

Impact of *Prosopis* (mesquite) invasion and clearing on ecosystem structure, function and agricultural productivity in semi-arid Nama Karoo rangeland, South Africa.

by
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DECLARATION

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own original work, that I am the sole author thereof (save to the extent explicitly otherwise stated), that reproduction and publication thereof by Stellenbosch university will not infringe any third party rights and that I have not previously, in its entirety or in part, submitted it for obtaining any qualification.

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ABSTRACT

I evaluated the impact of *Prosopis* invasion and clearing on ecological structure, function and agricultural productivity in heavily grazed Nama Karoo rangeland on two sheep farms near the town of Beaufort West in the Western Cape Province of South Africa. My aims were to (1) determine the effects of invasion and clearing on rangeland vegetation composition, diversity (alien and indigenous species richness) and structure (alien and indigenous species cover), soil vegetation cover (plant canopy and basal cover) and agricultural productivity (grazing capacity), (2) describe the vegetation processes that underlay the invasion and clearing impacts and (3) evaluate the success of clearing in facilitating unaided restoration of ecological structure, function and agricultural productivity in formerly invaded rangeland. I hypothesised that invasion would significantly change rangeland vegetation composition and structure, leading to greater alien species richness and cover and lower indigenous species richness and cover while clearing would lead to lower alien species diversity and cover and greater indigenous species richness and cover. In addition I hypothesized that invasion would reduce rangeland plant canopy and basal cover and grazing capacity while clearing would substantially increase them. Finally I predicted that vegetation composition, alien and indigenous species cover and richness, plant canopy and basal cover and grazing capacity would revert to pre-invasion status and levels within four to six years of clearing.

My results suggest that in heavily grazed Nama Karoo rangeland *Prosopis* invasion (~15 percent canopy cover) and clearing can significantly change rangeland vegetation composition, with invasion leading to greater alien species cover and lower indigenous species richness, while clearing leads to lower alien species richness and cover and greater indigenous species richness and cover. However invasion seems to have no effect on alien species richness and overall indigenous species cover. Clearing appears to facilitate the spontaneous restoration of alien species cover and indigenous species richness within four to six years but not species composition, alien species richness and indigenous species cover. In addition my results also indicate that *Prosopis* invasion can lower rangeland plant canopy and basal cover and grazing capacity while clearing, even under heavy grazing, can substantially raise them. Clearing however does not seem to facilitate the restoration of rangeland plant canopy and basal cover and grazing capacity to pre-invasion levels within four to six years after clearing.

OPSOMMING

Ek het die impak van *Prosopis* indringing en verwydering van indringers op ekologiese struktuur, funksie en landbou produktiwiteit in 'n swaar beweiende Nama Karoo gebied op twee skaapplase naby Beaufort-Wes in die Wes-Kaap provinsie van Suid-Afrika geëvalueer. My doelwitte was om (1) te bepaal wat die gevolge van die indringing en verwydering van indringers op die natuurlike plantegroei samestelling, diversiteit (uitheemse en inheemse spesiesrykheid) en struktuur (uitheemse en inheemse spesies bedekking) sal wees, sowel as die effek op plantegroei bedekking (kroon en basalebedekking) en landbou produktiwiteit (weidingkapasiteit), (2) die plantegroei prosesse te beskryf wat onderliggend deur die impakte van indringing en verwydering van indringers veroorsaak word, en (3) die sukses van die verwydering van indringers te evalueer deur die fasilitering van blote restorasie van ekologiese struktuur en funksie en landbou produktiwiteit in voorheen ingedringde gebiede. My hipotese is dat indringing 'n aansienlike verandering in natuurlike plantegroeisamestelling en struktuur sal veroorsaak, wat sal lei tot groter uitheemse spesiesrykheid en bedekking met minder inheemse spesiesrykheid en bedekking, terwyl die verwydering van indringers sou lei tot minder uitheemse spesie diversiteit en bedekking met 'n groter inheemse spesiesrykheid en bedekking. Verder vermoed ek dat indringing die natuurlike kroon- en basalebedekking en weidingkapasiteit sal verminder, terwyl die verwydering van indringers dit aansienlik sal verhoog. Ten slotte voorspel ek dat plantegroei samestelling, uitheemse en inheemse spesiesbedekking en -rykheid, kroon- en basalebedekking en weidingkapasiteit sou terugkeer na voor-indringing status en vlakke binne vier tot ses jaar na die verwydering van indringers.

My resultate daarop dat die indringing van *Prosopis* (~ 15 persent kroonbedekking) en die verwydering van indringers in swaar beweiende Nama Karoo gebiede 'n aansienlike verandering in die gebied se natuurlike plantegroei samestelling toon, waar indringing gelei het tot groter uitheemse spesiesbedekking en minder inheemse spesiesrykheid, terwyl die verwydering van indringers lei tot minder uitheemse spesiesrykheid en groter inheemse spesiesrykheid en -bedekking. Dit lyk egter of indringing geen effek op uitheemse spesiesrykheid en algehele inheemse spesiesbedekking het nie. Die verwydering van indringers blyk om die spontane herstel van indringerbedekking en inheemse spesiesrykheid binne vier tot ses jaar te fasiliteer, maar nie spesiesamestelling, uitheemse spesiesrykheid of inheemse spesiesbedekking nie. Benewens dui my resultate ook aan dat *Prosopis* indringing die natuurlike kroon- en basalebedekking sowel as weidingskapasiteit verlaag, terwyl die verwydering van indringers, selfs onder swaar beweiding, die bedekking aansienlik kan verhoog. Verwydering van indringers lyk egter nie asof dit die herstel van die gebied se natuurlike kroon- en

basalebedekking en weidingkapasiteit na voor-indringing vlakke toe kan fasiliteer binne vier tot ses jaar na die verwydering van indringers nie.

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CHAPTER 1

Research Background, Aims and Hypotheses

Research Background

Invasive alien plants (IAPs) are threatening the integrity of many natural and semi-natural ecosystems around the world (Le Maitre et al. 2000, Milton et al. 2003, Richardson and van Wilgen 2004, van Wilgen et al. 2008). Intact ecosystems provide a wide range of natural goods and services that are essential for human well-being (Millennium Ecosystem Assessment 2005). IAPs erode the natural capital (i.e. the stock of natural resources, such as biodiversity, soils, hydrological cycles, that enable ecosystems to provide goods and services into the future) that underlies the provision of ecosystem goods and services and threaten their flow to human societies and economies (Milton et al. 2003, Richardson and van Wilgen 2004, Reyers et al. 2008, Blignaut 2010). As a result, IAP control, impact prevention and, increasingly, the repair of IAP damaged ecosystems have become important tasks for a large number of conservation biologists and land managers worldwide (Richardson and van Wilgen 2004).

South Africa has a long history of problems with IAPs (Richardson and van Wilgen 2004). Some 153 IAP species have been introduced into South Africa from different parts of the world since 1652 (Binns et al. 2001). Early plant introductions, all of which were from Europe, resulted in only one IAP, *Pinus pinaster* (Binns et al. 2001). However 40 percent of introductions after 1830, when tree and shrub species were intentionally imported from areas with similar climate and/ecology to South Africa, have become serious invaders (Binns et al. 2001). IAPs now cover eight percent (10 million hectares) of South Africa and are expanding at a rate of five percent per year (Binns et al. 2001, van Wilgen et al. 2001). Many of the affected areas support natural and semi-natural ecosystems of great ecological and economic value (Richardson and van Wilgen 2004). IAPs are thought to have substantially eroded natural capital in these areas and lowered

the flow of critical ecosystem goods and services (Milton et al. 2003, Richardson and van Wilgen 2004, Reyers et al. 2008, Blignaut 2010).

Much of the concern in South Africa regarding IAPs has been on their effects on surface water yield (Le Maitre et al. 2000). It is estimated that IAPs may be responsible for the loss of around seven percent (3300 million cubic metres) of South Africa's annual river flow (Binns et al. 2001, Le Maitre et al. 2002). As rainfall in South Africa is low and erratic and most of the country is underlain by hard rock formations that perform poorly as ground water aquifers, the loss presents a serious and urgent water supply problem (Blignaut et al. 2007). In response, the South African government has launched an extensive and ambitious IAP control programme (van Wilgen et al. 1998, Binns et al. 2001, Le Maitre et al. 2002, Anon 2006, Marais and Wannenburg 2008). Dubbed Working for Water (WfW), the programme intends to secure threatened water resources by physically removing IAPs from South Africa's major catchment areas (Binns et al. 2001, Hobbs 2004, Anon 2006). The removal of IAPs from catchment areas is expected to lead to restoration of natural capital, improved hydrological function and enhanced river flow.

The WfW programme has grown to be the biggest conservation project in South Africa in terms of manpower, costs and impact (Hosking and du Preez 2002, Anon 2006). Millions have been spent and extensive areas cleared of IAPs under its aegis (Binns et al. 2001, Anon 2006, Marais and Wannenburg 2008, Turpie et al. 2008). However the future extent of the programme's activities is uncertain as it faces increasing competition for government funding from rival initiatives (Anon 2006, Turpie et al. 2008). The WfW programme will have to demonstrate its full environmental and socio-economic worth in order to compete effectively against its rivals (Turpie et al. 2008). However, despite the heavy investment of public funds and the widespread nature of its activities, the environmental and socio-economic benefits of the WfW programme have not been fully evaluated (Anon 2006, Turpie et al. 2008).

Research Problem

My research was developed and conducted as part of an ongoing five year (2008 - 2013) multidisciplinary project titled “The impacts of re-establishing indigenous plants and restoring the natural landscape on sustainable rural employment and land productivity through payment for environmental services”. The project, which is funded by the South African Water Research Commission, aims to evaluate the overall outcome of restoring natural capital (RNC) in South Africa (Blignaut 2010). Under the project, data from fifteen multidisciplinary studies conducted at diverse sites across South Africa will be brought together to test the hypothesis that:

“RNC improves water flow and water quality, land productivity, in some cases sequesters more carbon and, in general, increases both the socio-economic value of the land in situ, and in the surroundings of the restoration site, as well as the agricultural potential of the land.”

My study evaluated the project hypothesis in the site-specific context of IAP invasion and clearing in heavily grazed and degraded rangeland. The study site was in overgrazed Nama Karoo rangeland on two sheep farms (Brandwag and De Hoop) near the town of Beaufort West in the Western Cape Province of South Africa. Both farms were previously invaded by alien *Prosopis* trees. One of the farms, Brandwag, had been completely cleared of *Prosopis* by WfW teams at the time of my study while the neighbouring De Hoop farm still had standing *Prosopis* invasions of varying density and age.

Prosopis is an aggressive invasive woody tree that forms large and rampant infestations of dense thorn thickets that have serious economic, environmental and social impacts (Brown and Carter 1998, Zimmermann and Pasiecznik 2005). The invasive tree was introduced into South Africa in the late 1880s to provide shade, fodder, and fuel wood in arid regions (Zimmermann 1991, Zimmermann and Pasiecznik 2005). It quickly became widespread due to support for its dissemination and planting by the then Cape and

Transvaal forestry commissions (Roberts 2006). The two agencies imported large amounts of seed between 1897 and 1978 from the US, Mexico and Hawaii and distributed it to farmers as potted seedlings in a series of hugely successful planting programmes (Roberts 2006).

Large areas (>18 000 km²) of the Nama Karoo biome have been invaded by *Prosopis* (Richardson and van Wilgen 2004, Henderson 2007). The invasions have been particularly dense in areas with deep alluvial soils which are important aquifers for groundwater supply to farmers, livestock and rural settlements (Roberts 2006). Apart from impacting negatively on the hydrology of invaded areas, *Prosopis* is also thought to have displaced indigenous plant species and changed rangeland vegetation composition, structure and function (Roberts 2006). Very little empirical work (Saayman and Botha 2007) has been done to assess the ecological impacts of *Prosopis* invasion on Nama Karoo rangeland.

Large scale clearings of *Prosopis* have been undertaken in the Nama Karoo under the WfW programme (Zimmermann and Pasiecznik 2005). The clearings have been carried out using the standard WfW practice of reducing the above-ground biomass of alien plants and leaving the indigenous vegetation to recover without further intervention (Blanchard and Holmes 2008, Reinecke et al. 2008). The assumption behind the approach has been that alien plant removal alone is adequate for successful “self repair” in target ecosystems (Esler et al. 2008, Holmes et al. 2008). An evaluation of the clearing method in riparian fynbos vegetation has indicated that its success is largely circumstantial (Blanchard and Holmes 2008, Reinecke et al. 2008). It is unclear whether the method leads to successful ecological restoration in *Prosopis* invaded Nama Karoo rangeland (Saayman and Botha 2007).

In addition to water supply impacts, there is considerable concern in South Africa over the effects of IAPs on the nation’s grazing lands (Macdonald 2004). Raising livestock on natural pasture is the most widespread form of land use in South Africa (Macdonald

2004). The Nama Karoo, in particular, sustains an important meat- and wool-based small-stock industry (Palmer and Hoffman 1997). Ecological studies focused on assessing and quantifying the impact of *Prosopis* invasion and clearing on rangeland grazing value could provide a much needed basis (Richardson and van Wilgen 2004, Turpie 2004) for economic and financial evaluations of *Prosopis* clearing projects in Nama Karoo rangeland. Very few studies (Saayman and Botha 2007, van Wilgen et al. 2008) have attempted to quantify the impact of *Prosopis* invasion and clearing on Nama Karoo rangeland grazing capacity.

Research Aims and Hypotheses

The aims of my research were to (1) assess and describe the impacts of *Prosopis* invasion and clearing on the ecological structure, function and agricultural productivity of Nama Karoo rangeland, (2) describe the vegetation processes that underlay the invasion and clearing impacts and (3) evaluate the success of the WfW *Prosopis* clearing method in facilitating the unaided restoration of ecological structure, function and agricultural productivity in formerly invaded rangeland.

Based on evidence from literature (see Chapter two) I hypothesized that:

1. *Prosopis* invasion degraded natural capital (vegetation composition, diversity and structure), impaired ecological function (soil surface cover) and reduced agricultural potential (grazing capacity), while clearing reversed these negative effects.
2. Changes in rangeland vegetation composition, diversity and structure during invasion and after clearing were largely driven by changes in herbaceous plant species abundance.

3. Rangeland ecological structure, function and agricultural productivity reverted to pre-invasion conditions within four to six years of clearing.

Thesis Outline

The thesis consists of an introduction (Chapter 1), literature review (Chapter 2), three independent research papers (Chapters 3, 4 and 5) and a conclusion (Chapter 6). Since Chapters 3, 4 and 5 were prepared as stand-alone research papers there is some overlap in content between them. All the thesis chapters were largely my own work, however the data chapters were not written in the first person as I aim to submit them for publication as multi-authored research papers in collaboration with my supervisors. My supervisors, Professors Suzanne J. Milton and Karen J. Esler made comments and suggestions to refine and improve the draft manuscripts.

The contents of the chapters are as follows:

Chapter 1 Research Background, Aims and Hypotheses

This chapter provides background information about the study and presents the study aims and hypotheses.

Chapter 2 - *Prosopis* Ecology and the Working for Water Programme: A Literature Review

*This chapter reviews information on *Prosopis* taxonomy and ecology and South Africa's government-led WfW IAP control programme.*

Chapter 3 - Impact of *Prosopis* (mesquite) invasion and clearing on vegetation composition, diversity and structure in semi-arid Nama Karoo rangeland

This chapter evaluates the impact of Prosopis invasion and clearing on vegetation species composition, diversity, and structure.

Chapter 4 - Effect of *Prosopis* (mesquite) invasion and clearing on soil vegetation cover in degraded semi-arid Nama Karoo rangeland, South Africa.

This chapter assesses and quantifies the effects of Prosopis invasion and clearance on soil vegetation cover. Unlike Chapter 3 which looks at vegetation structure in terms of species cover (indigenous and alien species cover) this chapter looks at vegetation structure in terms of total vegetation cover (i.e. vegetation canopy and basal cover). Indigenous and alien species covers are indicators of vegetation community stability and resilience while total vegetation canopy and basal cover are important determinants of rainfall infiltration, runoff and erosion.

Chapter 5 - Impact of *Prosopis* (mesquite) invasion and clearing on the grazing capacity of degraded semi-arid Nama Karoo rangeland, South Africa.

This chapter assesses and quantifies the impact of Prosopis invasion and clearing on rangeland grazing capacity.

Chapter 6 – Conclusion

This chapter synthesizes the findings of the individual data chapters and presents an overall conclusion.

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CHAPTER 2

***Prosopis* Ecology and the Working for Water Programme: A Literature Review**

***Prosopis* Ecology**

Taxonomy

The genus *Prosopis* (Leguminosae subfam. Mimosoideae) consists of 44 tree and shrub species that are native to arid and semi-arid regions of North America (9 species), South America (31 species), northern Africa (1 species) and eastern Asia (3 species) (Burkart 1976, Pasiecznik et al. 2004, March et al. undated). The species are mostly thorny and have feathery foliage, tiny yellow (or white) flowers and thick pods (Pasiecznik et al. 2004). The complete taxonomy of the genus is provided by Burkart (1976).

In South Africa *Prosopis* species occur as large thorny shrubs or trees that can grow up to 10 metres tall (Pasiecznik et al. 2004). Six species have been recognized (Roberts 2006) although the exact number that has become naturalised is uncertain (Zimmermann 1991). Two species, *P. velutina* Wootan and *P. glandulosa* var. *torreyana* (L. Benson) M.C. Johnson, which constituted the bulk of the seeds imported into South Africa, are thought to be the most dominant (Roberts 2006). However extensive hybridization has occurred among introduced *Prosopis* species and generated considerable taxonomic confusion (Zimmermann 1991, Roberts 2006). As a result of the hybridization, particularly between *P. velutina* Wootan, *P. glandulosa* var. *torreyana* (L. Benson) M.C. Johnson, *P. juliflora* (Sw.) DC. and, to a lesser extent, *P. chilensis* (Molana) (Zimmermann 1991, Zimmermann and Pasiecznik 2005) many *Prosopis* populations in South Africa are composed of overlapping morpho-types that are difficult to classify into specific groupings (Roberts 2006). Many recent studies in South Africa have made no attempt to classify *Prosopis* populations further than the generic terms *Prosopis* or mesquite (Roberts 2006).

Distribution

Prosopis is highly invasive in both its native and introduced range (Pasiecznik et al. 2004). Several studies have described the pattern of *Prosopis* invasion in its native range using aerial photography (Robinson et al. 2008). These studies have demonstrated that *Prosopis* invasions generally follow a pattern of initial high patch initiation followed by coalescence, with most of the recruitment and coalescence occurring in the most mesic parts of the landscape (Robinson et al. 2008). Advancements in invasions have been observed to occur as "bursts", in response to highly favourable but irregular climatic events such as periods of exceptional rainfall and floods (March et al. undated).

Extensive areas have been invaded by *Prosopis* in South Africa (Henderson 2007). The invasions are particularly dense in the Northern Cape and parts of the Western Cape provinces (Coetzer and Hoffmann 1997, Henderson 2007). *Prosopis* trees are the most prominent invaders in the Nama Karoo (Henderson 2007) and cover more than 18 000 km² of the region's low lying alluvial plains and seasonal watercourses (Richardson and van Wilgen 2004).

Invasiveness

Prosopis has many features that enable it to invade and dominate marginal ecosystems (Hennessy et al. 1983). Many *Prosopis* species are phreatophytic and are thus able to utilise both near-surface soil moisture and groundwater at great depth (Nilsen et al. 1983, Ansley et al. 1992, Roberts 2006). In regions of extreme aridity where there is little or no recorded rainfall (e.g. the Sonoran desert of Southern California USA (Ansley et al. 1992)), *Prosopis* relies predominantly on its deep vertical roots for survival (Nilsen et al. 1983). These roots can extend to great depth (52m) where they tap into underground water sources (Nilsen et al. 1983). In wetter sites, such as semi-arid western Texas, where there is frequent wetting of surface soil horizons, *Prosopis* relies on shallow lateral roots and utilize the deep tap roots during drought (Jacoby et al. 1982, Ansley et al. 1992). The

ability to avoid water stress endowed by its rooting system has enhanced the competitive success of *Prosopis* in South Africa's semi-arid environments to the detriment of native vegetation (Roberts 2006).

Hybridization is also thought to enhance the competitiveness of *Prosopis* (Zimmermann and Pasiecznik 2005). Other features that contribute to the invasiveness of *Prosopis* are its immense reproductive potential (9-20 tonnes ha⁻¹ pods annually), the widespread dispersal and germination of seeds and seedlings under a wide range of temperature, moisture and soil conditions, ability to resprout from dormant stem buds following injury, spines, long seed dormancy, and the absence of natural enemies in newly invaded areas (Glendenning and Paulsen 1955, Zimmermann and Pasiecznik 2005, March et al. undated). Glendenning and Paulsen (1955) provide a detailed review of these attributes.

Impact on indigenous plant species

Prosopis competes for light, soil moisture and nutrients with understory vegetation in its native range (Meyer and Bovey 1986). Such competitive interactions are especially evident in arid to semi-arid areas where competition between woody plants and grass is critical (Jacoby et al. 1982). In a study conducted in Crane County, Texas Jacoby et al. (1982) found that although there were certain grasses that were adapted to shade conditions there were others which were shade intolerant and were thus inhibited by competition with *Prosopis*. Competition for soil water may lead to reduced herbaceous plant abundance and cover between *Prosopis* plants (Gibbens et al. 1986).

Prosopis trees may act as nurse plants for certain woody, forb and grass species (Ruthven 2001). Ruthven (2001) found greater grass and forb richness under *P. glandulosa* canopies as opposed to herb dominated interspaces in a south Texas shrub community. The microenvironments created underneath *Prosopis* canopies due to nitrogen fixation and shading provide ideal environments for the germination of certain woody and succulent species (Ruthven 2001). However this effect is dependent on the density of *Prosopis* plants (Ruthven 2001). Nitrogen extraction from the soil and incorporation into

woody plant tissues might inhibit further establishment of shrubs beneath *P. glandulosa* on sites with high *Prosopis* densities (Ruthven 2001).

Impact on grazing capacity

Studies conducted in the nineteen fifties and sixties in the United States demonstrated that *Prosopis* removal increased herbaceous forage production over the long term (Jacoby et al. 1982). This increase in forage production is thought to arise due to the release of grass from *Prosopis* competition (Ansley et al. 1992). In a study of *P. glandulosa* removal, McDaniel et al. (1982) found that the increase in production of more desirable perennial grasses occurred most significantly in areas formerly under *Prosopis* canopy and then expanded into the inter-space over the following years. It was also found that the institution of a growing season deferment and dormant season grazing regime following *Prosopis* control maximized the improvement in grazing capacity on rangeland in poor to fair condition (McDaniel et al. 1982). Deferment of grazing in the first growing seasons allows grasses the opportunity to increase vigour and set seed prior to the initiation of grazing in the dormant season (McDaniel et al. 1982). Herbicidal treatment of *P. glandulosa* infestations resulted in maximum increases in grazing capacity during the first three years, whereas no improvement was recorded three to four years after mechanical control (McDaniel et al. 1982).

Isolated *Prosopis* plants probably have a minor impact on grazing productivity and may even enhance production in the short term due to the nutritious seed pods and shade they provide (Campbell and Setter 2002). However the inevitable thickening of these infestations with time can result in a decrease in carrying capacity through loss of grass cover caused by replacement and by competition for limited water (Campbell and Setter 2002).

Impact on soil chemistry

Prosopis plants tend to accumulate soil nutrients beneath their canopies (Barth and Klemmedson 1982). This accumulation may result from several processes that include (a) absorption of nutrients by roots from beyond the crown area of the plant or from lower soil layers and substratum and eventual deposition of the litter under the crown, (b) fixation of nutrients by the plant or an associated symbiotic organism, (c) net import of nutrients by fauna that use the plants for nesting, resting, roosting or feeding, (d) movement by wind or water (Barth and Klemmedson 1982). However, since *Prosopis* trees seem to enrich the soil under their canopies at the expense of the soil nutrient capital in the open areas (Tiedemann and Klemmedson 1973) the overall nutrient status of invaded rangeland may compare unfavourably with uninvaded or cleared rangeland.

Studies conducted in the desert grasslands of the south western USA have shown that the clearing of *Prosopis* increases the amount and duration of supply of soil moisture (Tiedemann and Klemmedson 1973). This is because *Prosopis* trees use two to three times more water than natural herbaceous vegetation (Tiedemann and Klemmedson 1973). This effect may be felt both beneath the trees and in the open as *Prosopis* roots extend downwards and laterally (Tiedemann and Klemmedson 1973). Moisture depletion occurs rapidly near *Prosopis* tree bases with depth and distance from the tree (Jacoby et al. 1982). Studies in the rangelands of southern Arizona in the USA have found significant increases in moisture content of the upper 45 cm of soil at distances of 3, 6 and 10 metres from killed *Prosopis* trees compared to live ones (Tiedemann and Klemmedson 1973).

Prosopis is a nitrogen fixing legume that can directly affect soil nitrogen dynamics (Frias-Hernandez et al. 1999). There have been reports of higher levels of nitrogen in soils underneath *Prosopis* canopies than those in open areas (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). In central Mexico, Frias-Hernandez et al. (1999) have reported twice as high levels of nitrogen under *P. laevigata* as in open areas. Klemmedson and Tiedemann (1986) and

Tiedemann and Klemmedson (1973) reported three times greater nitrogen content under *P. juliflora* canopies in low rainfall savanna soils. In the California desert *Prosopis glandulosa* has been shown to fix about 30 kg N ha⁻¹ year⁻¹ (Geesing et al. 2000). Table 2.1 presents data from several studies on nitrogen concentrations in soils under and outside *Prosopis* canopies (Geesing et al. 2000).

Table 2.1. Nitrogen concentrations in soils under and outside *Prosopis* canopies (Geesing et al. 2000).

Location	Carbon concentration	
	Soil under <i>Prosopis</i> canopy	Soil outside <i>Prosopis</i> canopy
California	1.7 g N kg ⁻¹	0.2 g N kg ⁻¹
Arizona	0.49 g N kg ⁻¹	0.24 g N kg ⁻¹
India	0.49 g N kg ⁻¹	0.42 g N kg ⁻¹
Texas	1.3 g N kg ⁻¹	1.0 g N kg ⁻¹

The higher concentration of nitrogen under *Prosopis* canopy can be attributed to the deposition of nitrogen enriched litter (Frias-Hernandez et al. 1999). Due to its extensive root system *Prosopis* is able to absorb ammonium and nitrate ions from outside its canopy area and concentrate nitrogen in its tissue (Barth and Klemmedson 1982). Additionally *Prosopis* has the ability to form symbiotic relationships with nitrogen-fixing *Rhizobium*, thus increasing the nitrogen content of its litter and the cycling of nitrogen under its canopy (Frias-Hernandez et al. 1999). *P. velutina* has been reported to accumulate nitrogen at the rate of 112 g/m² per metre of height in a three year experiment in the Sonoran desert (Barth and Klemmedson 1982).

Gadzia and Ludwig (1983) found soils under *Prosopis* to have higher concentrations of calcium, magnesium, and potassium than those in open areas in southern New Mexico. However a study in the semi-arid highlands of central Mexico by Frias-Hernandez et al.

(1999) reported no difference in soil calcium content for soils under *P. laevigata* and in open areas. In the semi-arid highlands of Mexico, Frias-Hernandez et al. (1999) have found lower concentrations of magnesium in the soil under *P. laevigata* canopy than from soil in the intervening spaces. Tiedemann and Klemmedson (1973) also found more potassium in soils in the 0 to 4.5 cm layer under *Prosopis* than in the same layer in the open. However Frias-Hernandez et al. (1999) reported no difference in soil potassium content for soils under *P. laevigata* and away from *Prosopis* canopies in the semi-arid highlands of central Mexico.

Frias-Hernandez et al. (1999) found phosphorous to be two times greater under *Prosopis* trees than in open ground. The phosphorous concentration under *Prosopis* canopies could be a result of pumping of soluble phosphorous from deeper soil layers (Geesing et al. 2000). Legumes have also been found to be more efficient in obtaining phosphorous from insoluble sources due to the increased cation exchange capacity of their root systems that lowers the calcium activity of the soil solution facilitating the release of phosphorous from insoluble Ca-P compounds (Geesing et al. 2000).

A large number of studies have reported significantly higher carbon content in soils associated with *Prosopis* (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). In the desert grasslands of south eastern Arizona, Tiedemann and Klemmedson (2004) found that soils in areas under *Prosopis* had significantly higher carbon than those in areas where *Prosopis* had been removed. In central Mexico, Frias-Hernandez et al. (1999) reported twice as high total carbon content under *P. laevigata* than in open ground. *P. laevigata* was also found to increase the organic content of soils beneath its canopy in the same area (Reyes-Reyes et al. 2002). Klemmedson and Tiedemann (1986) and Tiedemann and Klemmedson (1973) reported three times greater carbon content under the canopy of *P. juliflora* in low rainfall savanna soils. Geesing et al. (2000) provide data from several studies on carbon concentrations in soils under and outside *Prosopis* canopies (Table 2.3).

Table 2.2. Carbon concentrations in soils under and outside *Prosopis* canopies (Geesing et al. 2000).

Location	Carbon concentration	
	Soil under <i>Prosopis</i> canopy	Soil outside <i>Prosopis</i> canopy
California	19g C kg ⁻¹	3.2g C kg ⁻¹
Arizona	5.0g C kg ⁻¹	2.7g C kg ⁻¹
India	3.1g C kg ⁻¹	1.9g C kg ⁻¹
Texas	15g C kg ⁻¹	13.8g C kg ⁻¹
New Mexico	2.1g C kg ⁻¹	1.3g kg ⁻¹

The carbon accumulation under *Prosopis* canopies could have been effected through absorption of bicarbonate and carbonate ions from outside the soil-plant systems by the plants' extensive root systems (Barth and Klemmedson 1982). Soils under *Prosopis velutina* have been found in a three year study to accumulate carbon at the rate of 0.11 kg/m² per metre of tree height in the Sonoran desert of the USA (Barth and Klemmedson 1982).

Impact on soil structure and respiration

A study in the desert grasslands of the south western US has reported findings of significantly lower bulk densities in the 0 to 4.5 cm soil layer beneath *Prosopis* trees in comparison to intervening openings (Tiedemann and Klemmedson 1973). In the highlands of central Mexico Frias-Hernandez et al. (1999) reported higher rates of carbon dioxide production after glucose application under *Prosopis* canopies than in open soil. They took this to be an indication of greater microbial mass under *Prosopis*. There is also generally much higher organic carbon under *Prosopis* which should provide larger quantities of energy yielding organic substrates (Virginia et al. 1982) for soil respiration compared with un-vegetated soil.

Impact on soil erosion

Prosopis invasion increases soil erosion while clearing reduces it by facilitating increased herbaceous plant cover (Bedunah and Sosebee 1986, Martin and Morton 1993, Reyes-Reyes et al. 2002). Bedunah and Sosebee (1986) reported significant reductions in erosion rates in rangeland sites where *Prosopis* had been controlled by shredding, mechanical grubbing, vibratilling, and foliar spraying with 2, 4, 5-T + picloram. Martin and Morton (1993) found that *Prosopis* free watersheds had higher herbaceous plant cover and lower soil movement rates than comparable *Prosopis* invaded watersheds.

The Working for Water Programme

The Working for Water (WfW) programme was established in September 1995 after intense lobbying by scientists concerned about the negative impact of invasive alien plants (IAPs) on South Africa's water resources (Binns et al. 2001, Hobbs 2004, Anon 2006). Considerable scientific evidence had accumulated indicating that IAPs were exerting more pressure on water resources than the indigenous vegetation they were displacing (Le Maitre et al. 2000, Binns et al. 2001, Hobbs 2004, Anon 2006). The scientists argued that South Africa's water resources, under critical pressure from a rapidly rising population and increased industrial, agricultural and luxury consumption, could be significantly restored by clearing IAPs from South Africa's major catchment areas (Binns et al. 2001, Anon 2006). Removing IAPs, they reasoned, would result in more water being available for percolation or runoff into the nation's groundwater reserves, streams and rivers (Binns et al. 2001, Hobbs 2004, Anon 2006). This would, in turn, mean more water for domestic, agricultural and industrial use (Binns et al. 2001).

The government was highly receptive of the scientists' argument (van Wilgen et al. 1998, Binns et al. 2001, Anon 2006). South Africa faces a serious water supply crisis (Binns et al. 2001) and any scheme proposing to restore water resources is bound to be taken seriously. The WfW programme, however, offered more than just an opportunity to

eradicate disruptive alien species and secure a threatened natural resource. It also provided a unique and innovative means to tackle South Africa's equally pressing socio-economic problem of chronic rural unemployment and poverty (Binns et al. 2001, Anon 2006, Hope 2006). By adopting a contracting policy that favoured disadvantaged local communities by offering minimal but living rates the programme provided the government with a vehicle for poverty alleviation and job creation (Hope 2006). As a result there has been tremendous support for the programme from South Africa's first democratically elected government and its successors.

The WfW programme started with an annual budget of R25 million at its inception in 1995 (Anon 2006). Over the years it has grown to be the biggest conservation project in South Africa in terms of manpower and impact (Hosking and du Preez 2002). By 2005 it was employing 32 000 people and running on a budget of R414 million per year (Anon 2006). The programme had by then cleared approximately 12% (1.2 million hectares) of the estimated 10.5 million hectares of infestations in the country (Macdonald 2004). The WfW programme is also acknowledged globally and has received numerous national and international awards (Macdonald 2004). It has become a model for other national programmes such as Working for Wetlands, Working on Fire and Working for Woodlands (Anon 2006).

The WfW programme has also been criticized (Binns et al. 2001, Anon 2006). Dr Beatrice Conradie, an economist with the University of Cape Town, considers the WfW programme as "stupid" when considered as an "engineering argument for water" (Anon 2006). According to her "it costs R100 investment in public funds for every R20 worth of water restored" through the programme (Anon 2006). Binns et al. (2001) have expressed their disquiet over the potential environmental effects of the massive plant clearance involved in the programme. According to them, the question of whether it is environmentally meritorious or problematic to clear alien plants and trees is still open to debate (Binns et al. 2001). They call for more research on the possible effects of the massive plant clearance on soil, flora and fauna (Binns et al. 2001). Dr Patricia Holmes, a biodiversity specialist with the City of Cape Town, criticized the programme's initial

rushed and unsystematic approach (Anon 2006). She noted in a 2003 audit that a lack of strategic ecological planning had resulted in the programme failing to focus on critical areas (Anon 2006). The programme had, instead, been spread too wide and unsystematically across the country with “disastrous” results (Anon 2006). The hasty beginnings also led to inadequate monitoring and record keeping during the early phases of the programme – a shortcoming that has made it difficult to evaluate the effectiveness of early clearing activities (Anon 2006).

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CHAPTER 3

Impact of *Prosopis* (mesquite) invasion and clearing on vegetation composition, diversity and structure in semi-arid Nama Karoo rangeland.

Abstract

We evaluated the impact of *Prosopis* invasion and clearing on vegetation species composition, diversity (alien and indigenous species richness), and structure (alien and indigenous species cover) in heavily grazed Nama Karoo rangeland on two sheep farms near the town of Beaufort West in the Western Cape Province of South Africa. Invasion (~15 percent *Prosopis* canopy cover) and clearing significantly altered rangeland species composition. The composition changes were however not substantial as they were mainly driven by changes in the relative abundance of species already present in the rangeland. Invasion changed species composition by reducing the abundance of the annual grass *Aristida adscensionis* and the non-succulent shrub *Pentzia incana* and by increasing the abundance of the annual and perennial grasses *Chloris virgata* and *Cynodon dactylon*. Clearing, on the other hand, changed rangeland species composition by increasing the abundance of the annual grass *A. adscensionis*, the perennial grasses *Eragrostis obtusa* and *C. dactylon* and the non succulent shrub *P. incana*. Plant species composition in cleared rangeland had not reverted to the pre-invasion state more than four years after clearing. Cleared rangeland mainly differed from the pre-invasion state by having higher abundances of the annual grass *A. adscensionis* and the perennial grasses *E. obtusa* and *C. dactylon* and a lower abundance of the non succulent shrub *P. incana*. Invasion did not

change the richness of alien species (three or four species) but increased their cover from 0.44 to 2 %. Clearing reduced alien species richness by one or two species and cover from 2 to 1 %. Alien species richness declined to below pre-invasion levels while species cover declined to pre-invasion levels after clearing. Invasion reduced the richness of indigenous species by six or seven species but did not affect total cover. Clearing increased indigenous species richness by between 10 and 15 species and cover from 65 to 100 %. Indigenous species richness in cleared rangeland reverted to the pre-invasion level (between 40 and 47 species) while cover remained 36 % higher than the pre-invasion level (i.e. 65 %) four to six years after clearing. Our results suggest that in heavily grazed Nama Karoo rangeland *Prosopis* invasion (~15 percent canopy cover) and clearing can significantly change rangeland species composition. Invasion can lead to greater alien species cover and less indigenous species richness, while clearing leads to lesser alien species richness and greater indigenous species richness and cover. However invasion seems to have no effect on alien species richness and overall indigenous species cover. Clearing appears to facilitate the spontaneous restoration of alien species cover and indigenous species richness within four to six years but not species composition, alien species richness and indigenous species cover.

Keywords: rangeland species composition, alien species richness, alien species cover, indigenous species richness, indigenous species cover, Working for Water (WfW)

Introduction

Large areas of South Africa (~10 million hectares) have been invaded by alien plants (Binns et al. 2001, van Wilgen et al. 2001). Much of the affected area, which is expanding at a rate of five percent per year (Binns et al. 2001, van Wilgen et al. 2001), supports natural and semi-natural ecosystems of great environmental and socio-economic importance (Le Maitre et al. 2000, Milton et al. 2003, Richardson and van Wilgen 2004, van Wilgen et al. 2008). Invasive alien plants (IAPs) are thought to have eroded the natural capital (i.e. the stock of natural resources) of these critical ecosystems and compromised their structure and function (Le Maitre et al. 2000, Milton et al. 2003, Richardson and van Wilgen 2004, van Wilgen et al. 2008).

The Nama Karoo occupies 28% (346 100 km²) of South Africa's land area and covers much of the central and western regions of the country (Palmer and Hoffman 1997, Hoffman 2000, Suttie et al. 2005). Large tracts (>180 000 km²) of Nama Karoo rangeland have been invaded by alien leguminous trees of the genus *Prosopis* (Richardson and van Wilgen 2004). The trees, which are indigenous to the Americas, were introduced into the area in the late 1880s to provide shade, fodder, and fuel wood (Zimmermann 1991, Palmer and Hoffman 1997, Richardson and van Wilgen 2004, Zimmermann and Pasiecznik 2005). However they have had serious negative environmental impacts (Zimmermann and Pasiecznik 2005). In many areas, invasive *Prosopis* trees have coalesced to form dense thorny thickets that are thought to have displaced indigenous plants and substantially changed rangeland composition, diversity and structure (Richardson and van Wilgen 2004, Richardson et al. 2005). Like many other plant invasions in South Africa's sparsely populated arid regions (Milton and Dean 1998), the processes and impacts of *Prosopis* invasion in the Nama Karoo have not been adequately studied.

Extensive 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 socio-economic 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 clearings will also result in the restoration of ecosystem structure and function in affected areas (Esler et al. 2008, Holmes et al. 2008). Very few studies (Saayman and Botha 2007) have tested this assumption in Nama Karoo rangeland.

We evaluated the impact of *Prosopis* invasion and clearing on vegetation species composition, diversity, and structure in heavily grazed Nama Karoo rangeland on two sheep farms near the town of Beaufort West in the Western Cape Province of South Africa. Our aims were to (1) determine the impacts of invasion and clearing on vegetation species composition, diversity (alien and indigenous species richness) and structure (alien and indigenous species cover), and (2) describe the vegetation changes that underlay the impacts. We hypothesised that invasion would significantly change rangeland species composition, leading to greater alien species richness and cover and lower indigenous species richness and cover while clearing would conversely change rangeland species composition leading to lower alien species richness and cover and greater indigenous species richness and cover. We also predicted that species composition and alien and indigenous species richness and cover in cleared rangeland would revert to pre-invasion status and levels within four to six years of clearing.

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*, *Prosopis juliflora*, and *Prosopis velutina*) have hybridized extensively (Zimmermann 1991) such that most populations in South Africa are

composed of overlapping morpho-types that are difficult to classify into distinct species (Roberts 2006). Many South African studies do not attempt 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"), about 30 kilometres north-east of the town of Beaufort West in the Western Cape Province of South Africa (Figure 3.1). 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*, *Ruschia*) and Asteraceae (*Eriocephalus*, *Pentzia*, *Pteronia*) interspersed with grasses (*Aristida*, *Enneapogon*, *Digitaria* and *Stipagrostis*) (Palmer and Hoffman 1997). Taller shrubs and trees (*Acacia karoo*, *Euclea undulata* and *Rhigozum obovatum*) occur intermittently (Palmer and Hoffman 1997).

The area receives a mean annual rainfall of 239 mm (calculated for the period 1878-2004) of rain per year (Kraaij and Milton 2006). Mean annual rainfall has however been generally higher than the long term average for the past eight years (2000 – 2008, Fig 3.2). Rainfall is highly seasonal with uni-modal 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*100 metre plots were set up during the WCDA experiment (viz. uninvaded & fenced, uninvaded & 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.

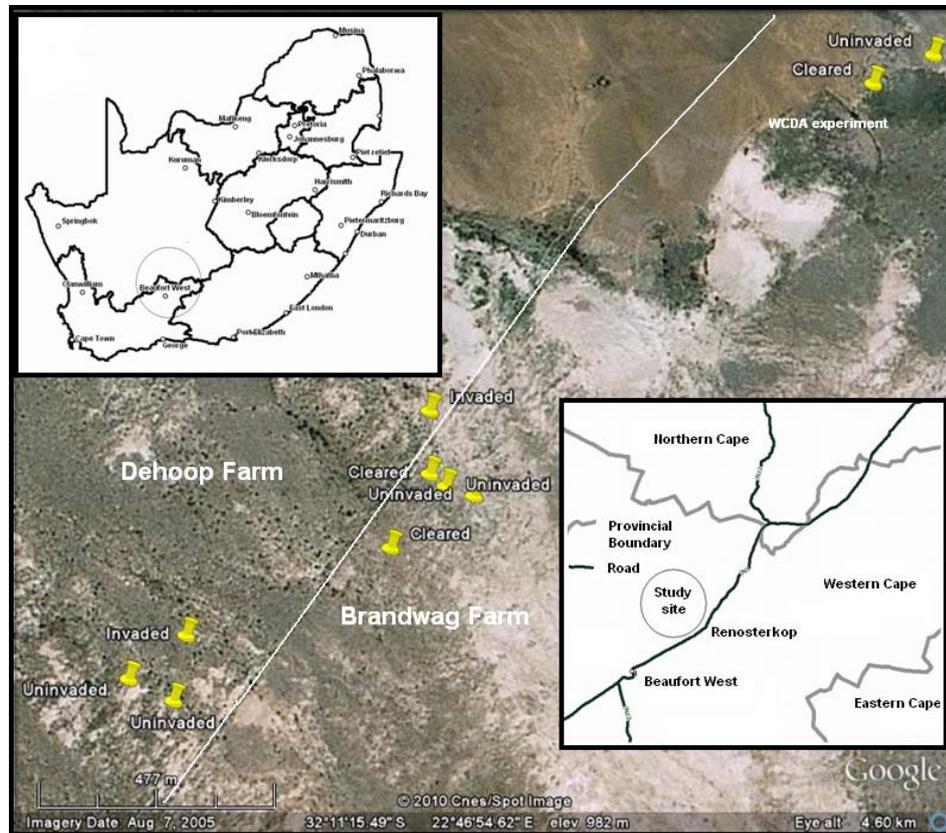


Figure 3.1 Map showing the location of the study site and the placement of sampling plots. Satellite image obtained from Google Earth (Version 5.1.3533.1731). Mountain View, CA: Google Inc. (2009).

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 Garlon® 4 herbicide (triclopyr ester) at a four percent 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.

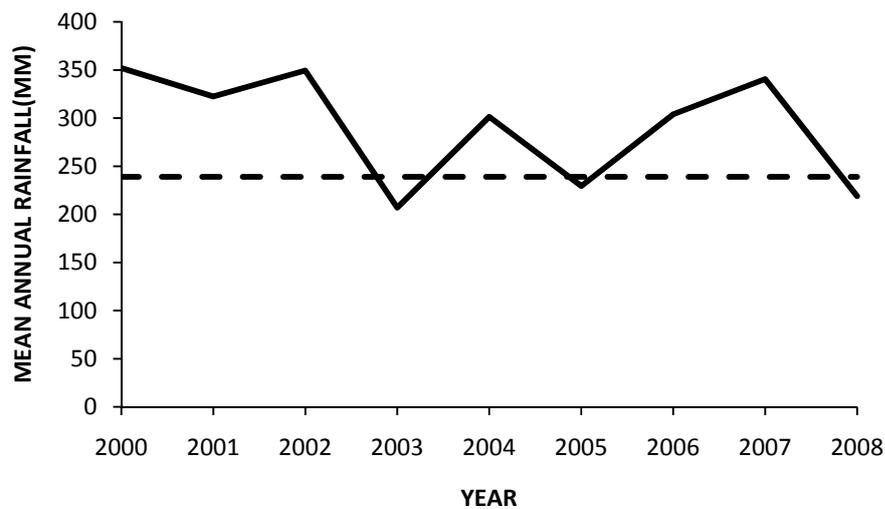


Figure 3.1 Mean annual rainfall for Beaufort West from 2000 to 2008 (South African Weather Service – unpublished data). The dashed line represents long term mean rainfall calculated over 126 years (1878-2004, Kraaij and Milton 2006).

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*100 metre 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 be as closely environmentally matched with the WCDA experimental site conditions as possible. To combat the problem of temporally un-replicated cleared plots inherited from the WCDA experiment, we pooled the 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 Brandwag while invaded sites (n = 2) were restricted to De Hoop (Figure 3.1). The invaded sites had comparable *Prosopis* tree size class distributions and an average cover of approximately 15%. Uninvaded sites (n = 5) were located on both De Hoop and Brandwag (Figure 3.1).

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

Data analysis

Plant species and functional type cover

Percent species covers per transect were calculated from intercept scores by dividing the total number of individual species intercepts in the top or lower canopy layers by 50 and multiplying the product by 100 (Herrick et al. 2005). Since the percent covers of individual plant species were evaluated independently, grouped species cover could exceed 100% (Fehmi 2010). Alien and indigenous species covers per transect were

calculated by summing the percent species covers of the individual alien and indigenous species that occurred along transects. Likewise, percent plant functional type covers per transect were determined by summing the individual percent species covers of species classified into six functional groups (viz. annual grass, perennial grass, annual herb, perennial herb, succulent shrub and non-succulent shrub). Mean alien and indigenous cover in uninvaded, invaded and cleared sites was calculated by averaging transect alien and indigenous species covers. Species were classified as alien or indigenous and grouped into functional types using published descriptions (Meredith 1955, Le Roux et al. 1994, Shearing and van Heerden 1994, Esler et al. 2006). The publications were also used to gather information on other species ecological attributes such as dispersal mode, habitat preference and interspecific competitiveness. *Prosopis* was excluded from all data sets.

Statistical analyses

Impact of invasion and clearing on vegetation composition

The impact of invasion and clearing on vegetation composition was evaluated by comparing plant species composition in uninvaded, invaded and cleared sites. Differences in species composition between uninvaded vs. invaded, invaded vs. cleared and uninvaded vs. cleared sites were taken to reflect invasion and clearing impacts. Uninvaded sites were regarded as representing pre-invasion states. Non-metric multidimensional scaling (NMDS, three dimensions, Bray-Curtis distances) was used to visually represent compositional relationships between sites while statistical significance was assessed using one way Analysis of Similarities (ANOSIM, sequential Bonferroni significance, 10 000 permutations, Bray-Curtis distances). NMDS is an ordination method that organises samples in multi-dimensional space according to compositional similarity (Kruskal 1964). NMDS results are displayed as two-dimensional diagrams in which compositionally similar sites are plotted near each other and dissimilar sites farther apart. ANOSIM is a non-parametric procedure that tests for significant differences between two or more multivariate groups (Clarke 1993). NMDS and ANOSIM analyses were conducted in the Paleontological Statistics Software Package for Education and Data Analysis (PAST, Hammer et al. 2001) using percent species cover per transect data.

The vegetation dynamics that underlay species composition changes during invasion and clearing were deduced from differences in the mean percent covers of the plant functional groups and species responsible for most of the compositional differences between uninvaded, invaded and cleared sites. Differences in mean percent cover of plant functional groups and species in uninvaded vs. invaded, invaded vs. cleared and uninvaded vs. cleared sites were taken to be the result (and thus indicative) of plant species composition changes caused by *Prosopis* invasion and clearing. Plant functional groups and species responsible for most (i.e. ~ 90%) of the compositional differences between sites were identified and ranked using Similarity of Percentage (SIMPER) analysis. SIMPER is a multivariate technique that ranks taxa according to their contribution to Bray Curtis dissimilarities between contrasted groups (Clarke 1993). SIMPER analyses were conducted in PAST using percent species cover per transect data.

Impact of invasion and clearing on alien and indigenous species richness

The impact of invasion and clearing on alien and indigenous species richness was determined by comparing alien and indigenous species richness in uninvaded vs. invaded, invaded vs. cleared and uninvaded vs. cleared sites. Comparisons were made using the Compare Diversities module in PAST (1000 bootstrap randomisations, Hammer et al. 2001). Compare Diversities computes a number of diversity indices for paired samples and statistically compares them through permutation or bootstrap randomisation (Hammer et al. 2001). Mean alien and indigenous species presence-absence data per site (derived from alien and indigenous species cover per site data) were used in the richness calculations and significance testing. The analyses excluded *Prosopis*.

The minimum species richness estimates calculated from sample-based line point intercept data (Herrick et al. 2005) were supplemented by statistically estimated “actual” species richness’. “Actual” species richness’ per transect were estimated using the program EstimateS Version 8 (10 000 randomisations with default settings, R. K. Colwell, downloaded from <http://purl.oclc.org/estimates>). Three estimators of species richness were used: Incidence-based coverage estimator (ICE, Chao et al. 2000), Chao 2 richness estimator (Chao 1984), and the second-order Jackknife richness estimator (Jackknife 2, Burnham and Overton 1979). Alien and indigenous species presence-absence data per transect (derived from alien and indigenous species cover per transect data) were used to

estimate the “actual” species richness’. The impacts of invasion and clearing on “actual” species richness were evaluated by comparing the means of the estimated richness’ in uninvaded vs. invaded, invaded vs. cleared and uninvaded vs. cleared sites. The significance of the differences were assessed using the One Way ANOVA via Randomisation test in the software package Resampling Procedures 1.3 (10 000 randomisations, David C. Howel, University of Vermont, downloaded from <http://www.uvm.edu/dhowell/statPages/Resampling/Resampling.html>). 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). Variation around means was expressed in standard errors.

Impact of invasion and clearing on vegetation structure

The impact of *Prosopis* invasion and clearing on vegetation structure was determined by comparing mean alien and indigenous species cover in uninvaded, invaded and cleared sites. The vegetation dynamics that underlay the observed alien and indigenous species cover changes were deduced from differences in mean alien and indigenous plant functional type and species cover between the sites. Cover differences between uninvaded vs. invaded, invaded vs. cleared and uninvaded vs. cleared sites were taken to represent the impacts of invasion and clearing. Alien and indigenous plant functional types whose mean cover differences tested significant were analysed to species level. The relative magnitudes of the vegetation changes were evaluated by considering the extents of the cover changes that were associated with them. Means and standard errors were calculated using the program PAST while the significance of differences in plant functional type and species covers was assessed using Resampling Procedures 1.3 (One Way ANOVA, 10 000 randomisations).

Results

Impact of invasion and clearing on vegetation composition

As expected, invasion and clearing altered plant species composition in affected rangeland. The composition changes were however not substantial. Clearing caused the greatest change in species composition. Plant species composition in cleared rangeland had not reverted to the pre-invasion state after more than four years. Although there was great overlap, the 95% NMDS confidence ellipses around uninvaded, invaded and cleared transects did not completely coincide with each other (Figure 3.3). The dissimilarities in species composition between uninvaded vs. invaded, invaded vs. cleared and uninvaded vs. cleared sites were significant ($R = 0.21, P < 0.001$; $R = 0.31, P < 0.001$; $R = 0.27, P < 0.001$). The greatest dissimilarity in species composition was between invaded vs. cleared sites (Overall average dissimilarity = 62%) followed by uninvaded vs. invaded (Overall average dissimilarity = 57%) and uninvaded vs. cleared (Overall average dissimilarity = 56%) sites.

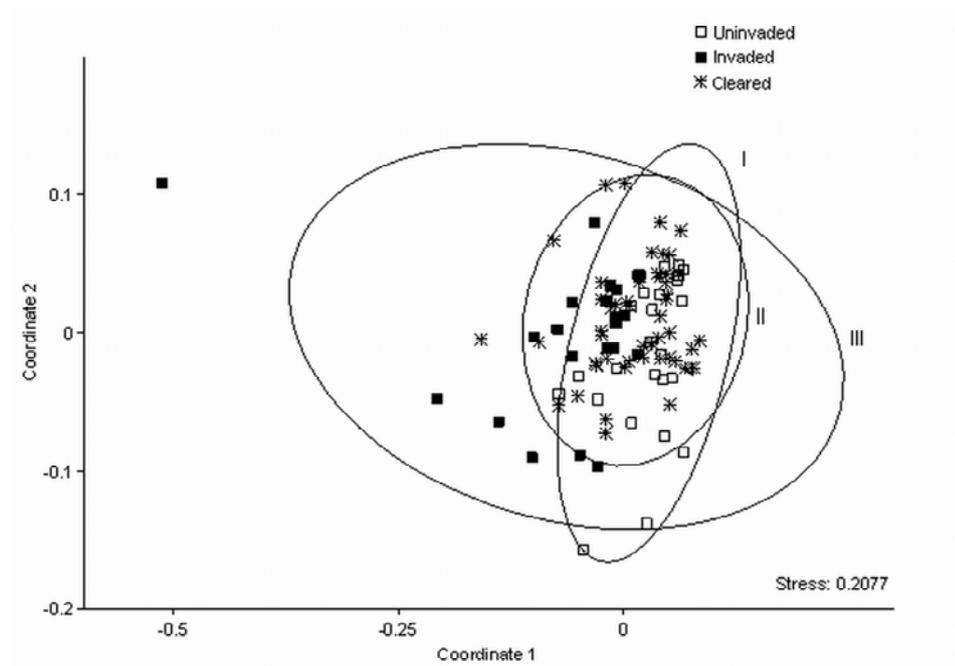


Figure 3.2 Three-dimensional NMDS plot showing plant species composition relationships between uninverted, inverted and cleared transects. Also shown are 95% confidence ellipses (I = uninverted, II = cleared and III = inverted).

The major vegetation changes that underlay species composition change during invasion were declines in abundance of the annual grass *Aristida adscensionis* and the non-succulent shrub *Pentzia incana* and increases in abundance of the annual and perennial grasses *Chloris virgata* and *Cynodon dactylon* (Table 3.1). Minor vegetation changes included reductions in abundance of the non succulent shrubs *Felicia muricata* and *Rosenia humilis* and increases in the abundance of the annual grass *Setaria verticillata* and the non-succulent shrubs *Lycium cinerium*, *Salsola tuberculata*, *Atriplex lindleyi*, *Kochia salsoloides*, *Lycium prunus-spinosa* and *Salsola calluna* (Table 3.1). Invasion completely displaced the annual grass *Tragus berteronianus* and facilitated the establishment of the non succulent shrub *Pentzia lanata* (Table 3.1).

Plant species compositional change after clearing was driven mainly by increases in the abundance of the annual grass *A. adscensionis*, the non-succulent shrub *P. incana*, and the perennial grasses *Eragrostis obtusa* and *C. dactylon* (Table 3.2). Other minor changes included increases in abundance of the annual grasses *S. verticillata*, the perennial grass *Eragrostis lehmanniana* and the non succulent shrubs, *L. cinerium* and *F. muricata* and declines in the annual grass *C. virgata* and the non succulent shrubs *P. lanata*, *L. prunus-spinosa*, *A. lindleyi*, *K. salsoloides*, and *S. tuberculata* (Table 3.2). Clearance facilitated the establishment of the annual and perennial grasses *T. berteronianus* and *E. obtusa* (Table 3.2).

Cleared rangeland differed mainly from uninvaded rangeland in having a lower abundance of the non succulent shrub *P. incana* and higher abundances of the annual grass *A. adscensionis* and the perennial grasses *E. obtusa* and *C. dactylon* (Table 3.3). Other minor differences included higher abundances of the annual grasses *C. virgata*, *T. berteronianus* and *S. verticillata*, the perennial grass *E. lehmanniana*, the alien annual herb *Medicago laciniata* and the non-succulent shrubs *F. muricata*, *Lycium cinerium*, *L. prunus-spinosa*, *L. oxycarpum* and *Asparagus retrofractus*, and lower abundances of non-succulent shrubs *R. humilis* and *S. tuberculata* (Table 3.3).

Table 3.1. Percent contributions to Bray-Curtis compositional dissimilarity and mean percent covers of 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

	% contribution to dissimilarity	Mean percent cover		
		Uninvaded	Invaded	Difference
Plant functional type				
Non succulent shrub	42.74	28.60	28.39	-0.21
Annual grass	35.15	27.88	27.13	-0.75
Perennial grass	8.49	2.96	6.45	3.49
Non succulent shrub				
<i>Pentzia incana</i>	17.52	17.80	13.40	-4.40
<i>Lycium cinerium</i>	6.24	4.12	4.18	0.06
<i>Felicia muricata</i>	3.03	1.84	1.27	-0.57
<i>Salsola tuberculata</i>	2.92	1.40	1.73	0.33
<i>Atriplex lindleyi</i>	2.78	0.20	1.82	1.62
<i>Kochia salsoloides</i>	2.59	0.36	1.45	1.09
<i>Pentzia lanata</i>	2.27	0.00	2.09	2.09
<i>Rosenia humilis</i>	2.24	1.88	0.27	-1.61
<i>Lycium prunus-spinosa</i>	1.74	0.32	1.45	1.13
<i>Salsola calluna</i>	1.41	0.68	0.73	0.05
Annual grass				
<i>Aristida adscensionis</i>	22.05	25.20	16.50	-8.70
<i>Chloris virgata</i>	10.70	1.88	9.45	7.57
<i>Setaria verticillata</i>	1.46	0.16	1.18	1.02
<i>Tragus berteronianus</i>	0.95	0.64	0.00	-0.64
Perennial grass				
<i>Cynodon dactylon</i>	8.49	2.96	6.45	3.49

Table 3.2. Percent contributions to Bray-Curtis compositional dissimilarity and mean percentage covers of 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.

	% contribution to dissimilarity	Mean percent cover		
		Invaded	Cleared	Difference
Plant functional type				
Annual grass	37.23	27.13	46.72	19.59
Non succulent shrub	30.51	25.66	27.55	1.89
Perennial grass	19.18	6.54	18.92	12.38
Annual grass				
<i>Aristida adscensionis</i>	26.00	16.50	39.80	23.30
<i>Chloris virgata</i>	7.39	9.45	3.85	-5.60
<i>Setaria verticillata</i>	2.29	1.18	1.69	0.51
<i>Tragus berteronianus</i>	1.56	0.00	1.38	1.38
Non succulent shrub				
<i>Pentzia incana</i>	10.84	13.40	14.10	0.70
<i>Lycium cinerium</i>	5.10	4.18	4.92	0.74
<i>Felicia muricata</i>	4.97	1.27	5.38	4.11
<i>Pentzia lanata</i>	2.27	2.09	1.08	-1.01
<i>Lycium prunus-spinosa</i>	2.04	1.45	1.38	-0.07
<i>Atriplex lindleyi</i>	1.88	1.82	0.08	-1.74
<i>Kochia salsoloides</i>	1.71	1.45	0.46	-0.99
<i>Salsola tuberculata</i>	1.69	1.73	0.15	-1.58
Perennial grass				
<i>Eragrostis obtusa</i>	8.21	0.00	7.54	7.54
<i>Cynodon dactylon</i>	7.84	6.45	7.92	1.47
<i>Eragrostis lehmanniana</i>	3.13	0.09	3.46	3.37

Table 3.3. Percent contributions to Bray-Curtis compositional dissimilarity and mean percentage covers of 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

	% contribution to dissimilarity	Mean percent cover		
		Uninvaded	Cleared	Difference
Plant functional type				
Non succulent shrub	34.60	28.04	29.86	1.82
Annual grass	32.22	27.88	46.72	18.84
Perennial grass	20.80	3.40	18.92	15.52
Annual herb	1.07	0.20	1.00	0.80
Non succulent shrubs				
<i>Pentzia incana</i>	13.89	17.80	14.10	-3.70
<i>Lycium cinerium</i>	5.97	4.12	4.92	0.80
<i>Felicia muricata</i>	5.79	1.84	5.38	3.54
<i>Rosenia humilis</i>	2.17	1.88	0.85	-1.03
<i>Salsola tuberculata</i>	1.63	1.40	0.15	-1.25
<i>Lycium prunus-spinosa</i>	1.52	0.32	1.38	1.06
<i>Asparagus retrofractus</i>	1.37	0.64	0.92	0.28
<i>Lycium oxycarpum</i>	1.21	0.04	1.08	1.04
<i>Pentzia lanata</i>	1.06	0.00	1.08	1.08
Annual grasses				
<i>Aristida adscensionis</i>	24.55	25.20	39.80	14.60
<i>Chloris virgata</i>	3.88	1.88	3.85	1.97
<i>Tragus berteronianus</i>	1.97	0.64	1.38	0.74
<i>Setaria verticillata</i>	1.82	0.16	1.69	1.53
Perennial grasses				
<i>Eragrostis obtusa</i>	8.91	0.12	7.54	7.42
<i>Cynodon dactylon</i>	8.41	2.96	7.92	4.96
<i>Eragrostis lehmanniana</i>	3.49	0.32	3.46	3.14

Annual herbs				
<i>Medicago laciniata</i>	1.07	0.20	1.00	0.80

Impact of invasion and clearing on alien species richness and cover

Invasion did not change the richness of alien species (three or four species) but increased their cover from 0.44 to 2 % (Figure 3.4). Clearing reduced alien species richness by one or two species and cover from 2 to 1 % (Figure 3.4). Alien species richness declined to below pre-invasion levels after clearing while species cover declined to pre-invasion levels. This situation persisted for more than four years after clearing. There was no significant difference in alien species richness (ICE richness $F = 2.24$ $P = 0.136$, Chao2 richness $F = 0.05$ $P = 0.839$, Jackknife 2 richness $F = 1.10$ $P = 0.292$) between uninvaded and invaded sites (Table 3.4). Mean alien species cover in invaded sites (2.18 ± 0.49 %) was significantly higher ($F = 20.08$, $P < 0.001$) than in uninvaded sites (0.44 ± 0.14 %). Cleared sites had significantly lower alien species richness (ICE richness $F = 90.51$ $P < 0.001$, Chao2 richness $F = 25.05$ $P < 0.001$, Jackknife 2 richness $F = 16.53$ $P < 0.001$) than invaded sites (Table 3.4). Cleared sites had mean alien species cover (1.08 ± 0.35 %) significantly lower ($F = 3.47$, $P = 0.051$) than invaded sites. Cleared sites had significantly fewer alien species (ICE richness $F = 15.12$ $P < 0.001$, Chao2 richness $F = 28.54$ $P < 0.001$, Jackknife 2 richness $F = 18.05$ $P < 0.001$) than uninvaded sites (Table 3.4).

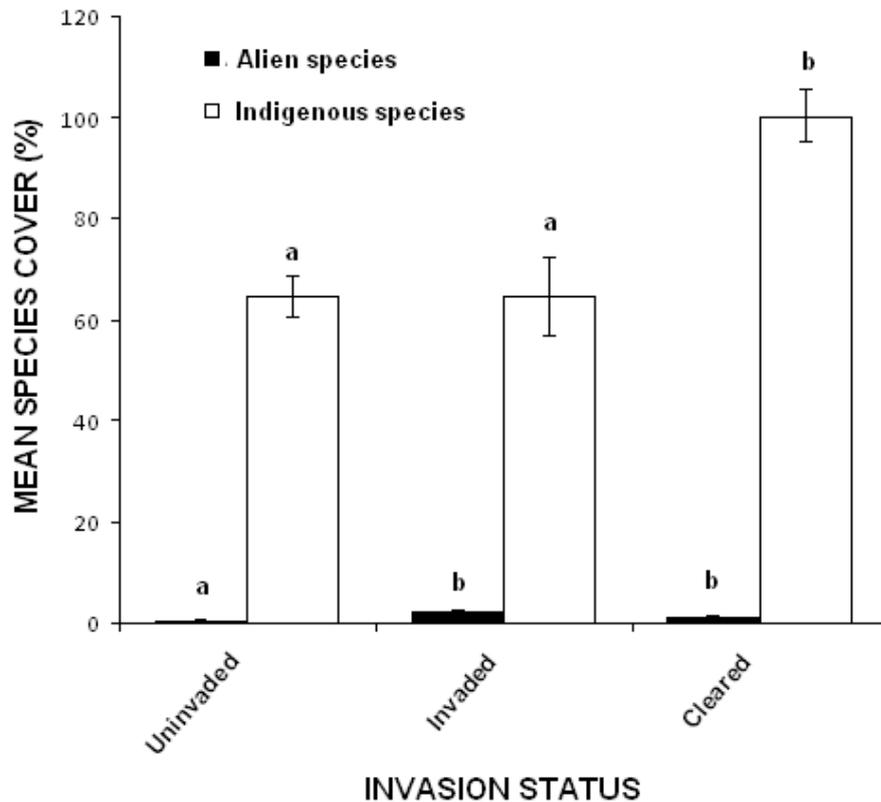


Figure 3.3 Comparison of alien and indigenous species covers for uninvaded (n = 5), invaded (n = 2) and cleared (n = 3) sites. The error bars are times one standard error. Significance determined by One Way ANOVA via randomisation.

The gain in alien species cover during invasion and the loss after clearing were solely due to increases and declines in abundance of the non succulent shrub *A. lindleyi*. The reduction in alien species cover after clearing was counteracted to a lesser extent by an accompanying increase in the cover of the alien annual herb *M. laciniata*. The third alien species, the non succulent shrub *Atriplex semibaccata* was not affected by invasion or clearing. *Atriplex lindleyi* had significantly different mean covers in uninvaded vs. invaded ($F = 31.369, P < 0.001$) and invaded vs. cleared sites ($F = 24.763, P < 0.001$) (Table 3.4). The mean cover of *M. laciniata* was significantly higher ($F = 5.28, P = 0.037$)

in cleared than in invaded sites (Table 3.5). There was no significant difference in the mean cover of *A. semibaccata* between uninvaded and invaded sites ($F = 1.51$, $P = 0.306$) and invaded and cleared sites ($F = 1.19$, $P = 0.456$) (Table 3.5).

Table 3.4. Comparison of plant species richness in uninvaded ($n = 5$), invaded ($n = 2$) and cleared sites ($n = 3$) sites near Beaufort West in the Western Cape Province of South Africa. Different superscript letters along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Uninvaded	Invaded	Cleared
Alien species			
Observed richness	3	3	2
ICE richness	2.85 ± 0.14^a	3.25 ± 0.25^a	1.98 ± 0.15^b
Chao 2 richness	2.33 ± 0.11^a	2.37 ± 0.19^a	1.48 ± 0.08^b
Jackknife 2 richness	3.43 ± 0.15^a	3.83 ± 0.39^a	2.42 ± 0.19^b
Indigenous species			
Observed richness	43 ^a	27 ^b	40 ^{ac}
ICE estimated richness	46.35 ± 0.70^a	30.54 ± 1.12^b	46.13 ± 1.17^{ac}
Chao 2 estimated richness	43.07 ± 0.98^a	35.86 ± 1.75^b	46.13 ± 1.17^{ac}
Jackknife 2 estimated richness	47.34 ± 1.65^a	30.30 ± 2.10^b	44.14 ± 2.68^{ac}

Table 3.5. Mean percent alien plant functional type and species cover in uninvaded (n = 5), invaded (n = 2) and cleared (n = 3) sites near Beaufort West in the Western Cape Province of South Africa. Different superscript letters along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Mean percent cover		
	Uninvaded	Invaded	Difference
Plant functional type			
Annual herb	0.20 ± 0.10 ^a	0.09 ± 0.09 ^a	-0.11
Non succulent shrub	0.24 ± 0.11 ^a	2.09 ± 0.46 ^b	1.85
Non succulent shrub			
<i>Atriplex lindleyi</i>	0.20 ± 0.10 ^a	1.82 ± 0.37 ^b	1.62
<i>Atriplex semibaccata</i>	0.04 ± 0.04 ^a	0.27 ± 0.27 ^a	0.23
	Invaded	Cleared	
Plant functional type			
Annual herb	0.09 ± 0.09 ^a	1.00 ± 0.36 ^b	0.91
Non succulent shrub	2.09 ± 0.46 ^a	0.08 ± 0.08 ^b	-2.01
Annual herb			
<i>Medicago laciniata</i>	0.09 ± 0.09 ^a	1.00 ± 0.36 ^b	0.91
Non succulent shrub			
<i>Atriplex lindleyi</i>	1.82 ± 0.37 ^a	0.08 ± 0.08 ^b	-1.74
<i>Atriplex semibaccata</i>	0.27 ± 0.27 ^a	0.00 ^a	-0.27

Table 3.6. Mean percent indigenous plant functional type and species cover in uninvaded (n = 5) vs. invaded (n = 2) sites near Beaufort West in the Western Cape Province of South Africa. Different superscript letters along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Mean percent cover		
	Uninvaded	Invaded	Difference
Plant functional type			
Annual grass	27.84 ± 1.92 ^a	27.09 ± 3.67 ^a	-0.75
Perennial grass	4.40 ± 0.81 ^a	6.55 ± 1.70 ^a	2.15
Annual herb	0.28 ± 0.10 ^a	0.36 ± 0.21 ^a	0.08
Perennial herb	0.12 ± 0.07 ^a	0.15 ± 0.27 ^a	0.03
Succulent shrub	0.27 ± 0.15 ^a	0.08 ± 0.08 ^a	-0.19
Non succulent shrub	0.28 ± 0.10 ^a	0.15 ± 0.27 ^a	-0.13

Table 3.7. Mean percent indigenous plant functional type and species cover in invaded (n = 2) vs. cleared (n = 3) sites near Beaufort West in the Western Cape Province of South Africa. Different superscript letters along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Mean percent cover		
	Invaded	Cleared	Difference
Plant functional type			
Annual grass	27.09 ± 3.67 ^a	46.69 ± 4.49 ^b	19.6
Perennial grass	6.55 ± 1.70 ^a	20.31 ± 3.21 ^b	13.76
Annual herb	0.36 ± 0.21 ^a	0.85 ± 0.34 ^a	0.49
Perennial herb	0.27 ± 0.15 ^a	0.46 ± 0.17 ^a	0.19
Succulent shrub	0.27 ± 0.15 ^a	0.08 ± 0.08 ^a	-0.19
Non succulent shrub	27.45 ± 3.06 ^a	31.62 ± 2.58 ^a	4.17
Annual grass			
<i>Aristida adscensionis</i>	16.45 ± 2.22 ^a	39.77 ± 4.63 ^b	23.32
<i>Tragus berteronianus</i>	0.00 ^a	1.38 ± 0.48 ^b	1.38
<i>Chloris virgata</i>	9.45 ± 1.85 ^a	3.85 ± 0.60 ^b	-5.6
<i>Setaria verticillata</i>	1.18 ± 0.76 ^a	1.69 ± 0.78 ^a	0.51
Perennial grass			
<i>Eragrostis obtusa</i>	0.00 ^a	7.54 ± 1.72 ^b	7.54
<i>Eragrostis lehmanniana</i>	0.09 ± 0.09 ^a	3.46 ± 1.01 ^b	3.37
<i>Aristida congesta</i>	0.00 ^a	0.46 ± 0.34 ^a	0.46
<i>Cynodon dactylon</i>	6.45 ± 1.64 ^a	7.92 ± 1.67 ^a	1.47
<i>Fingerhuthia africana</i>	0.00 ^a	0.31 ± 0.18 ^a	0.31
<i>Cenchrus ciliaris</i>	0.00 ^a	0.15 ± 0.15 ^a	0.15
<i>Stipagrostis ciliata</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08

Table 3.8. Mean percent indigenous plant functional type and species cover in uninvaded (n = 5) vs. cleared (n = 3) sites near Beaufort West in the Western Cape Province of South Africa. Different superscript letters along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Mean percent cover		
	Uninvaded	Cleared	Difference
Plant functional type			
Annual grass	27.84 ± 1.92 ^a	46.69 ± 4.49 ^b	18.85
Perennial grass	4.40 ± 0.81 ^a	20.31 ± 3.12 ^b	15.91
Annual herb	0.28 ± 0.10 ^a	0.85 ± 0.34 ^a	0.57
Perennial herb	0.12 ± 0.07 ^a	0.46 ± 0.17 ^b	0.34
Succulent shrub	0.28 ± 0.10 ^a	0.08 ± 0.08 ^a	-0.20
Non succulent shrub	30.92 ± 2.76 ^a	31.62 ± 2.58 ^a	0.70
Annual grass			
<i>Aristida adscensionis</i>	25.16 ± 1.88 ^a	39.77 ± 4.63 ^b	14.61
<i>Chloris virgata</i>	1.88 ± 0.37 ^a	3.85 ± 0.60 ^b	1.97
<i>Tragus berteronianus</i>	0.64 ± 0.18 ^a	1.38 ± 0.48 ^a	0.74
<i>Setaria verticillata</i>	1.18 ± 0.76 ^a	1.69 ± 0.78 ^b	0.51
Perennial grass			
<i>Eragrostis obtusa</i>	0.12 ± 0.07 ^a	7.54 ± 1.72 ^b	7.42
<i>Cynodon dactylon</i>	2.96 ± 0.81 ^a	7.92 ± 1.67 ^b	4.96
<i>Eragrostis lehmanniana</i>	0.32 ± 0.16 ^a	3.46 ± 1.01 ^a	3.14
<i>Aristida congesta</i>	0.00 ^a	0.46 ± 0.34 ^a	0.46
<i>Cenchrus ciliaris</i>	0.00 ^a	0.15 ± 0.15 ^a	0.15
<i>Sporobolus iocladius</i>	0.04 ± 0.04 ^a	0.15 ± 0.11 ^a	0.11
<i>Stipagrostis obtusa</i>	0.24 ± 0.11 ^a	0.23 ± 0.13 ^a	-0.01
<i>Fingerhuthia africana</i>	0.32 ± 0.16 ^a	0.31 ± 0.18 ^a	-0.01
<i>Sporobolus fimbriatus</i>	0.04 ± 0.04 ^a	0.00 ^a	-0.04
<i>Stipagrostis ciliata</i>	0.28 ± 0.10 ^a	0.08 ± 0.08 ^a	-0.20
Perennial herb			
<i>Galenia pubescens</i>	0.00 ^a	0.23 ± 0.13 ^b	0.23
<i>Blepharis capensis</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
<i>Ammocharis coranica</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
<i>Drosanthemum hispidum</i>	0.27 ± 0.15 ^a	0.08 ± 0.08 ^a	-0.19

Impact of invasion and clearing on indigenous species richness and cover

Invasion reduced the richness of indigenous species by six or seven species but did not affect total cover (Figure 3.4). Clearing increased indigenous species richness by between 10 and 15 species and cover from 65 to 100 % (Figure 3.4). Indigenous species richness in cleared rangeland reverted to the pre-invasion level (between 40 and 47 species) while cover remained 36 % higher than the pre-invasion level (i.e. 65 %) after more than four years after clearing (Figure 3.4). Indigenous species richness was significantly lower (Observed richness $P < 0.001$, ICE richness $F = 148.48$ $P < 0.001$, Chao2 richness $F = 14.76$ $P < 0.001$, Jackknife 2 richness $F = 35.59$ $P < 0.001$) in invaded than uninvaded sites (Table 3.4). There was no significant difference ($F = 0.00$, $P < 1.000$) in mean indigenous species cover between uninvaded (64.60 ± 4.09 %) and invaded sites (64.64 ± 7.80 %). Indigenous species richness was significantly higher (Observed richness $P < 0.001$, ICE richness $F = 90.51$ $P < 0.001$, Chao2 richness $F = 25.50$ $P < 0.001$, Jackknife 2 richness $F = 16.53$ $P < 0.001$) in cleared than invaded sites (Table 3.4). Mean indigenous species cover in cleared sites (100.23 ± 5.31 %) was significantly higher ($F = 14.95$, $P < 0.001$) than in invaded sites. There was no significant difference (Observed richness $P = 0.356$, ICE richness $F = 0.03$ $P = 0.866$, Chao2 richness $F = 3.64$ $P = 0.059$, Jackknife 2 richness $F = 1.18$ $P = 0.292$) in indigenous species richness in uninvaded and cleared sites (Table 3.4). Cleared sites had mean indigenous species cover significantly higher ($F = 27.06$, $P < 0.001$) than uninvaded sites.

There was no change in the cover of grasses, herbs and shrubs during invasion. The increase in indigenous species cover after clearing was due to increases in abundance of the annual grasses *A. adscensionis* and *T. berteronianus* and, to a lesser extent, the perennial grasses *E. obtusa* and *E. lehmanniana*. Indigenous species cover in cleared rangeland was higher than the pre-invasion level due to higher abundances of the annual grasses *A. adscensionis*, *C. virgata* and *S. verticillata*, perennial grasses *E. obtusa* and *C. dactylon* and the perennial herb *Galenia pubescens*. There was no significant difference ($F = 0.04$, $P = 0.857$, $F = 1.67$, $P = 0.212$, $F = 0.17$, $P = 0.753$, $F = 1.15$, $P = 0.356$, $F = 0.00$, $P = 1.000$, $F = 0.56$ $P = 0.466$) in mean annual grass, perennial grass, annual herb,

perennial herb, succulent shrub and non-succulent shrub cover between uninvaded and invaded sites (Table 3.6). Only indigenous annual and perennial grasses had significantly different mean covers ($F = 10.88$, $P = 0.079$, $F = 13.58$, $P < 0.001$) in invaded and cleared sites (Table 3.7). Of the annual and perennial grasses present in the study sites *A. adscensionis* ($F = 18.42$, $P < 0.001$), *T berteronianus* ($F = 6.99$, $P = 0.004$), *E. obtusa* ($F = 16.14$, $P < 0.001$) and *E. lehmanniana* ($F = 9.38$, $P < 0.001$) had significantly different mean covers in invaded and cleared sites (Table 3.7). Indigenous annual grasses ($F = 2.30$, $P < 0.001$), perennial grasses ($F = 40.33$, $P < 0.001$) and perennial herbs ($F = 4.97$, $P = 0.052$) had significantly different covers in uninvaded and cleared sites (Table 8). At species level, the annual grasses *A. adscensionis* ($F = 11.95$, $P = 0.001$), *C. virgata* ($F = 5.58$, $P = 0.005$) and *S. verticillata* ($F = 7.07$, $P = 0.009$), perennial grasses *E. obtusa* ($F = 18.42$, $P < 0.001$) and *C. dactylon* ($F = 18.42$, $P < 0.001$) and the perennial herb *G. pubescens* ($F = 18.42$, $P < 0.001$) had significantly different mean covers in uninvaded and cleared sites (Table 3.8).

Discussion

Several studies have shown that *Prosopis* invasion and clearing can strongly influence the composition, diversity and structure of understory or adjacent vegetation (Kincaid et al. 1959, Cable and Tschirley 1961, Scifres et al. 1974, Scifres and Polk 1974, Cable 1976, Tiedemann and Klemmedson 1977, Martin and Morton 1993, Ruthven 2001, Dean et al. 2002, Tiedemann and Klemmedson 2004, McClaran and Angell 2006, Pease et al. 2006, Simmons et al. 2008). Most of the studies were conducted in semi-arid, arid and desert rangelands in the Southern and South-western United States.

Impact of invasion and clearing on plant species composition

Species composition change during invasion involved both increases and decreases in grass and shrub abundance. This was probably because, while *Prosopis* trees generally compete with plants in their understory or neighbourhood for light, moisture and nutrients

(Tiedemann and Klemmedson 1977, Meyer and Bovey 1986) they also act as nurse plants for other sub-canopy species by creating ideal microhabitats via nitrogen fixation and shading (Ruthven 2001). For example, while the decline in the annual grass *A. adscensionis* during invasion was most likely due to competition for light (shading) from invading *Prosopis* trees the increases in the annual grasses *C. virgata* and *S. verticillata*, the perennial grass *C. dactylon* and the non-succulent shrubs *A. lindleyi* and *S. tuberculata* were most probably in response to the establishment of favourable environmental conditions in the sub canopies and neighbourhoods of the trees. *Aristida. adscensionis* performs poorly in shade (Varshney 1968) while *C. virgata*, *C. dactylon* and the alien non-succulent shrub *A. lindleyi* tolerate shade and are hardy colonisers of bare or disturbed soil (Le Roux et al. 1994, Shearing and van Heerden 1994, Esler et al. 2006). *Setaria verticillata* thrives in nitrogen-enriched shaded environments and *S. tuberculata* can withstand low moisture conditions (Le Roux et al. 1994, Shearing and van Heerden 1994, Esler et al. 2006). *Prosopis* trees, by denuding their neighbourhood of vegetation cover (Gibbens et al. 1986), enriching their sub-canopy with nitrogen and other soil nutrients (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) and lowering moisture content in surrounding soil (Tiedemann and Klemmedson 1973, Tiedemann and Klemmedson 1977, Jacoby et al. 1982), provide ideal conditions for the establishment and increase of such species.

Some of the species composition changes that occurred during invasion could have been caused indirectly by *Prosopis*. The loss of *A. adscensionis* due to shading by *Prosopis* trees, for example, could have intensified grazing pressure on the non-succulent shrub *P. incana* and led to its decline. *Pentzia incana* like *A. adscensionis* is resilient to heavy grazing and is an important component of forage production in overgrazed rangeland (Le Roux et al. 1994, Shearing and van Heerden 1994, Esler et al. 2006). Likewise, the non-succulent shrubs *L. cinereum* and *L. spinosum*, which produce small edible fruits, could have increased as a result of increased dispersal by birds perching on invading *Prosopis* trees (Dean et al. 2002, Milton et al. 2007, Iponga et al. 2009). However this advantage could have been limited as the steep angles of *Prosopis* canopies are thought to discourage maximum utilisation of the trees by birds (Dean et al. 2002).

The increases in the annual grasses *A. adscensionis*, *S. verticillata*, *T. berteronianus*, the perennial grasses *E. obtusa*, *C. dactylon*, *E. lehmanniana* and the non-succulent shrubs *P. incana*, *L. cinerium* and *F. muricata* that drove species composition change after clearing were most likely in response to the release of the species from *Prosopis* competition. In the case of the annual grasses *A. adscensionis* and *T. berteronianus*, and the perennial grasses *E. obtusa* and *E. lehmanniana* which are shade-intolerant (Varshney 1968, Klink and Joly 1989, Veenendaal et al. 1993), increases after clearing were most certainly due to cessation of shading. The increase in abundance of the grasses could have reduced the grazing pressure on the comparatively less palatable non-succulent shrubs *P. incana* and *F. muricata* and led to their increase. On the other hand, the increase in abundance of the abovementioned grasses could have led to the declines in the annual grass *C. virgata*, the alien herb *A. lindleyi* and the non-succulent shrubs *P. lanata*, *L. prunus-spinosa*, *K. salsoloides* and *S. tuberculata* through increased inter-specific competition for soil moisture. The annual grass *C. virgata* and the alien herb *A. lindleyi* are poor competitors that naturally occur in disturbed or bare areas denuded of competing plants (Le Roux et al. 1994, Shearing and van Heerden 1994, Esler et al. 2006). *Prosopis* invasion probably intensified the competition for soil water by denuding neighbouring soil of vegetation cover and exposing it to greater solar radiation heating and increased moisture loss. Soil moisture is the most important limiting factor in the Nama Karoo (Milton 1995).

The higher than usual grass cover in cleared rangeland was probably a legacy of *Prosopis* soil nutrient enrichment. *Prosopis* trees accumulate soil nutrients such as carbon, nitrogen, magnesium, potassium and phosphorous 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). Non succulent shrubs could have declined due to increased competition from grasses. Competition between grasses and woody plants is critical in arid and semi-arid areas (Jacoby et al. 1982, Milton 1995).

Impact of invasion and clearing on alien and indigenous species richness and cover

The alien flora of the Nama Karoo reflects the region's climate and economics (Milton and Dean 1998). Unpredictable and quantitatively variable rainfall (Milton and Dean 1998, Esler et al. 2008) has ensured a sparse alien flora while widespread livestock production has resulted in the domination of the flora by introduced livestock-dispersed forage species (Milton and Dean 1998). Despite being severely degraded, our study site had only three alien species (besides *Prosopis*), viz. the opportunistic short-lived annual herb, *M. laciniata* and the drought-tolerant non succulent shrubs *A. lindleyi* and *A. semibaccata*. All three invasive alien species were either dispersed unintentionally by livestock or deliberately introduced into the Nama Karoo to increase the livestock carrying capacity. *Medicago laciniata* was probably unintentionally introduced into the region from Mediterranean North Africa in about 2000 BP with the spread of the herding culture, while the *Atriplex* species were intentionally imported from Australia and introduced into Nama Karoo rangeland between 1860 and 1890 (Milton and Dean 1998).

Invasion by *Prosopis* probably raised alien species cover (i.e. *A. lindleyi* cover) by directly creating favourable environmental conditions and indirectly altering competition dynamics. *Atriplex lindleyi* competes poorly against indigenous species (Milton and Dean 1998). However in cases where indigenous species cover is reduced, either by overgrazing or drought, *A. lindleyi* has been observed to regenerate profusely from seed (Milton and Dean 1998). The cue for *A. lindleyi* seeds to break dormancy is provided by moisture and nitrogen (Milton and Dean 1998). *Prosopis* trees fix nitrogen (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) and considerably reduce indigenous vegetation cover and species richness in Nama Karoo rangeland (Dean et al. 2002).

The decrease in *A. lindleyi* cover during clearing was most likely due to increasing competition from indigenous grasses. Like *A. lindleyi* the indigenous annual grasses *A. adscensionis* and *T. berteronianus* and perennial grasses *E. obtusa* and *E. lehmanniana* are also adapted to colonising disturbed ground and so would have offered intense

competition. The increase in indigenous species cover was probably due to the release of the grasses from *Prosopis* competition.

Invasion and clearing affected the diversity and structure of indigenous vegetation by changing grass species richness and cover. *Prosopis* trees compete intensely with grasses for light and moisture (McClaran and Angell 2006, Simmons et al. 2008). However indigenous species cover at our study site could have remained constant during invasion due to an overall balance between the decline in the abundance of *Prosopis*-intolerant grasses (e.g. *A. adscensionis* and *T. berteronianus*) and the accompanying increase in the abundance of *Prosopis*-tolerant grass species such as *C. virgata*, *S. verticillata* and *C. dactylon*. Since the compensatory increases and declines in abundance would have occurred within one functional type, grasses, there would have been no significant cover changes at functional type level during invasion. Indigenous vegetation cover and richness probably increased after clearing due to the removal of *Prosopis* competition.

Conclusion

Our results suggest that in heavily grazed Nama Karoo rangeland *Prosopis* invasion (~15 percent canopy cover) and clearing can significantly change rangeland species composition, with invasion leading to greater alien species cover and less indigenous species richness, and clearing to lesser alien species richness and greater indigenous species richness and cover. However invasion seems to have no effect on alien species richness and overall indigenous species cover. Clearing appears to facilitate the spontaneous restoration of alien species cover and indigenous species richness within four to six years but not species composition, alien species richness and indigenous species cover.

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**Effect of *Prosopis* (mesquite) invasion and clearing on soil
vegetation cover in degraded semi-arid Nama Karoo
rangeland, South Africa.**

Abstract

We assessed the effects of *Prosopis* invasion and clearing on soil vegetation cover (plant canopy and basal cover) in heavily grazed Nama Karoo rangeland on two sheep farms near the town of Beaufort West in the Western Cape Province of South Africa. Invasion did not change rangeland plant canopy cover while clearing increased it from 42% to 76%. Plant canopy cover in cleared rangeland was still 40% higher than the pre-invasion level more than four years after clearing. Plant canopy cover remained constant during invasion due to a balance between increasing *Prosopis* cover and declining grass cover. The decline in grass cover during invasion was mainly due to the loss of the annual grass *Aristida adscensionis*. The gain in rangeland plant canopy cover after clearing was mainly driven by increases in the abundance of *A. adscensionis*. Invasion reduced rangeland plant basal cover from 3% to 1% while clearing, in turn, increased it to 11%. Cleared rangeland still had 8% more plant basal cover than uninvaded rangeland more than four years after clearing. The vegetation changes associated with the reduction in rangeland plant basal cover during invasion were of such small magnitudes that no distinct patterns could be detected at the functional type and species level. The increase in plant basal cover after clearing was mostly due to increases in the cover of *A. adscensionis* and some unidentified perennial grasses and non-succulent shrubs. Plant canopy cover increased steeply during invasion up to a threshold of 6.40% *Prosopis* canopy cover after which it fell sharply from 93 to 34%. Plant canopy cover rose, albeit at a less steep rate, after the

drop at the threshold. Plant basal cover did not change during invasion up to a threshold of 20.40% *Prosopis* canopy cover after which it fell from 2 % to 0%. Our findings suggest that *Prosopis* invasion can lower rangeland plant canopy and basal cover in overgrazed and degraded Nama Karoo rangeland while clearing *Prosopis* from such rangeland can, even under heavy grazing, substantially raise vegetation cover. Clearing however does not lead to restoration of pre-invasion vegetation cover status within four to six years after clearing.

Key words: invasive alien plants, canopy cover, basal cover, soil erosion, rainfall infiltration, overland flow, Working for Water (WfW)

Introduction

The Nama Karoo is the largest of the three biomes that comprise the Karoo-Namib ecoregion of Southern Africa (Palmer and Hoffman 1997). The biome covers 22.7% of the land area of southern Africa (Palmer and Hoffman 1997). In South Africa the region occupies 346 100 km² (28% of the country) and covers much of the central and western regions of the country where it supports extensive commercial sheep and goat production on natural rangeland (Palmer and Hoffman 1997, Hoffman 2000, Suttie et al. 2005).

Large areas of the Nama Karoo have been invaded by an array of invasive alien plants (IAPs, Richardson and van Wilgen 2004, Henderson 2007). Notable among the IAPs are leguminous trees of the genus *Prosopis* which cover at least 18 000 km² of the region's low lying alluvial plains and seasonal watercourses. *Prosopis*, which is native to North and Central America, was introduced into South Africa in the late 1880s to provide shade, fodder, and fuel wood in arid regions (Zimmermann 1991, Zimmermann and Pasiecznik 2005). However the alien trees have turned out to have serious environmental impacts (Zimmermann and Pasiecznik 2005). In many areas the trees have coalesced to form dense thorn thickets that are thought to have displaced indigenous species and

substantially changed ecosystem structure and function (Richardson and van Wilgen 2004, Richardson et al. 2005).

Extensive areas of the Nama Karoo have been cleared of *Prosopis* 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, Le Maitre et al. 2002). Most of the clearings have been carried out using the standard WfW practice of reducing the above-ground biomass of alien plants and leaving the indigenous vegetation to recover without further intervention (Blanchard and Holmes 2008, Reinecke et al. 2008). It is unclear, however, whether this method leads to successful restoration in *Prosopis* invaded Nama Karoo rangeland (Saayman and Botha 2007).

Very little is known about the processes and effects of *Prosopis* invasion and clearing on vegetation cover in Nama Karoo rangeland. However savanna "bush encroachment" and tree thinning studies in South Africa have shown that increases in woody plant abundance invariably suppress herbaceous plants while removal of all or some of the trees promotes herbaceous growth (Smit and Rethman 1999, Smit 2003, Smit 2005). The relationship is however complicated by the interplay of antagonistic negative and positive tree-herbaceous plant interactions at the individual tree sub-canopy level (Smit 2005). The abundance of herbaceous plants under tree canopies may be enhanced by the favorable microclimatic and nutrient conditions obtaining there while at the same time being suppressed by low irradiance and competition for other more limiting belowground resources (Scholes and Archer 1997). The net result of the positive and negative tree-herbaceous plant interactions usually depend on the tree's size/age and on tree density at the landscape level (Scholes and Archer 1997, Smit 2005).

Under small young trees, facilitation processes are usually more effective than competition, and herbaceous production is enhanced; however as trees and shrubs become larger, competitive processes usually overshadow facilitation and adversely affect

herbaceous production (Scholes and Archer 1997, Riginos et al. 2009). The positive effects of trees on herbaceous diversity and production are usually greater where there are a few trees than where there are no trees, but the trend is reversed at high tree densities (Scholes and Archer 1997, Riginos et al. 2009).

As a result of these complicated interactions herbaceous plant cover in semi-arid savanna does not decline in a simple way with increasing woody plant abundance during “bush encroachment” but is stable up to a certain critical level after which it begins to decrease with increasing tree density. Since herbaceous plants provide most of the vegetation cover in semi-arid rangelands (Herrick et al. 2005b) such threshold effects could also apply to *Prosopis* - soil vegetation cover impacts in Nama Karoo rangeland. Thresholds have been reported for *Prosopis* effects on herbaceous forage production in arid and semi-arid rangelands in the South and South-western United States (McDaniel et al. 1982, Warren et al. 1996).

Vegetation cover is an important determinant of rainfall infiltration, runoff and erosion (Elwell and Stocking 1976, Dunne et al. 1991, Zuazo and Pleguezuelo 2008). Plant canopy cover promotes infiltration and limits runoff by protecting the soil surface from raindrop impact which causes detachment of soil particles and physical crusting (Elwell and Stocking 1976, Herrick et al. 2005b). Basal cover on the other hand reduces the erosive ability of runoff by dissipating its power through deflection and obstruction (Rogers and Schumm 1991, Herrick et al. 2005b). Soil erosion is a severe problem in semi arid areas where seasonal and annual drought cycles limit the development of vegetation cover (Smith et al. 1962).

We assessed and evaluated the effects of *Prosopis* invasion and clearing on soil vegetation cover in heavily grazed Nama Karoo rangeland on two sheep farms near the town of Beaufort West in the Western Cape Province of South Africa. Our aims were to (1) determine the effects of invasion and clearing on soil vegetation cover (plant canopy and basal cover), and (2) describe the vegetation changes that underlay the effects. We

hypothesized that *Prosopis* invasion would lower plant canopy and basal cover while clearing would restore them to pre-invasion levels. Additionally, we expected the effects of *Prosopis* invasion on canopy and basal cover to intensify as invasions became denser.

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 *P. glandulosa*, *P. juliflora*, and *P. velutina*) have hybridized extensively (Zimmermann 1991) such that most populations in South Africa are composed of overlapping morpho-types 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"), about 30 kilometres north-east of the town of Beaufort West in the Western Cape Province of South Africa (Figure 4.1). 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*, *Ruschia*) and Asteraceae (*Eriocephalus*, *Pentzia*, *Pteronia*) interspersed with grasses (*Aristida*, *Enneapogon*, *Digitaria* and *Stipagrostis*) (Palmer and Hoffman 1997). Taller shrubs and trees (*Acacia karroo*, *Euclea undulata* and *Rhigozum obovatum*) occur intermittently (Palmer and Hoffman 1997).

The area receives a mean annual rainfall of 239 mm (calculated for the period 1878-2004) of rain per year (Kraaij and Milton 2006). Mean annual rainfall has however been generally higher than the long term average for the past eight years (2000 – 2008, Fig 4.2). Rainfall is highly seasonal with uni-modal peaks occurring from December to March (Palmer and Hoffman 1997).

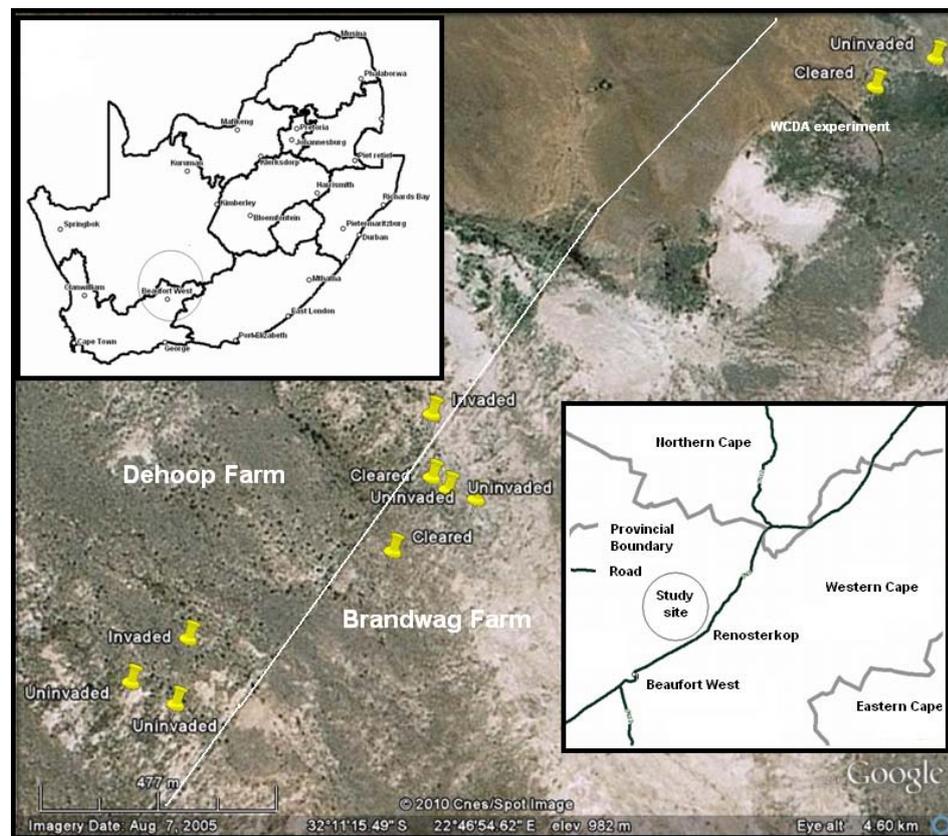


Figure 4.1 Map showing the location of the study site and the placement of sampling plots. Satellite image obtained from Google Earth (Version 5.1.3533.1731). Mountain View, CA: Google Inc. (2009).

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*100 metre plots were set up during the WCDA experiment (viz. uninvaded & fenced, uninvaded & 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 Garlon ® 4 herbicide (triclopyr ester) at a four percent 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, ground 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.

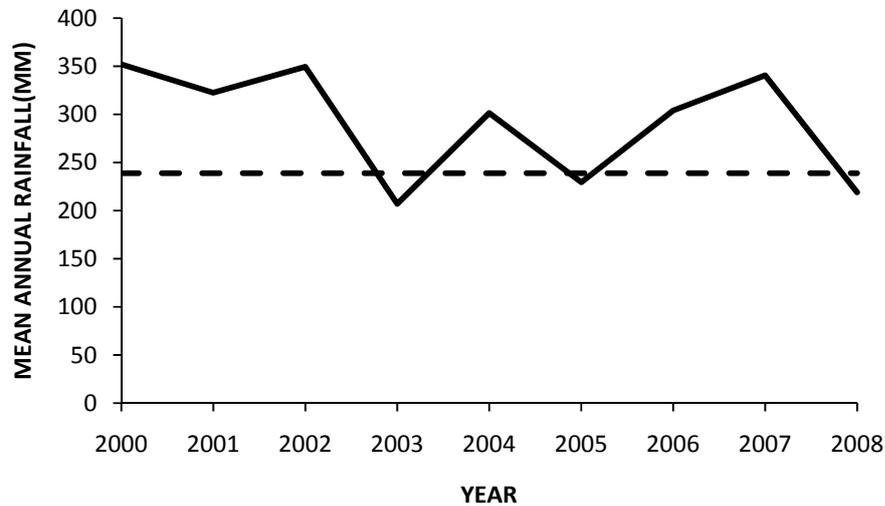


Figure 4.2 Mean annual rainfall for Beaufort West from 2000 to 2008 (South African Weather Service – unpublished data). The dashed line represents long term mean rainfall calculated over 126 years (1878-2004, Kraaij and Milton 2006).

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*100 metre 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 be as closely environmentally matched with the WCDA experimental site conditions as possible. To combat the problem of temporally

un-replicated cleared plots inherited from the WCDA experiment, we pooled the 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 Brandwag while invaded sites (n = 2) were restricted to De Hoop (Figure 4.1). 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 (Figure 4.1).

Line-point intercepts were used to measure the proportion of the soil surface that was covered by plants (Herrick et al. 2005a). In each plot, five 100-metre transects were laid out at 10 metre intervals along a 50-metre east-west trending base line. Two 50-point line-point intercept readings were made along each 100-metre transect using 50-metre tape. A total of 50, 20 and 30 50-metre line-point intercepts were set up on uninvaded, invaded and cleared sites respectively.

Data analysis

Plant canopy and basal cover

Plant canopy cover referred to the proportion of the ground surface covered by plant parts (leaf, stem, and flower etc., Herrick et al. 2005a). Percent canopy cover per transect was calculated by dividing the number of plant canopy intercepts by 50 and multiplying by 100 (Herrick et al. 2005a). Basal cover referred to the proportion of the soil surface that was covered by plant bases (Herrick et al. 2005a). Percent basal cover per transect was calculated in the same manner as canopy cover.

Species and functional type canopy and basal cover

Species canopy/basal covers per transect were determined by dividing the number of individual species canopy/basal intercepts by 50 and multiplying by 100 while plant

functional type (annual grass, perennial grass, annual herb, perennial herb, succulent shrub, non-succulent shrub and tree) canopy/basal covers per transect were calculated by summing up the canopy covers of species falling within each of the functional groups. Species were classified into functional types using published descriptions (Meredith 1955, Le Roux et al. 1994, Shearing and van Heerden 1994, Esler et al. 2006).

Statistical analyses

Effect of *Prosopis* invasion and clearing on rangeland soil vegetation cover

The effect of *Prosopis* invasion and clearing on rangeland soil vegetation cover was evaluated by comparing mean plant canopy and basal cover in uninvaded, invaded and cleared plots. Differences between uninvaded vs. invaded, invaded vs. cleared and uninvaded vs. cleared plots were taken to represent the impacts of invasion and clearing. Likewise the vegetation dynamics that underlay plant canopy and basal cover changes following invasion and clearing were deduced from differences in the mean plant species and functional type canopy and basal covers between the plots. Plant functional types whose mean canopy and basal covers tested significant were analysed to species level. The relative importance of the vegetation changes were evaluated by considering the magnitude of the changes in plant canopy and basal cover values associated with them.

Means and standard errors were calculated using the Paleontological Statistics Software Package for Education and Data Analysis (PAST, Hammer et al. 2001). Significance was assessed by One Way ANOVA via Randomisation (10 000 randomisations) using the software Resampling Procedures 1.3 (David C. Howel, University of Vermont, downloaded from <http://www.uvm.edu/dhowell/statPages/Resampling/Resampling.html>). Differences were considered significant at $p \leq 0.05$. Non-parametric randomisation (Manly 1997) was used because the data was non-normal. Normality was tested using the Shapiro-Wilk test (Shapiro and Wilk 1965).

Effect of increasing invasion density on plant canopy and basal cover

The effect of increasing invasion density on plant canopy and basal cover was determined from the relationship between increasing *Prosopis* cover and plant canopy and basal cover. The relationship between increasing *Prosopis* cover and plant canopy and basal cover was assessed by segmented (piecewise) linear regression using the program SegReg (R.J Oosterbaan, International Institute for Land Reclamation and Improvement, downloaded from <http://www.waterlog.info/segreg.htm>). Segmented regression applies linear regressions to data that do not have strong linear relations by introducing one or more breakpoints (Oosterbaan 1994). Separate linear regressions are then performed for the separate linear segments. SegReg selects, based on significance and maximal explanation of variation, the best fitting break-point and linear regressions from seven predefined functions (Oosterbaan 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).

Results

Effect of invasion and clearing on plant canopy cover

Invasion did not change rangeland plant canopy cover while clearing increased it from 42% to 76% (Figure 4.3). Plant canopy cover in cleared rangeland was still 40% higher than the pre-invasion level more than four years after clearing (Figure 4.3). Average plant canopy cover did not differ significantly ($F = 0.43$, $P = 0.563$) between uninvaded (45.35 ± 2.50 %) and invaded (42.00 ± 4.05 %) sites. Cleared sites had significantly higher ($F = 37.92$, $P < 0.001$) average plant canopy cover (76.31 ± 3.28 %) than invaded sites.

Average plant canopy cover in cleared sites was significantly higher ($F = 57.58$, $P < 0.001$) than in uninvaded sites.

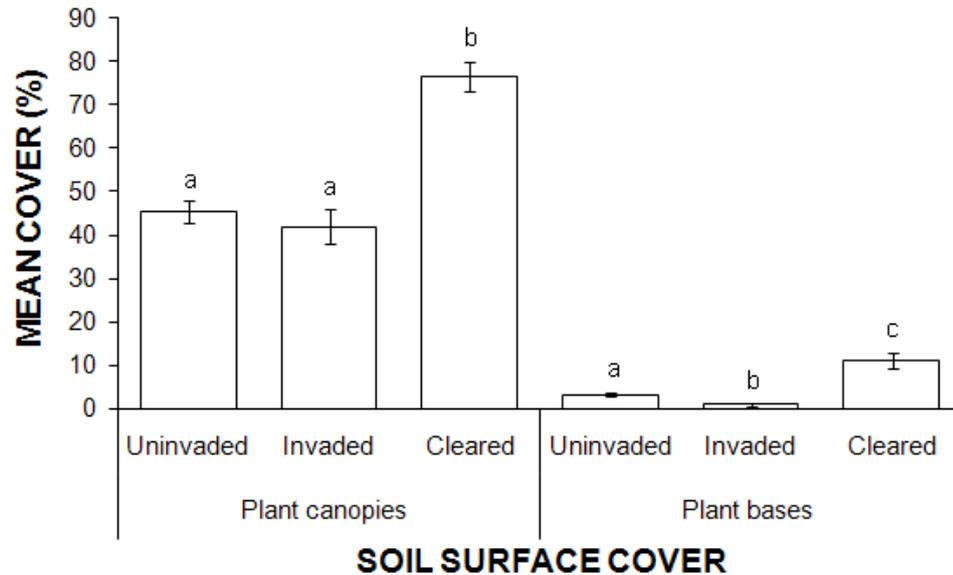


Figure 4.3 Mean plant canopy and basal cover for uninvaded ($n = 5$), invaded ($n = 2$) and cleared ($n = 3$) sites. The error bars are times one standard error. Significance determined by One Way ANOVA via randomisation.

Plant canopy cover remained constant during invasion mainly due to equilibrium between increasing *Prosopis* cover and declining grass cover. The decline in grass cover was mainly due to the loss of the annual grass *Aristida adscensionis* and to a much lesser extent some unidentified perennial grasses. Only the annual grass *A. adscensionis* ($F = 12.24$, $P = 0.001$) and *Prosopis* ($F = 58.09$, $P < 0.001$) had significantly different mean canopy covers in uninvaded and invaded sites (Table 4.1). The difference in *Prosopis* covers between uninvaded and invaded sites (15.12 %) was almost the same as the difference in grass canopy cover (13.06 %, Table 4.1). Although perennial grasses had

significantly ($F = 6.00$, $P = 0.016$) different mean canopy covers in uninvaded and invaded sites there were no significant differences at species level (Table 4.1).

The gain in rangeland plant canopy cover after clearing was mainly driven by increases in the abundance of the annual grass *A. adscensionis* and to much lesser extents the annual grass *Setaria verticillata*, the perennial grasses *Eragrostis obtusa*, *Cynodon dactylon* and *Eragrostis lehmanniana* and the non succulent shrubs *Felicia muricata*, *Lycium prunus-spinosa* and *Atriplex lindleyi*. Clearing was also accompanied by reductions in the cover of invasive *Prosopis* trees, and to a much lesser extent the succulent shrub *Phyllobolus splendens* and the non succulent shrub *Salsola tuberculata*. The annual grasses *A. adscensionis* ($F = 13.53$, $P = 0.001$) and *S. verticillata* ($F = 6.85$, $P = 0.008$), the perennial grasses *E. obtusa* ($F = 8.79$, $P = 0.006$), *C. dactylon* ($F = 4.97$, $P = 0.038$) and *E. lehmanniana* ($F = 4.35$, $P = 0.036$), the succulent shrub *P. splendens* ($F = 5.58$, $P = 0.030$) the non succulent shrubs *F. muricata* ($F = 4.48$, $P = 0.042$), *S. tuberculata* ($F = 10.90$, $P = 0.003$), *L. prunus-spinosa* ($F = 6.85$, $P = 0.008$) and *A. lindleyi* ($F = 7.08$, $P = 0.029$) and *Prosopis* ($F = 26.87$, $P < 0.001$) had significantly different mean canopy covers in invaded and cleared sites (Table 4.2).

The canopy cover in cleared rangeland was higher than the pre-invasion level mainly due to a higher abundance of the annual grasses *A. adscensionis* and to a lesser extent the annual grass *S. verticillata*, the perennial grass *E. obtusa* and unidentified succulent shrubs. Mean canopy cover was significantly different in cleared and uninvaded sites for the annual grasses *A. adscensionis*, ($F = 12.81$, $P < 0.001$) and *S. verticillata* ($F = 6.85$, $P = 0.008$) and the perennial grass *E. obtusa* ($F = 28.80$, $P < 0.001$, Table 4.3). Although succulent shrubs had significantly ($F = 7.28$, $P = 0.008$) different mean canopy covers in cleared and uninvaded sites the difference does not occur at species level (Table 4.3).

Table 4.1. Mean percent canopy covers of 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 along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Uninvaded	Invaded	Difference
Plant functional type			
Annual grass	20.90 ± 1.60 ^a	10.17 ± 1.95 ^b	-10.73
Perennial grass	3.00 ± 0.51 ^a	0.67 ± 0.38 ^b	-2.33
Annual herb	0.25 ± 0.13 ^a	0.17 ± 0.17 ^a	-0.08
Perennial herb	0.05 ± 0.05 ^a	0.17 ± 0.17 ^a	0.12
Succulent shrub	1.05 ± 0.26 ^a	1.00 ± 0.39 ^a	-0.05
Non succulent shrub	19.50 ± 1.96 ^a	13.83 ± 2.19 ^a	-5.67
Tree (<i>Prosopis</i>)	0.05 ± 0.05 ^a	15.17 ± 3.70 ^b	15.12
Annual grass			
<i>Aristida adscensionis</i>	18.80 ± 1.58 ^a	8.00 ± 1.92 ^b	-10.80
<i>Chloris virgata</i>	1.65 ± 0.35 ^a	2.17 ± 0.87 ^a	0.52
<i>Tragus berteronianus</i>	0.45 ± 0.17 ^a	0.00 ^a	-0.45
Perennial grass			
<i>Cynodon dactylon</i>	1.80 ± 0.51 ^a	0.67 ± 0.38 ^a	-1.13
<i>Stipagrostis obtusa</i>	0.35 ± 0.14 ^a	0.00 ^a	-0.35
<i>Eragrostis obtusa</i>	0.10 ± 0.07 ^a	0.00 ^a	-0.10
<i>Sporobolus iocladius</i>	0.05 ± 0.05 ^a	0.00 ^a	-0.05
<i>Stipagrostis ciliata</i>	0.30 ± 0.11 ^a	0.00 ^a	-0.30
<i>Fingerhuthia africana</i>	0.15 ± 0.11 ^a	0.00 ^a	-0.15
<i>Eragrostis lehmanniana</i>	0.10 ± 0.07 ^a	0.00 ^a	-0.10
<i>Cenchrus ciliaris</i>	0.05 ± 0.05 ^a	0.00 ^a	-0.05

Table 4.2. Mean percent canopy covers of 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 along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Invaded	Cleared	Difference
Plant functional type			
Annual grass	10.17 ± 1.95 ^a	37.46 ± 4.44 ^b	27.29
Perennial grass	0.67 ± 0.38 ^a	14.00 ± 2.32 ^b	13.33
Annual herb	0.17 ± 0.17 ^a	0.62 ± 0.29 ^a	0.45
Perennial herb	0.17 ± 0.17 ^a	0.00 ^a	-0.17
Succulent shrub	1.00 ± 0.39 ^a	0.15 ± 0.11 ^b	-0.85
Non succulent shrub	13.83 ± 2.19 ^a	21.46 ± 2.10 ^b	7.63
Tree (<i>Prosopis</i>)	15.17 ± 3.70 ^a	1.77 ± 0.50 ^b	-13.40
Annual grass			
<i>Aristida adscensionis</i>	8.00 ± 1.92 ^a	34.00 ± 4.69 ^b	26.00
<i>Setaria verticillata</i>	0.00 ^a	0.85 ± 0.40 ^b	0.85
<i>Tragus berteronianus</i>	0.00 ^a	1.00 ± 0.46 ^a	1.00
<i>Chloris virgata</i>	2.17 ± 0.87 ^a	1.85 ± 0.43 ^a	-0.32
Perennial grass			
<i>Eragrostis obtusa</i>	0.00 ^a	5.92 ± 1.35 ^b	5.92
<i>Cynodon dactylon</i>	0.67 ± 0.38 ^a	3.69 ± 0.90 ^b	3.02
<i>Eragrostis lehmanniana</i>	0.00 ^a	2.77 ± 0.89 ^b	2.77
<i>Stipagrostis ciliata</i>	0.00 ^a	0.62 ± 0.47 ^a	0.62
<i>Stipagrostis obtusa</i>	0.00 ^a	0.23 ± 0.13 ^a	0.23
<i>Fingerhuthia africana</i>	0.00 ^a	0.31 ± 0.18 ^a	0.31
<i>Cenchrus ciliaris</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
<i>Aristida congesta</i>	0.00 ^a	0.15 ± 0.11 ^a	0.15
<i>Sporobolus iocladius</i>	0.00 ^a	0.15 ± 0.11 ^a	0.15
Succulent shrubs			
<i>Phyllobolus splendens</i>	2.83 ± 0.52 ^a	1.31 ± 0.37 ^b	-1.52
Non succulent shrub			
<i>Felicia muricata</i>	0.17 ± 0.17 ^a	2.92 ± 0.88 ^b	2.75

<i>Salsola tuberculata</i>	1.67 ± 0.64 ^a	0.15 ± 0.11 ^b	-1.52
<i>Lycium prunus-spinosa</i>	0.00 ^a	0.08 ± 0.08 ^b	0.08
<i>Atriplex lindleyi</i>	0.67 ± 0.28 ^a	1.00 ± 0.46 ^b	0.33
<i>Lycium cinerium</i>	3.00 ± 0.83 ^a	5.85 ± 1.00 ^a	2.85
<i>Kochia salsoloides</i>	1.33 ± 0.71 ^a	0.46 ± 0.20 ^a	-0.87
<i>Asparagus retrofractus</i>	0.00 ^a	0.85 ± 0.45 ^a	0.85
<i>Rosenia humilis</i>	0.00 ^a	0.85 ± 0.30 ^a	0.85
<i>Lycium oxycarpum</i>	0.00 ^a	0.85 ± 0.40 ^a	0.85
<i>Pentzia lanata</i>	0.00 ^a	0.69 ± 0.33 ^a	0.69
<i>Aridaria noctiflora</i>	0.67 ± 0.28 ^a	0.31 ± 0.31 ^a	-0.36
<i>Zygophyllum gilfillanii</i>	0.00 ^a	0.31 ± 0.31 ^a	0.31
<i>Salsola calluna</i>	0.17 ± 0.17 ^a	0.31 ± 0.18 ^a	0.14
<i>Selago geniculata</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
<i>Eriocephalus</i> sp.	0.00 ^a	0.08 ± 0.08 ^a	0.08

Table 4.3. Mean percent canopy covers of 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 along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Uninvaded	Cleared	Difference
Plant functional type			
Annual grass	20.90 ± 1.60 ^a	37.46 ± 4.44 ^b	16.56
Perennial grass	3.00 ± 0.51 ^a	14.00 ± 2.32 ^b	11.00
Annual herb	0.25 ± 0.13 ^a	0.62 ± 0.29 ^a	0.37
Perennial herb	0.05 ± 0.05 ^a	0.00 ^a	-0.05
Succulent shrub	1.05 ± 0.26 ^a	0.15 ± 0.11 ^b	-0.90
Non succulent shrub	19.50 ± 1.96 ^a	21.46 ± 2.10 ^a	1.96
Tree (<i>Prosopis</i>)	0.05 ± 0.05 ^a	1.77 ± 0.50 ^b	1.72
Annual grass			
<i>Aristida adscensionis</i>	18.80 ± 1.58 ^a	37.00 ± 4.69 ^b	18.20
<i>Setaria verticillata</i>	0.00 ^a	0.85 ± 0.40 ^b	0.85
<i>Chloris virgata</i>	1.65 ± 0.35 ^a	1.85 ± 0.43 ^a	0.20
<i>Tragus berteronianus</i>	0.45 ± 0.17 ^a	1.00 ± 0.46 ^a	0.55
Perennial grass			
<i>Eragrostis obtusa</i>	0.10 ± 0.07 ^a	5.92 ± 1.35 ^b	5.82
<i>Cynodon dactylon</i>	1.80 ± 0.51 ^a	3.69 ± 0.90 ^a	1.89
<i>Eragrostis lehmanniana</i>	0.10 ± 0.07 ^a	2.77 ± 0.89 ^a	2.67
<i>Stipagrostis ciliata</i>	0.30 ± 0.11 ^a	0.62 ± 0.47 ^a	0.32
<i>Fingerhuthia africana</i>	0.15 ± 0.11 ^a	0.31 ± 0.18 ^a	0.16
<i>Cenchrus ciliaris</i>	0.05 ± 0.05 ^a	0.08 ± 0.08 ^a	0.03
<i>Sporobolus iocladius</i>	0.05 ± 0.05 ^a	0.15 ± 0.11 ^a	0.10
<i>Aristida congesta</i>	0.00 ^a	0.15 ± 0.11 ^a	0.15
<i>Stipagrostis obtusa</i>	0.35 ± 0.14 ^a	0.23 ± 0.13 ^a	-0.12
Succulent shrub			
<i>Phyllobolus splendens</i>	0.85 ± 0.26 ^a	1.31 ± 0.37 ^a	0.46

Effect of invasion and clearing on plant basal cover

Invasion reduced rangeland plant basal cover from about 3% to 1% while clearing, in turn, increased it to 11% (Figure 4.3). Cleared rangeland still had 8% more plant basal cover than uninvaded rangeland more than four years after clearing (Figure 4.3). Average plant basal cover in invaded sites (1.00 ± 0.39 %) was significantly lower ($F = 6.14$, $P = 0.015$) than in uninvaded sites (3.32 ± 0.51 %). Cleared sites had significantly higher ($F = 16.31$, $P = 0.010$) average plant basal cover (11.00 ± 1.73 %) than invaded sites. Average plant basal cover in cleared sites was significantly higher ($F = 25.93$, $P < 0.001$) than in uninvaded sites.

The vegetation changes associated with the reduction in rangeland plant basal cover during invasion were of such small magnitudes that no distinct patterns could be detected at the functional type and species level. There was no significant difference in annual grass ($F = 2.74$, $P = 0.103$), perennial grass ($F = 2.45$, $P = 0.182$), annual herb ($F = 0.30$, $P = 1.000$), succulent shrub ($F = 1.28$, $P = 0.564$) and non-succulent shrub ($F = 2.05$, $P = 0.167$) mean plant basal cover between uninvaded and invaded sites (Table 4.4).

The increase in plant basal cover after clearing was due to increases in the cover of the annual grass *A. adscensionis* and some unidentified perennial grasses and non-succulent shrubs. The annual grass *A. adscensionis* ($F = 5.10$, $P = 0.029$), perennial grasses ($F = 7.08$, $P = 0.016$) and non-succulent shrubs ($F = 9.07$, $P = 0.005$) had significantly different mean basal covers in cleared and invaded sites (Table 4.5). Although perennial grasses and non-succulent shrubs had significantly different mean basal covers in cleared and invaded sites the difference did not occur at species level (Table 4.5).

Plant basal cover was higher in cleared than uninvaded rangeland because of higher covers of the annual grass *A. adscensionis* and the non-succulent shrubs *Pentzia lanata*, *Rosenia humilis* and *Lycium oxycarpum*. The annual grass *A. adscensionis* ($F = 8.19$, $P = 0.005$) and the non-succulent shrubs *P. lanata* ($F = 5.54$, $P = 0.051$), *R. humilis* ($F = 6.77$,

$P = 0.015$) and *L. oxycarpum* ($F = 4.84$, $P = 0.048$) had significantly different mean basal covers in cleared and invaded sites (Table 4.6).

Table 4.4. Mean percent basal covers of 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 along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Uninvaded	Invaded	Difference
Plant functional type			
Annual grass	1.05 ± 0.29^a	0.17 ± 0.17^a	-0.88
Perennial grass	0.35 ± 0.12^a	0^a	-0.35
Annual herb	0.05 ± 0.05^a	0^a	-0.05
Succulent shrub	0.15 ± 0.08^a	0.17 ± 0.17^a	0.02
Non succulent shrub	1.65 ± 0.36^a	0.67 ± 0.28^a	-0.98

Table 4.5. Mean percent basal covers of 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 along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Invaded	Cleared	Difference
Plant functional type			
Annual grass	0.17 ± 0.17 ^a	3.42 ± 0.81 ^b	3.25
Perennial grass	0.00 ^a	2.25 ± 0.59 ^b	2.25
Annual herb	0.00 ^a	0.17 ± 0.12 ^a	0.17
Succulent shrub	0.17 ± 0.17 ^a	0.08 ± 0.08 ^a	-0.09
Non succulent shrub	0.67 ± 0.28 ^a	4.67 ± 0.92 ^b	4.00
Tree (<i>Prosopis</i>)	0.00 ^a	0.17 ± 0.12 ^a	0.17
Annual grass			
<i>Aristida adscensionis</i>	0.17 ± 0.17 ^a	2.83 ± 0.82 ^b	2.66
<i>Chloris virgata</i>	0.00 ^a	0.17 ± 0.12 ^a	0.17
Non succulent shrub			
<i>Pentzia incana</i>	0.50 ± 0.26 ^a	2.25 ± 0.62 ^a	1.75
<i>Lycium cinerium</i>	0.17 ± 0.17 ^a	0.58 ± 0.25 ^a	0.41
<i>Felicia muricata</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
<i>Pentzia lanata</i>	0 ^a	0.25 ± 0.14 ^a	0.25
<i>Rosenia humilis</i>	0.00 ^a	0.42 ± 0.21 ^a	0.42
<i>Lycium oxycarpum</i>	0.00 ^a	0.33 ± 0.20 ^a	0.33
<i>Asparagus retrofractus</i>	0.00 ^a	0.17 ± 0.17 ^a	0.17
<i>Pteronia erythrochaeta</i>	0.00 ^a	0.17 ± 0.12 ^a	0.17
Perennial grass			
<i>Eragrostis obtusa</i>	0.00 ^a	0.83 ± 0.32 ^a	0.83
<i>Cynodon dactylon</i>	0.00 ^a	0.33 ± 0.16 ^a	0.33
<i>Eragrostis lehmanniana</i>	0.00 ^a	0.83 ± 0.34 ^a	0.83
<i>Cenchrus ciliaris</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
<i>Stipagrostis ciliata</i>	0.00 ^a	0.17 ± 0.12 ^a	0.17
<i>Stipagrostis obtusa</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08

Table 4.6. Mean percent basal covers of 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 along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

	Uninvaded	Cleared	Difference
Plant functional type			
Annual grass	1.05 ± 0.29 ^a	3.42 ± 0.81 ^b	2.37
Perennial grass	0.35 ± 0.12 ^a	2.25 ± 0.59 ^b	1.90
Annual herb	0.05 ± 0.05 ^a	0.17 ± 0.12 ^a	0.12
Succulent shrub	0.15 ± 0.08 ^a	0.08 ± 0.08 ^a	-0.07
Non succulent shrub	1.65 ± 0.36 ^a	4.67 ± 0.92 ^b	3.02
Tree (<i>Prosopis</i>)	0.00 ^a	0.17 ± 0.12 ^a	0.17
Annual grass			
<i>Aristida adscensionis</i>	0.80 ± 0.25 ^a	2.83 ± 0.82 ^b	2.03
<i>Chloris virgata</i>	0.10 ± 0.07 ^a	0.17 ± 0.12 ^a	0.07
<i>Tragus berteronianus</i>	0.05 ± 0.05 ^a	0.00 ^a	-0.05
Perennial grass			
<i>Eragrostis obtusa</i>	0.00 ^a	0.83 ± 0.32 ^b	0.83
<i>Cynodon dactylon</i>	0.15 ± 0.08 ^a	0.33 ± 0.16 ^a	0.18
<i>Eragrostis lehmanniana</i>	0.05 ± 0.05 ^a	0.83 ± 0.34 ^b	0.78
<i>Fingerhuthia africana</i>	0.05 ± 0.05 ^a	0.00 ^a	-0.05
<i>Cenchrus ciliaris</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
<i>Aristida congesta</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
<i>Stipagrostis ciliata</i>	0.10 ± 0.07 ^a	0.17 ± 0.12 ^a	0.07
<i>Stipagrostis obtusa</i>	0.00 ^a	0.08 ± 0.08 ^a	0.08
Non succulent shrub			
<i>Rosenia humilis</i>	0.00 ^a	0.42 ± 0.21 ^b	0.42
<i>Lycium oxycarpum</i>	0.00 ^a	0.33 ± 0.20 ^b	0.33
<i>Pentzia lanata</i>	0.00 ^a	0.25 ± 0.14 ^b	0.25
<i>Pentzia incana</i>	1.30 ± 0.29 ^a	2.25 ± 0.62 ^a	0.95
<i>Lycium cinerium</i>	0.25 ± 0.13 ^a	0.58 ± 0.25 ^a	0.33
<i>Asparagus retrofractus</i>	0.00 ^a	0.17 ± 0.17 ^a	0.17
<i>Pteronia erythrochaeta</i>	0.00 ^a	0.17 ± 0.12 ^a	0.17

Effect of increasing invasion density on plant canopy and basal cover

The relationship between *Prosopis* cover and rangeland canopy cover conformed to the Type 6 function in SegReg (Figure 4.4), i.e. an increase in plant canopy cover occurred steeply before a threshold of 6.40% *Prosopis* canopy cover, after which it fell and then increased less steeply (Figure 4.4). Rangeland canopy cover fell sharply from 93 to 34 % after the threshold.

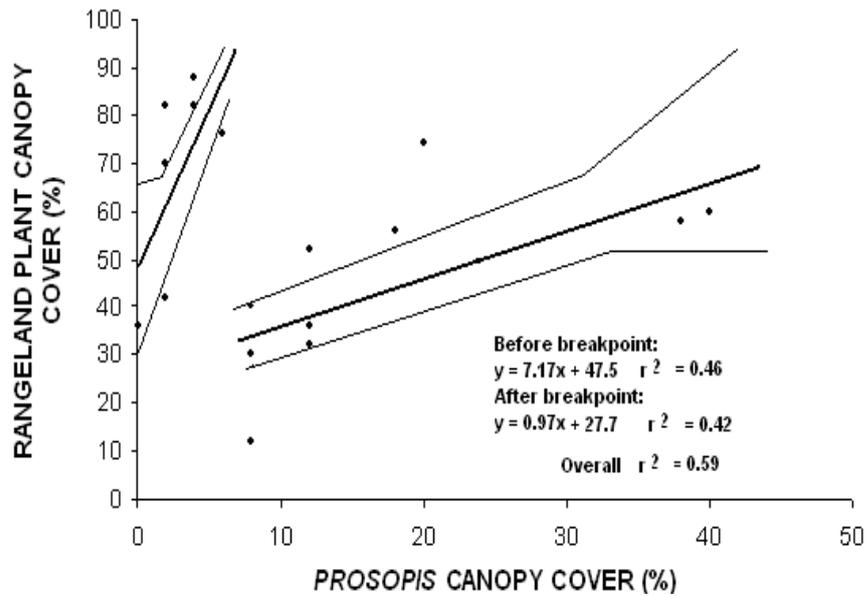


Figure 4.4 Segmented regression analysis showing the relationship between *Prosopis* cover and rangeland canopy cover. Also shown are the standard (least-squares) regression equations and 95% confidence intervals.

The relationship between *Prosopis* cover and plant basal cover conformed to the Type 5 function in SegReg (Figure 4.5). Plant basal cover did not change during invasion up to a threshold of 20.40% *Prosopis* canopy cover after which it fell sharply from 2 % to 0% (Figure 4.5).

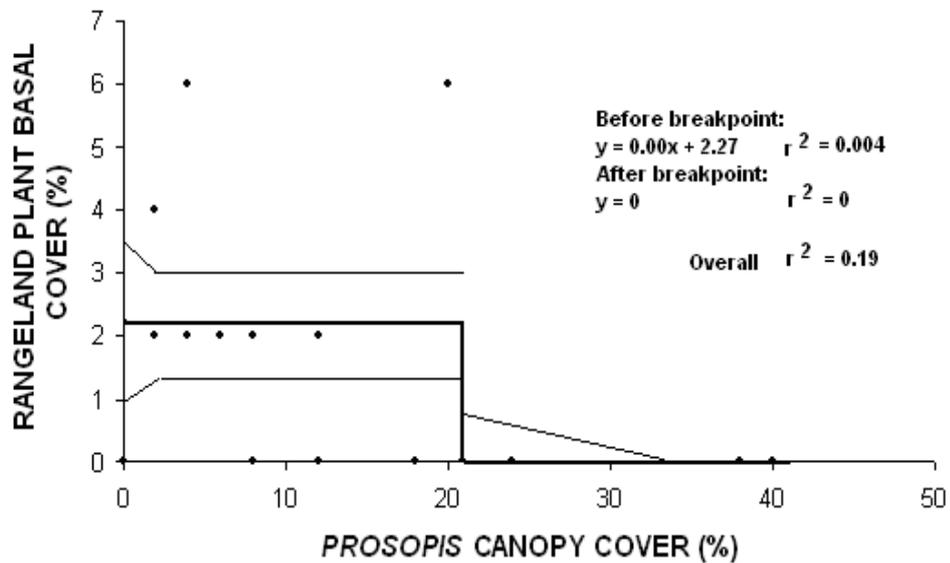


Figure 4.5 Segmented regression analysis showing the relationship between *Prosopis* cover and rangeland plant basal cover. Also shown are the standard (least-squares) regression equations and 95% confidence intervals.

Discussion

Prosopis trees have been documented to reduce grass abundance in their understory and neighbourhood (McDaniel et al. 1982, McClaran and Angell 2006, Simmons et al. 2008). As a result we expected changes in rangeland plant canopy and basal cover during invasion and clearing at our study site to be mainly driven by changes in grass abundance with invasion reducing plant canopy and basal cover and clearing restoring the covers to

pre-invasion levels. Our results confirmed most of the expectations except that invasion did not result in a decrease in rangeland canopy cover and clearing did not restore canopy and basal cover to pre-invasion levels. Instead increasing *Prosopis* canopy cover during invasion compensated for lost grass canopy cover and kept rangeland plant canopy cover constant while clearing increased plant canopy and basal cover to extents far above pre-invasion levels.

Plant canopy and basal cover changes during invasion and clearing at our study site were mainly due to changes in the abundance of the annual grass *A. adscensionis*. The grass, which due to its resilience to overgrazing (Esler et al. 2006) dominated our heavily grazed study site, is shade-intolerant and a poor inter-specific competitor for moisture and nutrients (Varshney 1968). Invading *Prosopis* trees extract soil moisture and nutrients from far beyond their crown areas through extensive lateral root systems (Tiedemann and Klemmedson 1973) and most likely reduced *A. adscensionis* cover in the neighbouring open areas by competing with the grass for moisture and nutrients. The balance between increased *Prosopis* canopy cover and lost *A. adscensionis* cover appears to have been a serendipitous outcome that does not occur at *Prosopis* covers higher or lower than those at our study site (i.e. greater or lesser than 15 % *Prosopis* cover, see discussion on the effect of increasing *Prosopis* invasion density on plant canopy and basal cover below). The increase in canopy and basal covers after clearing to levels surpassing pre-invasion conditions probably resulted from elevated soil fertility in cleared rangeland. *Prosopis* trees accumulate soil nutrients such as carbon, nitrogen, magnesium, potassium and phosphorous 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 in our study site could have been more fertile than uninvaded rangeland and consequently supported greater grass production and canopy cover.

Grasses usually contribute the most to canopy and basal cover in semi-arid rangelands (Herrick et al. 2005b). Invading *Prosopis* trees have a threshold effect on rangeland grass production where they do not seem to have any significant effect until their cover surpasses certain thresholds (McDaniel et al. 1982, Warren et al. 1996). This

phenomenon probably explains the complex threshold effects that characterised relationships between *Prosopis* cover and rangeland plant canopy and basal cover at our study site. The steep rise in plant canopy cover during early stages of invasion (below the 6% *Prosopis* cover threshold) was probably due to the incorporation of invading *Prosopis* tree cover into overall rangeland canopy cover without any loss to the original grass cover. However once *Prosopis* cover exceeded the 6% cover threshold and invasive trees began to displace grasses overall rangeland canopy cover fell. The less rapid increase in rangeland canopy cover after the threshold was most likely solely due to increasing *Prosopis* tree cover. The same process probably occurred with basal cover which remained constant up to a threshold of 20% *Prosopis* cover after which it collapsed as invading *Prosopis* trees began to reduce grass cover.

Conclusion

Our findings suggest that *Prosopis* invasion can lower rangeland plant canopy and basal cover in overgrazed and degraded Nama Karoo rangeland while clearing *Prosopis* from such rangeland can, even under heavy grazing, substantially raise it. Clearing however does not lead to restoration of pre-invasion status within four to six years after clearing.

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Impact of *Prosopis* (mesquite) invasion and clearing on the grazing capacity of degraded semi-arid Nama Karoo rangeland, South Africa

Abstract

We assessed the impact of *Prosopis* invasion and clearing on the grazing capacity of heavily grazed Nama Karoo rangeland on two sheep farms in the Beaufort West district of the Western Cape Province of South Africa. Invasion (~15 percent *Prosopis* canopy cover) reduced grazing capacity by 34% while 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 in 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*. The relationship between increasing *Prosopis* cover and rangeland grazing capacity exhibited a threshold effect. Rangeland grazing capacity declined sharply by 42% after invading *Prosopis* trees reached a 6% canopy cover threshold. Increasing *Prosopis* cover did not influence grazing capacity below and above this threshold. Our results indicate that *Prosopis* invasion (>13% mean canopy cover) can lower grazing capacity in overgrazed and degraded Nama Karoo rangeland while clearing

Prosopis from such rangeland can, even under heavy grazing, substantially improve grazing capacity within reasonable time frames.

Key words: agricultural productivity, invasive aliens, overgrazing, Working for Water (WfW)

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). IAPs cover an estimated eight percent (10 million hectares) of the country and are expanding at a rate of five percent per year (Binns et al. 2001, van Wilgen et al. 2001). Much of the area affected by IAPs 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 eco-region 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 km² 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, to date, 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 socio-economic 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.

The costs of controlling IAPs are usually very high and cannot be met through private effort or normal government department conservation budgets (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 socio-economic worth to compete effectively (Turpie 2004). The benefits of clearing invasive *Prosopis* trees from Nama Karoo rangeland have not, as yet, 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 clearing 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 and 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*, *Prosopis juliflora*, and *Prosopis velutina*) have hybridized extensively (Zimmermann 1991) such that most populations in South Africa are composed of overlapping morpho-types 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"), about 30 kilometres north-east of the town of Beaufort West in the Western Cape Province of South Africa (Figure 5.1). 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*, *Ruschia*) and Asteraceae (*Eriocephalus*, *Pentzia*, *Pteronia*) interspersed with grasses (*Aristida*, *Enneapogon*, *Digitaria* and *Stipagrostis*) (Palmer and Hoffman 1997). Taller shrubs and trees (*Acacia karroo*, *Euclea undulata* and *Rhigozum obovatum*) occur intermittently (Palmer and Hoffman 1997).

The area receives a mean annual rainfall of 239 mm (calculated for the period 1878-2004) of rain per year (Kraaij and Milton 2006). Mean annual rainfall has however been generally higher than the long term average for the past eight years (2000 – 2008, Fig 5.2). Rainfall is highly seasonal with uni-modal peaks occurring from December to March (Palmer and Hoffman 1997).

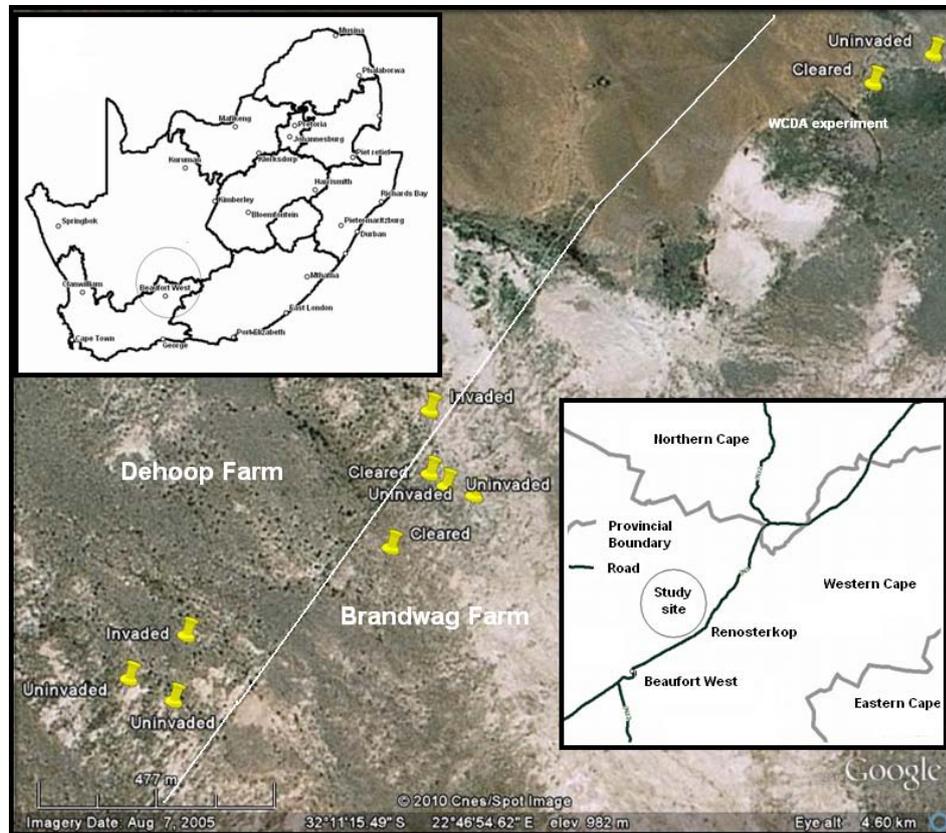


Figure 5.1 Map showing the location of the study site and the placement of sampling plots. Satellite image obtained from Google Earth (Version 5.1.3533.1731). Mountain View, CA: Google Inc. (2009).

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*100 metre plots were set up during the WCDA experiment (viz. uninvaded & fenced, uninvaded & 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 Garlon ® 4 herbicide (triclopyr ester) at a four percent 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, ground 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.

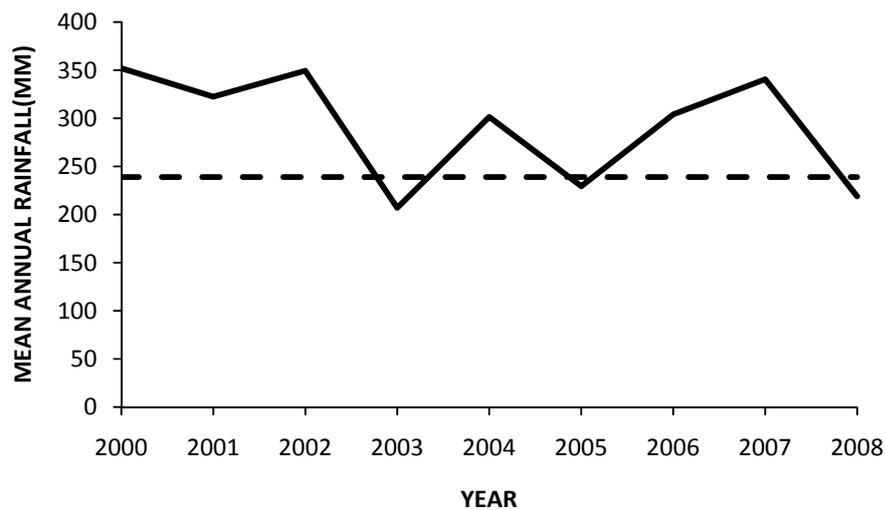


Figure 5.2 Mean annual rainfall for Beaufort West from 2000 to 2008 (South African Weather Service – unpublished data). The dashed line represents long term mean rainfall calculated over 126 years (1878-2004, Kraaij and Milton 2006).

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*100 metre 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 be as closely environmentally matched with the WCDA experimental site conditions as possible. To combat the problem of temporally un-replicated cleared plots inherited from the WCDA experiment, we pooled the 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 Brandwag while invaded sites (n = 2) were restricted to De Hoop (Figure 5.1). 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 (Figure 5.1).

Estimates of species cover were obtained using line-point intercepts (Herrick et al. 2005). In each plot, five 100-metre transects were laid out at 10 metre intervals along a 50-metre east-west trending base line. Two 50-point line-point intercept readings were made along each 100-metre transect using 50-metre tape. A total of 50, 20 and 30 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 (LSU, 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 the number of LSUs per 100 hectares 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 summed up to give that functional type's contribution per transect. Range condition indices, which are calculated by summing up 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 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 while 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. Howel, 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 was 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 (R.J. 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* (~15 percent canopy cover) reduced rangeland grazing capacity by 34%, whereas clearing, even under heavy grazing, improved it by 110% within four to six years (Figure 5.3). Average current grazing capacity on invaded sites (2.56 ± 0.25 LSU 100ha^{-1}) was 34% lower ($F = 17.68$, $P = 0.013$) than on uninvaded sites (3.87 ± 0.21 LSU 100ha^{-1}). Cleared sites had an average current grazing capacity (5.39 ± 0.30 LSU 100ha^{-1}) 110% higher ($F = 17.68$, $P < 0.001$) than invaded sites (2.56 ± 0.25 LSU 100ha^{-1}). Cleared rangeland had a grazing capacity that was significantly higher than uninvaded rangeland (Figure 5.3). The average grazing capacity in cleared sites (5.39 ± 0.30 LSU

100ha⁻¹) was 39% higher ($F = 17.68, P = 0.003$) than in uninvaded sites (3.87 ± 0.21 LSU 100ha⁻¹).

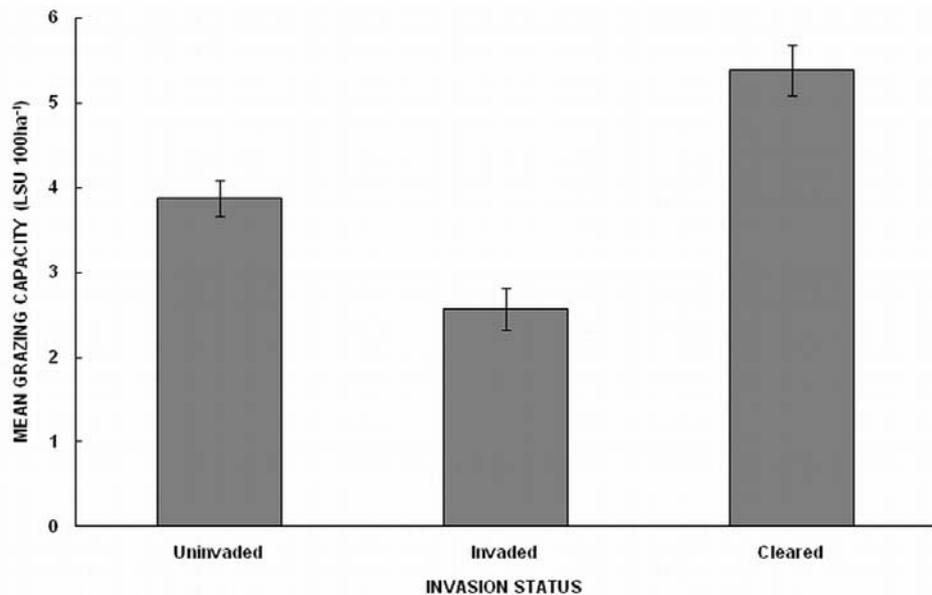


Figure 5.3 Mean current grazing capacities for uninvaded ($n = 5$), invaded ($n = 2$) and cleared ($n = 3$) sites near Beaufort West in the Western Cape Province of South Africa. The error bars are times one standard error. All differences are significant at $P \leq 0.05$ (One Way ANOVA $F = 17.68, P < 0.001$ followed by Tukey's pairwise comparisons).

Vegetation dynamics underlying changes in rangeland grazing capacity

Much of the loss in grazing capacity during invasion was due to the displacement of the annual grass *Aristida adscensionis* which dominated herbaceous forage production in the study site. Invading *Prosopis* trees offset about 59 percent of the forage lost due to 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 5.1). 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 5.1). The difference between the average range condition scores for *Prosopis* in uninvaded and invaded sites was lower than the difference for *A. adscensionis* (Table 5.1).

Most of the improvement in rangeland grazing capacity after *Prosopis* clearing was due to increases in abundance of the annual grass *A. adscensionis*, the perennial grass *Cynodon dactylon* and the establishment of the perennial grasses *Eragrostis obtusa* and *Eragrostis lehmanniana*. 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 5.2). However, at species level, only two annual grasses, *A. adscensionis* ($F = 14.92, P = 0.001$) and *T. berteronianus* ($F = 4.53, P = 0.039$) 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 5.2). *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 5.2). 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 5.2). Annual forbs increased after clearing while succulent shrubs declined but both had very little impact on grazing capacity due to their extremely low occurrences (Table 5.2). The loss of grazing capacity due to the removal of *Prosopis* trees was smaller than the overall gain in grazing capacity that followed clearing (Table 5.2).

Grazing capacity in cleared rangeland was higher than in uninvaded rangeland due to a higher abundance of the annual grasses, *A. adscensionis*, *C. virgata*, *S. verticillata* 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 5.3). At species level, the annual grasses, *A. adscensionis* ($F = 12.75$, $P > 0.001$), *C. virgata* ($F = 6.33$, $P = 0.014$), *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 5.3).

Table 5.1. Mean range condition scores and standard errors 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 along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

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

Table 5.2. Mean range condition scores and standard errors for different plant functional types, and species in invaded (n = 2) vs. cleared (3) sites near Beaufort West in the Western Cape Province of South Africa. Different superscript letters along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

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

<i>Lessertia annularis</i>	0 ^a	0.48 ± 0.33 ^a	0.48
<i>Sonchus oleraceus</i>	0 ^a	0.23 ± 0.18 ^a	0.23
<i>Medicago laciniata</i>	0 ^a	0.24 ± 0.17 ^a	0.24
Succulent shrubs			
<i>Drosanthemum uniflorum</i>	0 ^a	0.18 ± 0.18 ^a	0.18
<i>Phyllobolus splendens</i>	0.55 ± 0.55 ^a	0 ^a	-0.55
<i>Delosperma spp.</i>	2.50 ± 1.37 ^a	0.69 ± 0.38 ^a	-1.81

Table 5.3. Mean range condition scores and standard errors 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 along the rows denote significantly different values at $P \leq 0.05$ (One Way ANOVA via Randomisation).

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

<i>Lessertia annularis</i>	0 ^a	0.48 ± 0.33 ^a	0.48
<i>Sonchus oleraceus</i>	0 ^a	0.23 ± 0.18 ^a	0.23
<i>Medicago laciniata</i>	0.16 ± 0.09 ^a	0.24 ± 0.17 ^a	0.08
Succulent shrubs			
<i>Drosanthemum uniflorum</i>	0.35 ± 0.19	0.18 ± 0.18 ^a	-0.17
<i>Delosperma spp.</i>	2.70 ± 0.8 ^a	0.69 ± 0.38 ^a	-2.01

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 5.4). The break point in the data occurred at 6.18% *Prosopis* canopy cover. Current grazing capacity dropped by 42% (- 2.15 LSU/100ha) at the breakpoint.

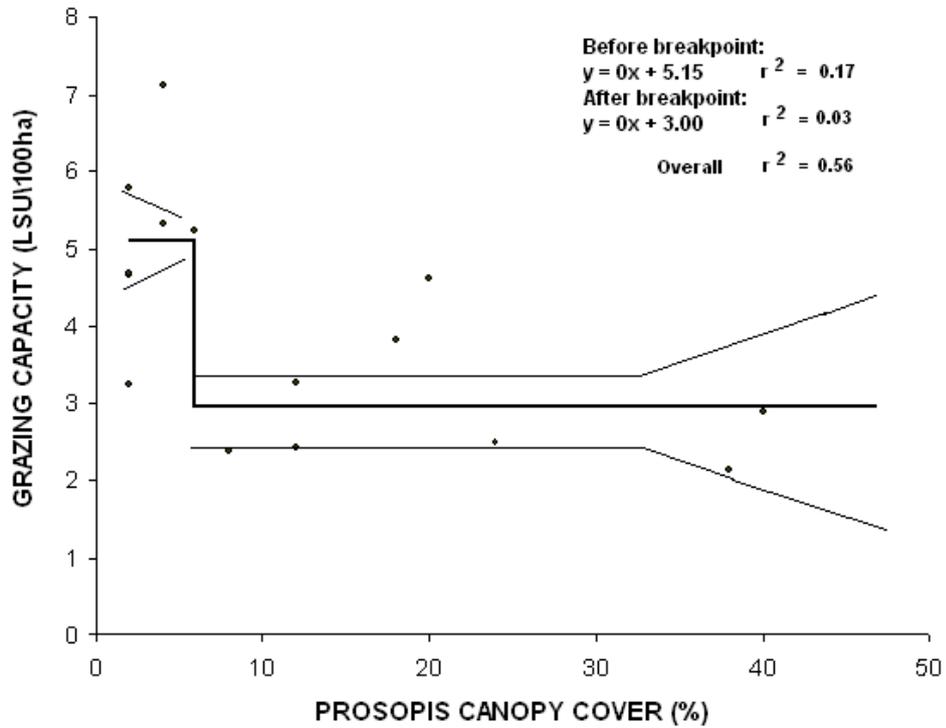


Figure 5.4 Segmented regression analysis showing the relationship between *Prosopis* cover and current grazing capacity. Also shown are the standard (least-squares) regression equations and 95% confidence intervals.

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 semi-arid rangelands in the Southern and South-

western United States. Similar results were also reported for bush encroached and thinned savanna rangeland (Scholes and Archer 1997, Smit 2005).

***Prosopis* invasion effects on grazing capacity**

In the Rolling Plains of Texas in the USA, McDaniel et al. (1982) found detectible decline in forage production when *Prosopis* canopy increased beyond 15 to 20 percent. Warren et al. (1996) reported a 17 percent cover threshold for *Prosopis* impact on forage production in the Chihuahuan desert. The relatively low threshold in our study site could have been due to the effects of overgrazing. Overgrazing could have suppressed the increase in the abundance of palatable herbs and grasses adapted to micro-environments 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 our study.

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 our 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 the heavy grazing at our study site and dominate forage production.

Prosopis trees produce nutritious seed pods that are eaten by livestock (Campbell and Setter 2002). Isolated trees may even enhance production in the short term (Campbell and Setter 2002). However the inevitable thickening of infestations with time results in a decrease in carrying capacity through loss of grass cover caused by replacement and by competition for limited water (Campbell and Setter 2002). Although invading *Prosopis*

trees in our 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 percent of the forage lost due to 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 our study site, grazing capacity increased by a dramatic 110% within six years of *Prosopis* clearing. The associated increases in *A. adscensionis* and *E. obtusa* were probably due to 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 colonize 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 phosphorous 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 in our 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 our 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 due to *Prosopis* clearing may be less than recorded during our study. In addition, grazing capacity gains due to 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 while clearing *Prosopis* from such rangeland can, even under heavy grazing, substantially improve grazing capacity within reasonable time frames. 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 increased 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 benefits may be subject to yearly seasonal fluctuation and more prolonged decline during drought years. Additionally, the grazing capacity benefit due to enhanced soil fertility in cleared rangeland will most likely decline in the long term.

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CHAPTER 6

Conclusion

Key findings

I evaluated the impact of *Prosopis* invasion and clearing on ecosystem structure, function and agricultural productivity in heavily grazed Nama Karoo rangeland on two sheep farms near Beaufort West in the Western Cape Province of South Africa. My aims were to (1) determine the effects of invasion and clearing on rangeland species composition, diversity (alien and indigenous species richness) and structure (alien and indigenous species cover), soil vegetation cover (plant canopy and basal cover) and agricultural productivity (grazing capacity), (2) describe the vegetation processes that underlay the invasion and clearing impacts and (3) evaluate the success of clearing in facilitating unaided restoration of ecological structure, function and agricultural productivity in formerly invaded rangeland.

My results suggest that *Prosopis* invasion (~15 percent canopy cover) and clearing significantly change rangeland vegetation composition. The composition changes are however not substantial as they are mainly driven by changes in the relative abundance of species already present in the rangeland. Invasion mainly changes species composition by reducing the abundance of shade intolerant grasses and over-browsed non-succulent shrubs and by increasing the abundance of grasses adapted to shaded nitrogen-enriched environments. Clearing, on the other hand, changes rangeland species composition by increasing the abundance of grasses previously suppressed by *Prosopis* and non succulent shrubs relieved from intense browsing. Invasion leads to greater alien species cover and less indigenous species richness, while clearing leads to lesser alien species richness and greater indigenous species richness and cover. However invasion has no effect on alien species richness and overall indigenous species cover. Clearing facilitates the spontaneous restoration of alien species cover and indigenous species richness to pre-invasion levels within four to six years but not species composition, alien species richness and indigenous

species cover. Cleared rangeland mainly differs from the pre-invasion state by having a higher abundance of grasses. Alien species richness declines to below pre-invasion levels while indigenous species cover remains higher than the pre-invasion level four to six years after clearing.

Invasion lowers rangeland plant canopy and basal cover while clearing substantially increases it. The decline in rangeland canopy and basal cover during invasion is mainly due to loss of grass cover while the gain after clearing is driven by increases in grass and non succulent shrub cover. Clearing however does not lead to the restoration of pre-invasion plant canopy and basal cover within four to six years after clearing. Canopy and basal cover in cleared rangeland is higher than the pre-invasion level mainly due to a higher abundance of grasses and succulent shrubs.

Invasion (>15 % mean canopy cover) lowers grazing capacity while clearing, even under heavy grazing, substantially improves grazing capacity within reasonable time frames. Much of the loss and gain in grazing capacity during invasion and clearing is due to the displacement of grasses. Grazing capacity in cleared rangeland is higher than the pre-invasion level rangeland due to higher grass abundance.