difference (Table 1). The difference between the average range condition scores



**Figure 2:** Mean current grazing capacities for uninvaded ( $n = 5$ ), invaded ( $n = 2$ ) and cleared ( $n = 3$ ) sites near Beaufort West in the Western Cape province of South Africa. The error bars are times one SE. All differences are significant at  $P \leq 0.05$  (one-way ANOVA;  $F = 17.68$ ,  $P < 0.001$  followed by Tukey's pairwise comparisons)

for *Prosopis* in uninvaded and invaded sites was lower than the difference for *A. adscensionis* (Table 1).

Most of the improvement in rangeland grazing capacity after *Prosopis* clearing was caused by increases in abundance of the annual grass *A. adscensionis*, the perennial grass *Cynodon dactylon* (L.) Pers. and the establishment of the perennial grasses *Eragrostis obtusa* Munro ex. Stampf and *E. lehmanniana* Nees. Annual grasses ( $F = 23.91$ ,  $P < 0.001$ ), perennial grasses ( $F = 14.95$ ,  $P = 0.001$ ), annual forbs ( $F = 5.32$ ,  $P = 0.020$ ), succulent shrubs ( $F = 13.91$ ,  $P = 0.002$ ) and *Prosopis* trees ( $F = 26.08$ ,  $P < 0.001$ ) had significantly different mean range condition scores in invaded and cleared sites (Table 2). However, at species level, only two annual grasses, *A. adscensionis* ( $F = 14.92$ ,  $P = 0.001$ ) and *Tragus berteronianus* Schult. ( $F = 4.53$ ,  $P = 0.039$ ) and three perennial grasses, *C. dactylon* ( $F = 5.04$ ,  $P = 0.026$ ), *E. obtusa* ( $F = 8.70$ ,  $P = 0.005$ ) and *E. lehmanniana* ( $F = 5.78$ ,  $P = 0.015$ ) had significantly different average range condition scores in invaded and cleared sites (Table 2). *Aristida adscensionis*, *C. dactylon*, *E. obtusa* and *E. lehmanniana* accounted for the bulk of the range condition scores of grasses in uninvaded and invaded sites and also the greatest differences (Table 2). Although the annual grass *T. berteronianus* re-established after clearing, its abundance was so low that it contributed very little to the increase in grazing capacity. The mean range condition scores for *T. berteronianus* in invaded and cleared sites and the difference between them were extremely small compared to the scores and differences for *A. adscensionis*, *C. dactylon*, *E. obtusa* and *E. lehmanniana* (Table 2). Annual forbs increased after clearing, whereas succulent shrubs declined but both had very little impact on grazing capacity as a result of their extremely low occurrences (Table 2). The loss of grazing capacity caused by the removal of *Prosopis* trees was smaller than the overall gain in grazing capacity that followed clearing (Table 2).

Grazing capacity in cleared rangeland was higher than in uninvaded rangeland as a result of higher abundance

**Table 1:** Mean range condition scores and SE for different plant functional types, and species in uninvaded ( $n = 5$ ) vs invaded ( $n = 2$ ) sites near Beaufort West in the Western Cape province of South Africa. Different superscript letters within a row denote significantly different values at  $P \leq 0.05$  (one-way ANOVA via randomisation)

Functional type and species	Uninvaded	Invaded	Difference
<b>Plant functional type</b>			
Annual grasses	27.97 ± 1.99 <sup>a</sup>	15.23 ± 2.25 <sup>b</sup>	-12.74
Perennial grasses	12.95 ± 2.20 <sup>a</sup>	4.59 ± 2.05 <sup>a</sup>	-8.36
Annual forbs	0.73 ± 0.25 <sup>a</sup>	0.11 ± 0.11 <sup>a</sup>	-0.62
Perennial forbs	0.49 ± 0.27 <sup>a</sup>	1.62 ± 0.85 <sup>a</sup>	1.13
Succulent shrubs	3.63 ± 0.9 <sup>a</sup>	3.58 ± 1.44 <sup>a</sup>	-0.05
Non-succulent shrubs	66.12 ± 6.13 <sup>a</sup>	51.66 ± 8.19 <sup>a</sup>	-14.46
Trees ( <i>Prosopis</i> )	0.03 ± 0.03 <sup>a</sup>	7.58 ± 1.85 <sup>b</sup>	7.55
<b>Annual grass species</b>			
<i>Aristida adscensionis</i>	24.79 ± 1.9 <sup>a</sup>	11.52 ± 2.48 <sup>b</sup>	-13.27
<i>Chloris virgata</i>	2.48 ± 0.55 <sup>a</sup>	3.20 ± 1.28 <sup>a</sup>	0.72
<i>Setaria verticillata</i>	0.23 ± 0.14 <sup>a</sup>	0.19 ± 0.19 <sup>a</sup>	-0.04
<i>Tragus berteronianus</i>	0.16 ± 0.09 <sup>a</sup>	0 <sup>a</sup>	-0.16

**Table 2:** Mean range condition scores and SE for different plant functional types, and species in invaded ( $n = 2$ ) vs cleared ( $n = 3$ ) sites near Beaufort West in the Western Cape province of South Africa. Different superscript letters within a row denote significantly different values at  $P \leq 0.05$  (one-way ANOVA via randomisation)

Functional type and species	Invaded	Cleared	Difference
<b>Plant functional type</b>			
Annual grasses	15.23 ± 2.25 <sup>a</sup>	51.12 ± 4.85 <sup>b</sup>	35.89
Perennial grasses	4.59 ± 2.05 <sup>a</sup>	54.49 ± 8.65 <sup>b</sup>	49.9
Annual forbs	0.11 ± 0.11 <sup>a</sup>	1.89 ± 0.52 <sup>b</sup>	1.78
Perennial forbs	1.62 ± 0.85 <sup>a</sup>	0.50 ± 0.3 <sup>a</sup>	-1.12
Succulent shrubs	3.58 ± 1.44 <sup>a</sup>	0.64 ± 0.36 <sup>b</sup>	-2.94
Non-succulent shrubs	51.66 ± 8.19 <sup>a</sup>	70.85 ± 6.47 <sup>a</sup>	19.19
Trees ( <i>Prosopis</i> )	7.58 ± 1.85 <sup>a</sup>	0.92 ± 0.28 <sup>b</sup>	-6.66
<b>Annual grass species</b>			
<i>Aristida adscensionis</i>	11.52 ± 2.48 <sup>a</sup>	41.87 ± 5.18 <sup>b</sup>	30.35
<i>Tragus berteronianus</i>	0 <sup>a</sup>	1.60 ± 0.51 <sup>b</sup>	1.60
<i>Chloris virgata</i>	3.20 ± 1.28 <sup>a</sup>	4.77 ± 0.74 <sup>a</sup>	1.57
<i>Setaria verticillata</i>	0.19 ± 0.19 <sup>a</sup>	1.96 ± 0.91 <sup>a</sup>	1.77
<b>Perennial grass species</b>			
<i>Eragrostis obtusa</i>	0 <sup>a</sup>	22.16 ± 5.07 <sup>b</sup>	22.16
<i>Cynodon dactylon</i>	4.59 ± 2.05 <sup>a</sup>	16.80 ± 3.55 <sup>b</sup>	12.21
<i>Eragrostis lehmanniana</i>	0 <sup>a</sup>	11.22 ± 3.15 <sup>b</sup>	11.22
<i>Aristida congesta</i>	0 <sup>a</sup>	0.48 ± 0.35 <sup>a</sup>	0.48
<i>Cenchrus ciliaris</i>	0 <sup>a</sup>	0.82 ± 0.82 <sup>a</sup>	0.82
<i>Fingerhuthia africana</i>	0 <sup>a</sup>	0.25 ± 0.74 <sup>a</sup>	1.25
<i>Sporobolus iocladius</i>	0 <sup>a</sup>	0.47 ± 0.33 <sup>a</sup>	0.47
<i>Stipagrostis ciliata</i>	0 <sup>a</sup>	0.36 ± 0.36 <sup>a</sup>	0.36
<b>Annual forbs</b>			
<i>Gazania krebsiana</i>	0 <sup>a</sup>	0.18 ± 0.12 <sup>a</sup>	0.18
<i>Lepidium africanum</i>	0.11 ± 0.11 <sup>a</sup>	0.21 ± 0.12 <sup>a</sup>	0.1
<i>Lessertia annularis</i>	0 <sup>a</sup>	0.48 ± 0.33 <sup>a</sup>	0.48
<i>Sonchus oleraceus</i>	0 <sup>a</sup>	0.23 ± 0.18 <sup>a</sup>	0.23
<i>Medicago laciniata</i>	0 <sup>a</sup>	0.24 ± 0.17 <sup>a</sup>	0.24
<b>Succulent shrubs</b>			
<i>Drosanthemum uniflorum</i>	0 <sup>a</sup>	0.18 ± 0.18 <sup>a</sup>	0.18
<i>Phyllobolus splendens</i>	0.55 ± 0.55 <sup>a</sup>	0 <sup>a</sup>	-0.55
<i>Delosperma</i> spp.	2.50 ± 1.37 <sup>a</sup>	0.69 ± 0.38 <sup>a</sup>	-1.81

of the annual grasses *A. adscensionis*, *Chloris virgata* Sw., *Setaria verticillata* (L.) P.Beauv. and *T. berteronianus* and the perennial grasses *E. obtusa*, *E. lehmanniana*, and *C. dactylon*. However, *C. virgata*, *S. verticillata*, and *T. berteronianus* affected grazing capacity to very small extents. Annual grasses ( $F = 25.2$ ,  $P < 0.001$ ), perennial

grasses ( $F = 30.95$ ,  $P < 0.001$ ), annual forbs ( $F = 5$ ,  $P = 0.03$ ), succulent shrubs ( $F = 10.51$ ,  $P = 0.002$ ) and *Prosopis* trees ( $F = 26.08$ ,  $P < 0.001$ ) had significantly different mean range condition scores in uninvaded and cleared sites (Table 3). At species level, the annual grasses *A. adscensionis* ( $F = 12.75$ ,  $P < 0.001$ ), *C. virgata*

**Table 3:** Mean range condition scores and SE for different plant functional types, and species in uninvaded ( $n = 5$ ) vs cleared ( $n = 3$ ) sites near Beaufort West in the Western Cape province of South Africa. Different superscript letters within a row denote significantly different values at  $P \leq 0.05$  (one-way ANOVA via randomisation)

Functional type and species	Uninvaded	Cleared	Difference
<b>Plant functional type</b>			
Annual grasses	27.97 ± 1.99 <sup>a</sup>	51.12 ± 4.85 <sup>b</sup>	23.15
Perennial grasses	12.95 ± 2.20 <sup>a</sup>	54.49 ± 8.65 <sup>b</sup>	41.54
Annual forbs	0.73 ± 0.25 <sup>a</sup>	1.89 ± 0.52 <sup>b</sup>	1.16
Perennial forbs	0.49 ± 0.27 <sup>a</sup>	0.50 ± 0.3 <sup>a</sup>	0.01
Succulent shrubs	3.63 ± 0.90 <sup>a</sup>	0.64 ± 0.36 <sup>b</sup>	-3.63
Non-succulent shrubs	66.12 ± 6.13 <sup>a</sup>	70.85 ± 6.47 <sup>a</sup>	4.73
Trees ( <i>Prosopis</i> )	0.03 ± 0.03 <sup>a</sup>	0.92 ± 0.28 <sup>b</sup>	0.89
<b>Annual grass species</b>			
<i>Aristida adscensionis</i>	24.79 ± 1.9 <sup>a</sup>	41.87 ± 5.18 <sup>b</sup>	17.08
<i>Tragus berteronianus</i>	0.16 ± 0.09 <sup>a</sup>	1.60 ± 0.51 <sup>b</sup>	1.44
<i>Chloris virgata</i>	2.48 ± 0.55 <sup>a</sup>	4.77 ± 0.74 <sup>b</sup>	2.29
<i>Setaria verticillata</i>	0.23 ± 0.14 <sup>a</sup>	1.96 ± 0.91 <sup>b</sup>	1.73
<b>Perennial grass species</b>			
<i>Eragrostis obtusa</i>	0.44 ± 0.22 <sup>a</sup>	22.16 ± 5.07 <sup>b</sup>	21.72
<i>Cynodon dactylon</i>	7.42 ± 2.09 <sup>a</sup>	16.80 ± 3.55 <sup>b</sup>	9.38
<i>Eragrostis lehmanniana</i>	0.49 ± 0.27 <sup>a</sup>	11.22 ± 3.15 <sup>b</sup>	10.73
<i>Aristida congesta</i>	0 <sup>a</sup>	0.48 ± 0.35 <sup>a</sup>	0.48
<i>Cenchrus ciliaris</i>	0.27 ± 0.27 <sup>a</sup>	0.82 ± 0.82 <sup>a</sup>	0.55
<i>Fingerhuthia africana</i>	1.22 ± 0.62 <sup>a</sup>	1.25 ± 0.74 <sup>a</sup>	0.03
<i>Sporobolus iocladius</i>	0.15 ± 0.15 <sup>a</sup>	0.47 ± 0.33 <sup>a</sup>	0.32
<i>Stipagrostis ciliata</i>	1.39 ± 0.53 <sup>a</sup>	0.36 ± 0.36 <sup>a</sup>	-1.03
<b>Annual forbs</b>			
<i>Gazania krebsiana</i>	0 <sup>a</sup>	0.18 ± 0.12 <sup>a</sup>	0.18
<i>Lepidium africanum</i>	0.07 ± 0.05 <sup>a</sup>	0.21 ± 0.12 <sup>a</sup>	0.14
<i>Lessertia annularis</i>	0 <sup>a</sup>	0.48 ± 0.33 <sup>a</sup>	0.48
<i>Sonchus oleraceus</i>	0 <sup>a</sup>	0.23 ± 0.18 <sup>a</sup>	0.23
<i>Medicago laciniata</i>	0.16 ± 0.09 <sup>a</sup>	0.24 ± 0.17 <sup>a</sup>	0.08
<b>Succulent shrubs</b>			
<i>Drosanthemum uniflorum</i>	0.35 ± 0.19	0.18 ± 0.18 <sup>a</sup>	-0.17
<i>Delosperma</i> spp.	2.70 ± 0.8 <sup>a</sup>	0.69 ± 0.38 <sup>a</sup>	-2.01

( $F = 6.33$ ,  $P = 0.014$ ), *S. verticillata* ( $F = 5.35$ ,  $P < 0.017$ ) and *T. berteronianus* ( $F = 11.74$ ,  $P < 0.001$ ) and the perennial grasses *C. dactylon* ( $F = 5.93$ ,  $P = 0.016$ ), *E. obtusa* ( $F = 28.38$ ,  $P < 0.001$ ) and *E. lehmanniana* ( $F = 17.74$ ,  $P < 0.001$ ) had significantly different average range condition scores in uninvaded and cleared sites (Table 3).

### Response of rangeland grazing capacity to increasing *Prosopis* cover

The relationship between *Prosopis* cover and rangeland grazing capacity exhibited a threshold effect. Rangeland grazing capacity sharply declined by 42% at 6% *Prosopis* canopy cover. *Prosopis* cover did not influence grazing capacity below and above the threshold. The relationship between *Prosopis* cover and grazing capacity conformed to the Type 5 function in SegReg (Figure 3). The break point in the data occurred at 6.18% *Prosopis* canopy cover. Current grazing capacity dropped by 42% (-2.15 LSU 100 ha<sup>-1</sup>) at the breakpoint.

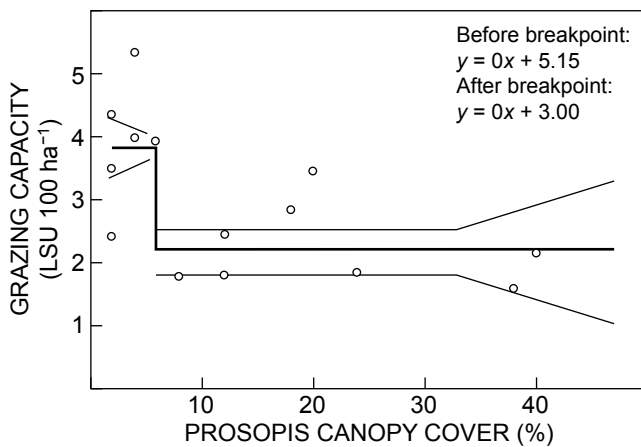
### Discussion

Our results were in general agreement with much of the available literature on the impact of *Prosopis* invasion and control on rangeland grazing capacity (Cable and Tschirley 1961, Busby and Schuster 1971, Tiedemann and

Klemmedson 1973, Scifres and Polk 1974, Cable 1976, Dahl et al. 1978, Jacoby et al. 1982, McDaniel et al. 1982, Heitschmidt and Dowhower 1991, East and Felker 1993, Martin and Morton 1993, Laxson et al. 1997, Ruthven 2001, McClaran and Angell 2006, Simmons et al. 2008). Much of this literature dealt with the effects of *Prosopis* invasion and control on herbaceous forage production in arid and semiarid rangelands in the southern and south-western USA.

### *Prosopis* invasion effects on grazing capacity

In the Rolling Plains of Texas in the USA, McDaniel et al. (1982) found a detectable decline in forage production when *Prosopis* canopy increased beyond 15–20%. Warren et al. (1996) reported a 17% cover threshold for *Prosopis* impact on forage production in the Chihuahuan desert. The relatively low threshold recorded in this study could have been caused by the effects of overgrazing. Overgrazing could have suppressed the increase in the abundance of palatable herbs and grasses adapted to microenvironments under *Prosopis* canopies or tolerant of *Prosopis* competition (Jacoby et al. 1982, Ruthven 2001) that would have accompanied invasion and offset the loss of intolerant species. Such offsetting could have maintained forage levels constant during invasion up to a higher threshold in *Prosopis* cover than the 6% in this study.



**Figure 3:** Segmented regression analysis showing the relationship between *Prosopis* cover and current grazing capacity. Also shown are the standard (least-squares) regression equations and 95% confidence intervals

Invading *Prosopis* trees have been found to lower forage production by competing for light, moisture, and nutrients with annual (Simmons et al. 2008) and perennial grasses (McDaniel et al. 1982, McClaran and Angell 2006). In overgrazed rangeland invading *Prosopis* trees probably accentuate the overall forage loss by displacing grasses that would have persisted under the heavy grazing. This was borne out in this study by the annual grass *A. adscensionis* whose suppression accounted for the bulk of the loss in grazing capacity during *Prosopis* invasion. *Aristida adscensionis*, which is resilient to overgrazing (Esler et al. 2006), was able to persist under heavy grazing at the study site and dominate forage production.

*Prosopis* trees produce seed pods that are eaten by livestock and isolated trees may even enhance production in the short term by enriching the soil with nitrogen and other nutrients (Campbell and Setter 2002). However, the inevitable thickening of infestations with time results in a decrease in carrying capacity through loss of grass cover through shading and competition for limited soil water (Campbell and Setter 2002). Although invading *Prosopis* trees at the study site contributed positively to rangeland grazing capacity, they did not counteract the overall decline in grazing capacity as *Prosopis* trees offset only about 59% of the forage lost through the suppression of the annual grass *A. adscensionis*.

#### **Prosopis clearing effects on grazing capacity**

Several other studies have reported increases in grazing capacity after *Prosopis* clearing or control (Cable and Tschirley 1961, McDaniel et al. 1982, Martin and Morton 1993, Laxson et al. 1997). Laxson et al. (1997) reported a 45% increase in herbaceous standing crop two years after *Prosopis* clearing. First-year results from near Matador, Texas, showed a 46% forage increase following *Prosopis* control by herbicidal spraying (Dahl et al. 1978). McDaniel et al. (1982) found that aerial herbicide spraying resulted in a 7% and 16% increase in grazing capacity over a four-year period on light and heavy *Prosopis*-infested

pasture, respectively. In this study, grazing capacity increased by a dramatic 110% within six years of *Prosopis* clearing. The increases in *A. adscensionis* and *E. obtusa* that underlay grazing capacity increase at the site were probably occasioned by the release of the grasses from *Prosopis* competition. *Aristida adscensionis* and *E. obtusa* are resilient to overgrazing (Esler et al. 2006) and could have increased after *Prosopis* clearing to establish a new equilibrium with the ongoing heavy grazing at the study site. The more palatable *E. lehmanniana* and *C. dactylon* probably owed their establishment to the protection from grazing afforded by the thorny stems and branches of felled *Prosopis* trees. Together with *T. berteronianus*, the two grass species, which colonise bare and compacted soils (Esler et al. 2006), could also have benefited from the disturbance to the soil and vegetation caused by *Prosopis* clearing activities.

The higher grazing capacity in cleared compared to uninvaded rangeland probably reflected the legacy effects of *Prosopis* invasion on soil fertility. *Prosopis* trees accumulate soil nutrients such as carbon, nitrogen, magnesium, potassium and phosphorus under their canopies (Tiedemann and Klemmedson 1973, Barth and Klemmedson 1982, Gadzia and Ludwig 1983, Klemmedson and Tiedemann 1986, Frias-Hernandez et al. 1999, Geesing et al. 2000, Reyes-Reyes et al. 2002). As a result, cleared rangeland at the study site could have been more fertile than uninvaded rangeland and consequently supported greater grass production.

Although *Prosopis* clearing led to considerable gains in grazing capacity in this study, this outcome probably would not persist in the same measure throughout and across the years. Much of the gain in forage production following *Prosopis* clearing was based on the annual grass *A. adscensionis*. Annual grasses disappear seasonally from Karoo rangeland during drier periods of the year and for prolonged periods during summer-drought years (Esler et al. 2006). During such periods grazing capacity gain after *Prosopis* clearing may be less than recorded in this study. In addition, grazing capacity gains caused by enhanced post-invasion soil fertility will decline in the years proceeding clearing as the ecological processes maintaining heightened soil fertility will no longer be operational (Klemmedson and Tiedemann 1986).

#### **Conclusion**

Based on our findings, we concluded that *Prosopis* invasion (>15% mean canopy cover) can lower grazing capacity in overgrazed and degraded Nama Karoo rangeland, whereas clearing *Prosopis* from such rangeland can, even under heavy grazing, substantially improve grazing capacity within 4–6 years. Invading *Prosopis* trees exacerbate the overall loss of grazing capacity in overgrazed rangeland by displacing remnant grazing-resilient grasses. *Prosopis* clearing releases grazing-resilient grasses from competition and may enable less resilient perennial grasses to establish under the protection of felled trunks and branches. Grazing capacity improvement after clearing may also be additionally promoted by *Prosopis*-enhanced soil fertility in cleared rangeland. However, because much of the gain in



grazing capacity after *Prosopis* clearing is based on annual grasses, the magnitude of the benefits may vary with yearly and seasonal fluctuation in rainfall. In addition, the grazing capacity benefit derived from enhanced soil fertility in cleared rangeland will most likely decline in the long term.

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