

**UNGULATE BROWSING AS AN ECOSYSTEM PROCESS:
BROWSER-PLANT-SOIL INTERACTIONS IN A SOUTHERN
AFRICAN SAVANNA**

by

Dario Arturo Fornara

Submitted in partial fulfillment of the requirements for the Degree of Doctor
of Philosophy in the Faculty of Natural & Agricultural Science

University of Pretoria

Pretoria

March 2005

SUMMARY

Ungulate browsing and its ecological effects at plant, population, community, and ecosystem levels were addressed in a eutrophic southern African savanna. This was to test predictions of prevailing hypotheses, which are based on research in boreal and temperate forests. Changes in plant morpho-functional traits and population structure of a staple palatable species, *Acacia nigrescens* Miller were addressed over a two-year survey among vegetation stands with very different histories of attack from herbivores. Moreover browser-induced effects on functional composition of a woody plant community were addressed along a strong browsing gradient. Nutrient cycling was investigated through measurements of leaf litter decomposition rates, as well as soil and leaf chemistry analyses. Finally, a modelling approach was used to make predictions on plant productivity and changes in soil nutrient availability under ungulate browsing according to opposite plant defensive traits (i.e. tolerance vs resistance).

I found evidence that long-term selective browsing may negatively affect soil nutrient pool, at least in the vicinity of palatable woody plants. I proposed this might be due to the drastic reduction of leaf-twig litter mass returned to the soil, which likely decreased decomposer activity and negatively affected N mineralization rates. Hence, the processes responsible for a loss of nutrients in the soil were different from those proposed for northern hemisphere scenarios, which were instead due to decreased litter quality. However, I found evidence of high plant resilience in heavily browsed sites where *Acacia* stands shown (1) higher leaf N during the main growing season, (2) higher N release from leaf litter, (3) high concentrations of nitrate (NO₃) and ammonium (NH₄), and (4) similar, or even faster, litter decomposition rates than in lightly browsed sites. Firstly, this suggests that tree pruning triggers and maintains a fast nutrient cycling within the plant-browser system. The accelerating effect is supported by high mass compensatory growth abilities from highly palatable, fast-growing *Acacia* trees that produce highly decomposable litter. Secondly, browsing may have a long-term decelerating effect on N cycling through quantitative changes in litter production rather than through qualitative changes in litter chemistry. Further studies should better address processes related to soil nutrient cycling to confirm such hypothesis. I discuss how the interactive effects of browsing-grazing-soil fertility may influence nutrient cycling through different ecological processes.

ACKNOWLEDGEMENTS

I would like to thank my advisor Johan du Toit, firstly for giving me the opportunity to work in one of the most incredible environmental settings I've ever been in, namely the open savanna woodlands of the Tshokwane section of the Kruger National Park. Thanks for your guidance and expert suggestions during the planning of my PhD project, as well as for the straight forward advises about what was most important to investigate according to the main goals of my research study.

I would like to thank Elmarie Cronje, Elizabé Els and Martin Haupt for helping and supporting me with many administrative and logistic tasks. Many thanks for your assistance and willingness to help whenever I needed it during my three years spent at the Mammal Research Institute. Thanks also to Halszka Hrabar for the interesting discussions we had about plant-animal interactions in African savannas. Thanks to all for the nice chats we had during the daily coffee breaks in the MRI tea room.

I was given financial support by an Outgoing Fellowship Program from Milan University in Italy through which I started my first year of PhD studies in South Africa. The University of Pretoria contributed, as well with a grant that covered some living expenses.

I've learnt a great deal during my training period of 6 months at the Department of Ecological Modelling - UFZ- Center for Environmental Research, Leipzig, Germany. This has only been possible through a Marie Curie Fellowship Program funded by the European Community for students being already enrolled in their PhD studies.

I really appreciated the logistic support offered by the Head of the Tshokwane Ranger Section, Steven Whitfield, who was always ready to give me information about faunistic and floristic aspects of the savanna landscape type I had surveyed during my fieldwork. Harry Biggs, Nick Zambatis, Navashni Govender, and Sandra MacFadyen of the Kruger Park scientific staff provided me with useful information, permits and data on rainfall, fire regimes and GIS maps.

Thanks to Peter Weisberg, Steve Higgins, Richard Bardgett and the two external examiners, Prof. Robert Naiman and Prof. John Pastor for suggestions and useful comments, which have greatly improved the quality of my scientific work.

I would like to thank my family, which has always supported me in many different ways since my decision to pursue a PhD in South Africa. My father really enjoyed visiting me here, and he will never forget the game drives and the bush life. My sister loved large mammalian browsers, especially elephants and giraffes. She has always encouraged me in my studies though she will never understand why I have studied their impact on vegetation.

Finally, a very special thank to Valeria Cenini who has spent these years with me in South Africa, assisting me in the field work, proposing ideas, contributing to data input, taking care of many different things and sharing with me all the amazing adventures we experienced in the Kruger National Park. I'll never forget the time spent together working in savanna and enjoying romantic African sunsets. Without her I would never have completed my PhD successfully or enjoyed South Africa so much.

CONTENTS

DECLARATION.....	i
SUMMARY.....	ii
ACKNOWLEDGEMENTS.....	iii
CHAPTER 1.....	1
Introduction.....	1
1.1 Background and justification.....	1
1.2 Ungulate browsing and <i>Acacia</i> tree responses	2
1.3 Browsing effects on plant community composition.....	3
1.4 Plant-browser-soil interactions: nutrient cycling at the ecosystem level.....	4
1.5 References.....	8
CHAPTER 2.....	12
Study area.....	12
2.1 Kruger National Park at a glance.....	12
2.2 Study area: the Tshokwane section of the Kruger Park.....	15
2.3 Site description and research assumptions.....	15
2.4 References.....	17
CHAPTER 3.....	19
Responses of a woody plant community to long-term browsing by indigenous ungulates in a southern African savanna.....	19
3.1 Introduction.....	20
3.2 Methods.....	21
3.3 Data analysis.....	23
3.4 Results.....	24
3.4.1 Browsing intensity.....	24

3.4.2	Grazing intensity.....	24
3.4.3	Population structure of <i>Acacia nigrescens</i>	25
3.4.4	Effects of browsing on spinescence, palatability and evergreenness.....	30
3.4.5	Vegetation community composition and species distribution.....	30
3.5	Discussion.....	32
3.5.1	Browsing-grazing gradient.....	32
3.5.2	Browsing effect on population structure of <i>Acacia nigrescens</i>	32
3.5.3	Browsing effect on vegetation community composition.....	33
3.6	Conclusion.....	35
3.7	References.....	36
CHAPTER 4	42
Ungulate browsing as an ecosystem process: plant-soil-browser interactions in a southern African savanna	42
4.1	Introduction.....	43
4.2	Methods.....	45
4.2.1	Browsing/grazing intensity.....	45
4.2.2	Litter decomposition: August placement.....	46
4.2.3	Litter decomposition across species and sites.....	46
4.2.4	Litter biomass, soil depth and soil nutrient pool.....	47
4.2.5	Termite activity.....	47
4.3	Data analysis.....	48
4.4	Results.....	49
4.4.1	Litter decomposition rates - August placement.....	49
4.4.2	June placement.....	50
4.4.3	Soil analysis and litter composition.....	51
4.4.4	Visitation of termites to litter bags.....	51
4.5	Discussion.....	59
4.6	References.....	62

CHAPTER 5.....	67
Plant tolerance, resistance and phenology: responses from	
<i>Acacia nigrescens</i> to ungulate browsing in an African savanna.....	67
5.1 Introduction.....	68
5.2 Methods.....	70
5.2.1 Mass compensation and morpho-functional traits.....	70
5.2.2 Annual net shoot growth, leaf N and tree phenology...	71
5.3 Data analysis.....	72
5.4 Results.....	73
5.4.1 Mass compensation and morpho-functional traits.....	73
5.4.2 Annual net shoot growth, leaf N and phenology.....	73
5.5 Discussion.....	80
5.6 Conclusion.....	83
5.7 References.....	83
 CHAPTER 6.....	 89
Ungulate browsing and its effects on suppressed juvenile forms of	
woody species in a eutrophic African savanna.....	89
6.1 Introduction.....	90
6.2 Methods.....	92
6.2.1 Compensatory growth and leaf N.....	93
6.2.2 Net annual height growth, density and gulliver	
distribution.....	94
6.3 Data analysis.....	95
6.4 Results.....	95
6.4.1 Compensatory growth ability.....	95
6.4.2 Morpho-functional traits.....	96
6.4.3 Gullivers demography and distribution.....	96
6.5 Discussion.....	104
6.5.1 Gulliver resprouting abilities.....	104
6.5.2 Morpho-functional traits.....	105

6.5.3 Gulliver distribution and abundance.....	106
6.6 Conclusion.....	107
6.7 References.....	108
CHAPTER 7.....	113
Ungulate browsing and plant defensive traits: modelling changes in plant productivity and soil nutrient availability in savanna.....	113
7.1 Introduction.....	114
7.1.1 Conceptual definition.....	116
7.1.2 Assumptions.....	116
7.2 Operational definition.....	119
7.2.1 Specific formulae of the ALLOCATE model.....	119
7.2.2 Aspects related to the plant-browser system in a semi-arid eutrophic savanna.....	122
7.3 Results.....	126
7.4 Discussion.....	135
7.4.1 Tolerance vs resistance: plant biomass and soil nutrient availability.....	135
7.4.2 Plant community composition and nutrient cycling.....	136
7.5 References.....	138
CHAPTER 8.....	145
8.1 Conclusion.....	145
8.2 References.....	151