

# Large herbivores alter semi-arid savanna structure through soil nutrient mediation

Lessons from a natural experiment with abandoned kraals

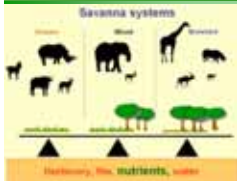
**C van der Waal, A Kool, S Meijer, E Kohi, H de Kroon, IMA Heitkönig, FW de Boer, F van Langevelde, CC Grant, MJS Peel, R Slotow, AK Skidmore, HJ de Knecht, E Mwakiwa, Y Pretorius, SE van Wieren, HHT Prins**

*Resource Ecology Group, Wageningen University., Wageningen, The Netherlands, Department of Experimental Plant Ecology, Radboud University Nijmegen, The Netherlands; Scientific Services, Kruger National Park, Skukuza, RSA; Agricultural Research Council - RFI, Nelspruit, RSA; Biological and Conservation Sciences, Westville Campus, University of KwaZulu-Natal, Durban, RSA; International Institute for Geo-information Science and Earth Observation, Enschede, The Netherlands*

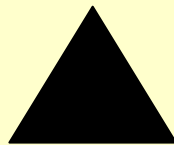
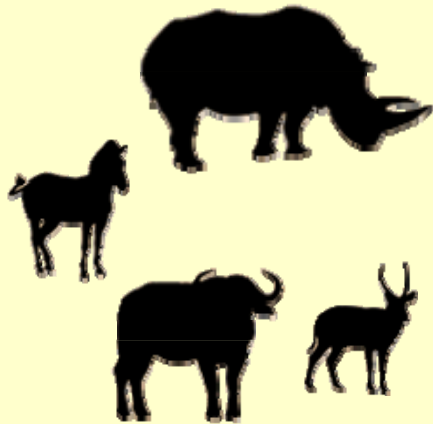
**A Tembo production**



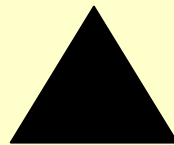
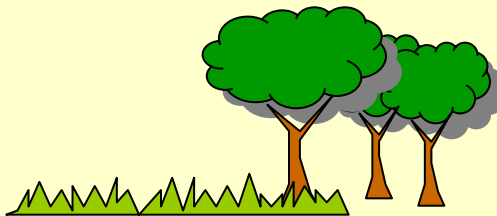
# Vegetation structure governs plant and animal productivity



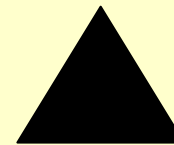
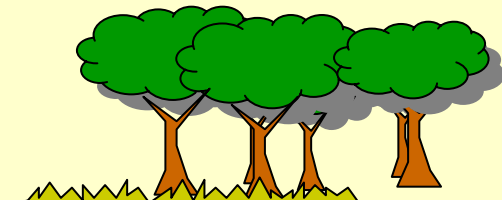
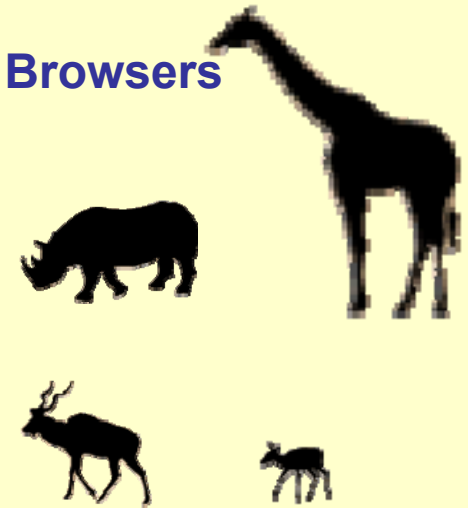
**Grazers**



**Mixed**

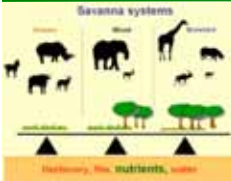


**Browsers**



**Herbivory, fire, nutrients, water**

# Herbivores affect vegetation structure and soil nutrients (1)



**Vegetation structure largely governs plant and animal productivity.**

**Scholes & Archer 1997 *Ann Rev Ecol Syst***

**Sankaran *et al* 2004 *Ecol Lett***

**Sankaran *et al* 2005 *Glob Ecol Biogeogr***

**The direct effect of large herbivores on vegetation structure is well documented, e.g. ...**

**Scholes and Archer 1997 *Ann Rev Ecol Syst***

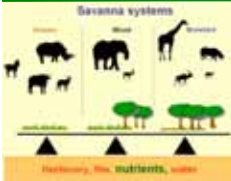
**Van Langevelde *et al* 2003 *Ecology***

**... but indirect effects, e.g. through fire, are not**

**Holdo *et al* 2007 *J of Ecol***

**Waldram *et al* 2008 *Ecosystems***

# Herbivores affect vegetation structure and soil nutrients (2)



Herbivores may also alter vegetation growth forms through soil nutrient changes ...

**Wilson & Tilman 1993 *Ecology***

**Bokdam 2001 *J Vegetation Sci***

... and may strongly affect local nutrient availability

**De Mazancourt *et al* 1998 *Ecology***

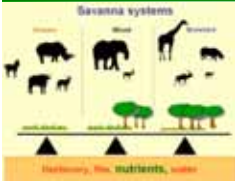
**Augustine *et al* 2003 *Ecol Applic***

**Bardgett & Wardle 2003 *Ecology***

**So:**

**How do herbivores impact on vegetation structure in savannas?**

# Herbivores affect vegetation structure and soil nutrients (3)

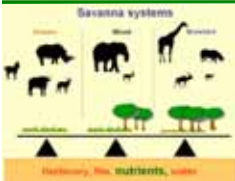


## Relevant issues:

- nutrient cycling rate determines N and P availability for plant uptake
- on fertile soils: herbivores increase nutrient cycling rates & plant productivity
- on infertile soils: herbivores decrease nutrient cycling rates & plant productivity
- herbivores forage here and deposit dung there
- tree cover correlates negatively with N availability
- co-existing grasses outcompete woody seedlings if N high

(Bardgett & Wardle 2003, Augustine & McNaughton 2006, Singer & Schoenecker 2003, Sankaran *et al* 2008, Higgins *et al* 2000)

# Herbivores influence savanna structure through soils



**We test that:**

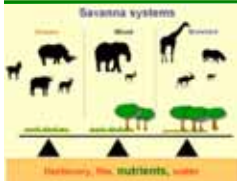


**Large herbivores can potentially influence savanna structure through soil mediation.**

**If so, then two conditions must be met:**

- (1) large herbivores significantly affect local soil nutrient levels**
- (2) soil nutrient levels significantly affect woody recruitment**

# Natural experiment: abandoned cattle kraals and control sites



## Associated Private Nature Reserves (APNR)

< 1970



> 1970



After 40  
years:

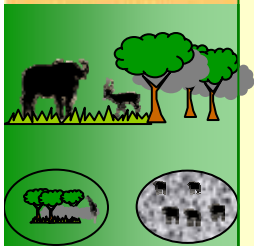
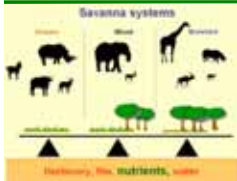
High levels of N, P, K, Ca and Mg

Locally high plant production potential

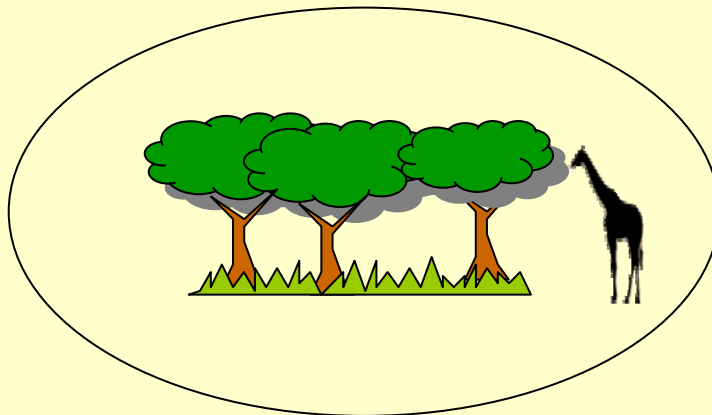
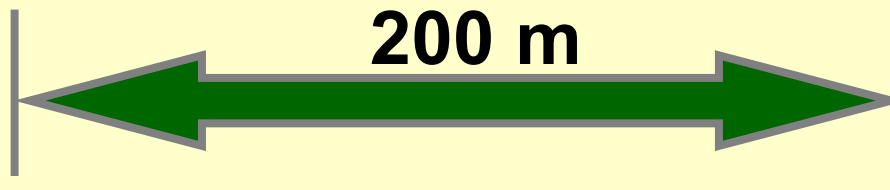
Locally high quality forage

Very low tree densities

# Natural experiment: abandoned cattle kraals and control sites

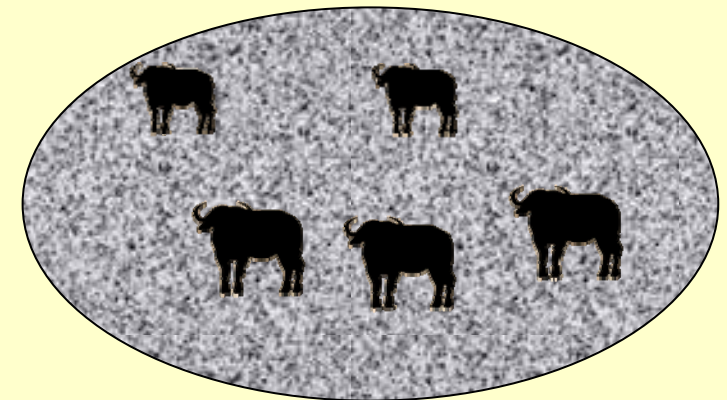


## Associated Private Nature Reserves (APNR)



**Paired control area**

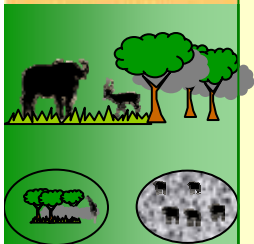
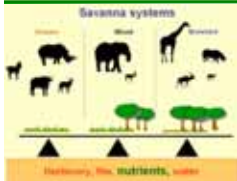
**n = 9**



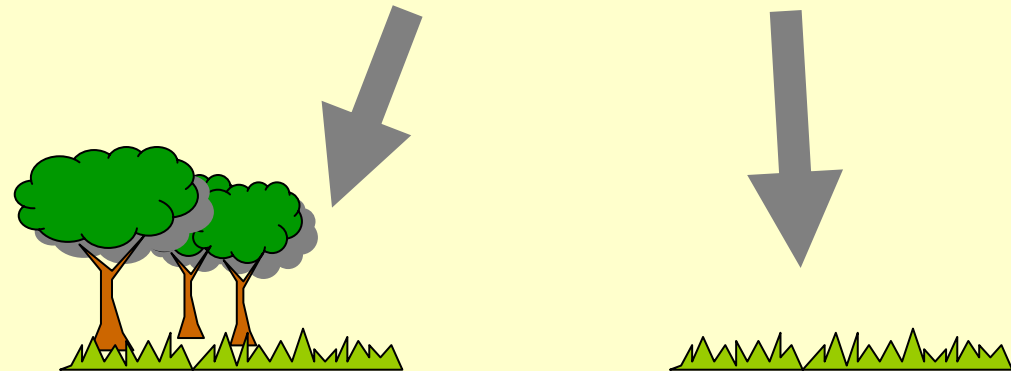
**Cattle 'kraal' site**

**∅ = 10-30m; n = 9**

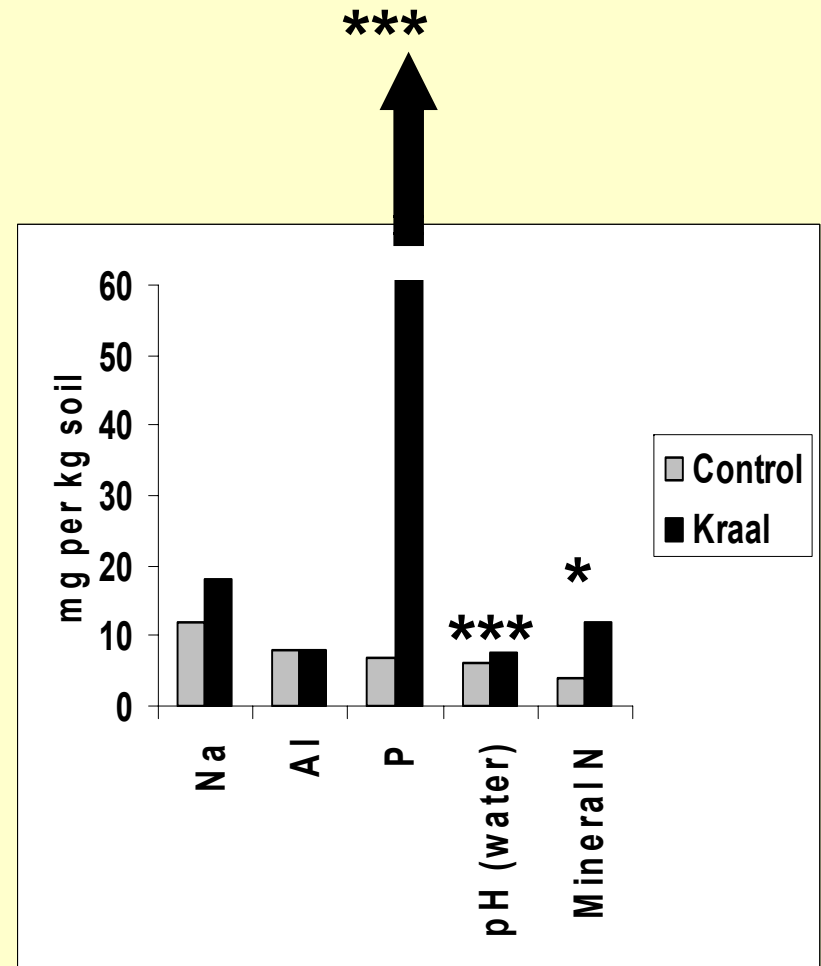
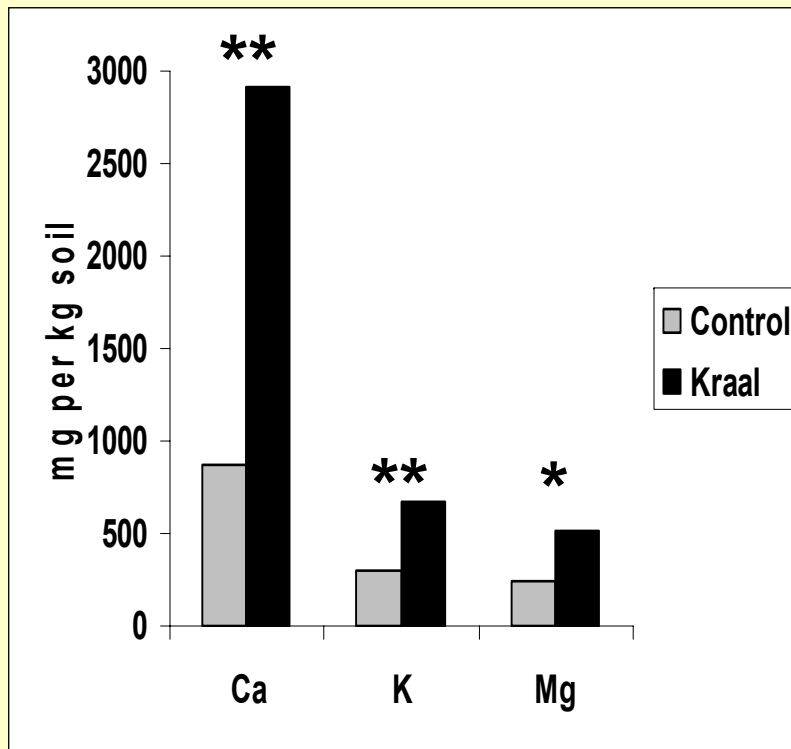
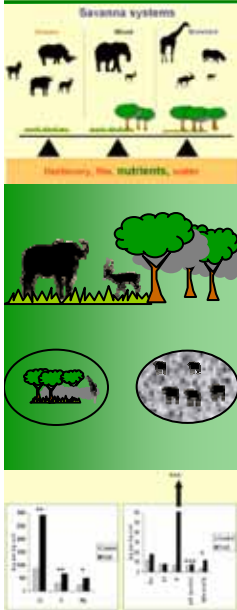
# Vegetation structure contrasts



Vegetation structure	Control	Kraal	<i>P</i>
Woody density (# / ha)	200 - 3000	0 - 100	***
Woody leaf biomass (kg / ha)	107 - 1553	0 - 2	***
Herbaceous biomass (kg/ha)	781	928	ns

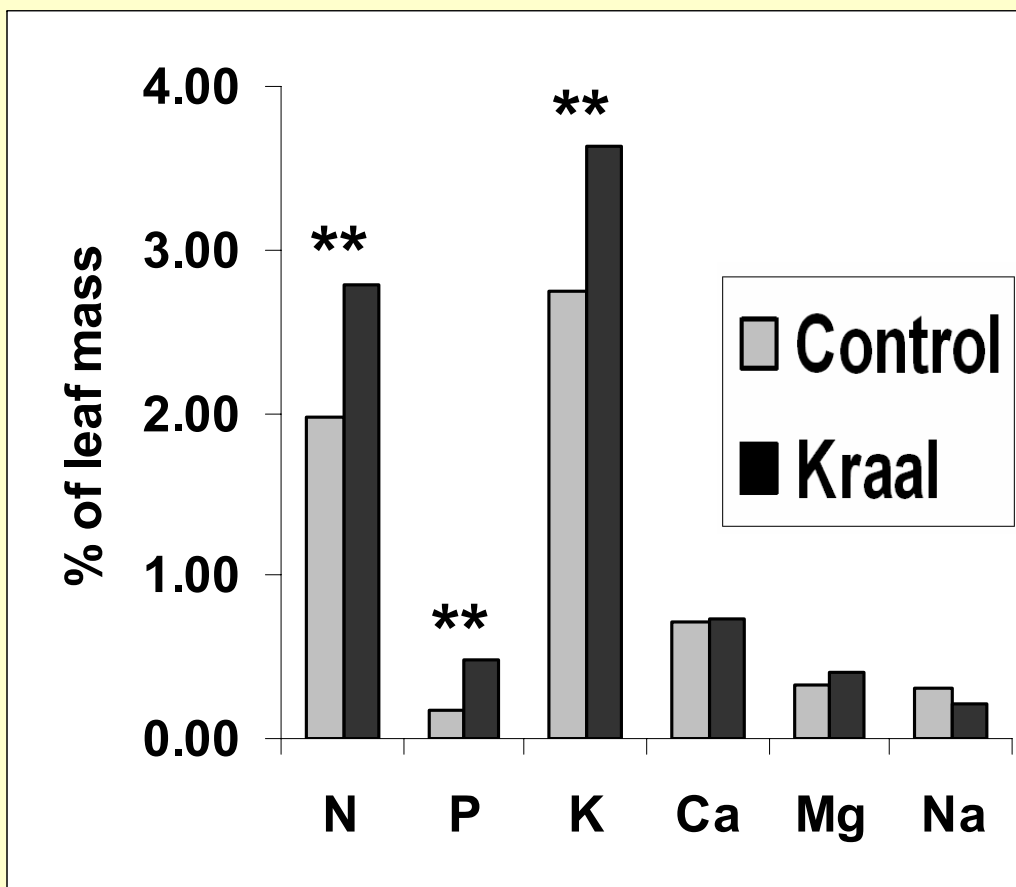
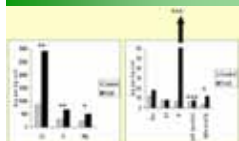
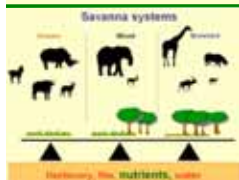


# Top soil differences

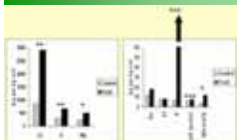
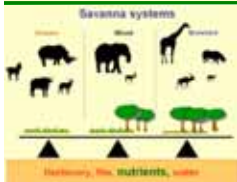


**N mineralization rate Kraal = 0.55 vs 0.18 mg N kg soil<sup>-1</sup> d<sup>-1</sup>**  
**Maize growth rate Kraal = 4.75 vs 1.95 g month<sup>-1</sup>**

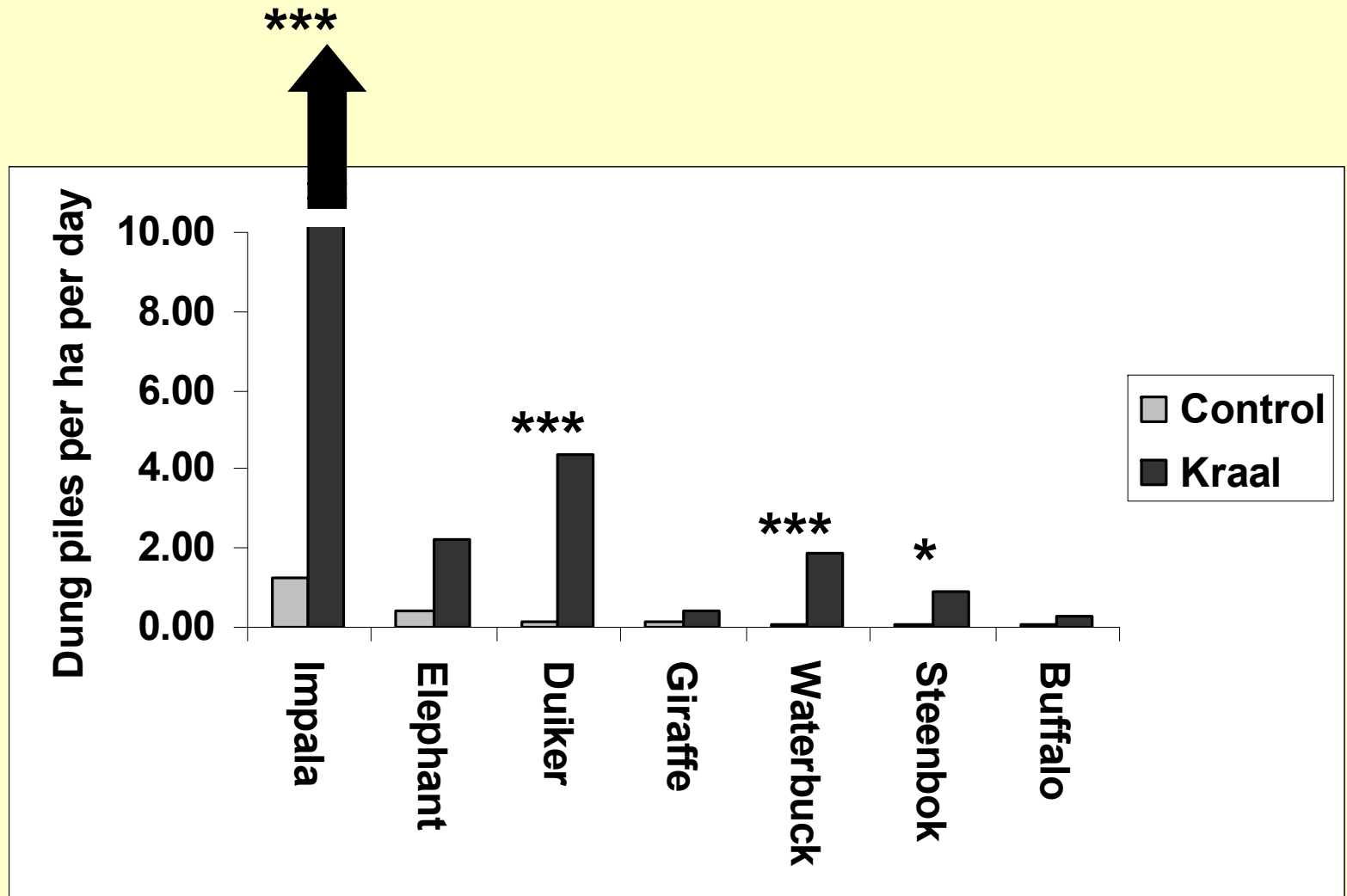
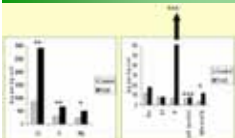
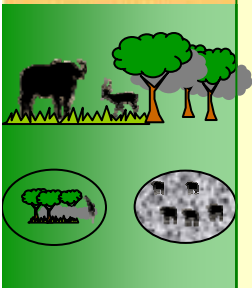
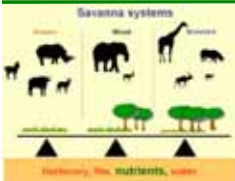
# *Urochloa mosambicensis* leaf chemistry



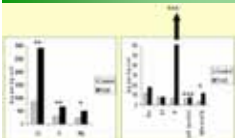
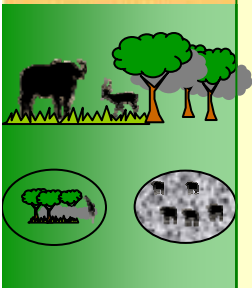
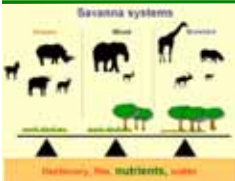
# Nice food – nice dung



# Dung deposition rates

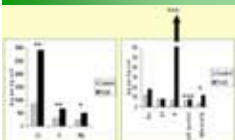
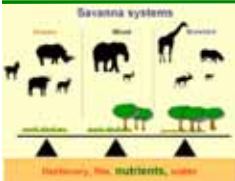


# Dung deposition rates



*Pim van Hooft*

# Dung deposition rates

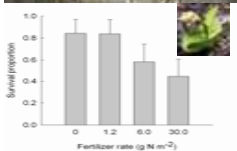
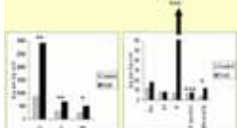
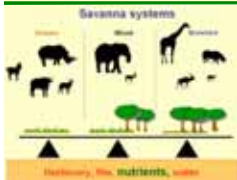


**From:**

- dung pile deposition rates
- mean dung pile mass
- %N in dung

**N deposition kraal: 1.2 g N m<sup>-2</sup> y<sup>-1</sup>**  
**control: 0.1 g N m<sup>-2</sup> y<sup>-1</sup>**

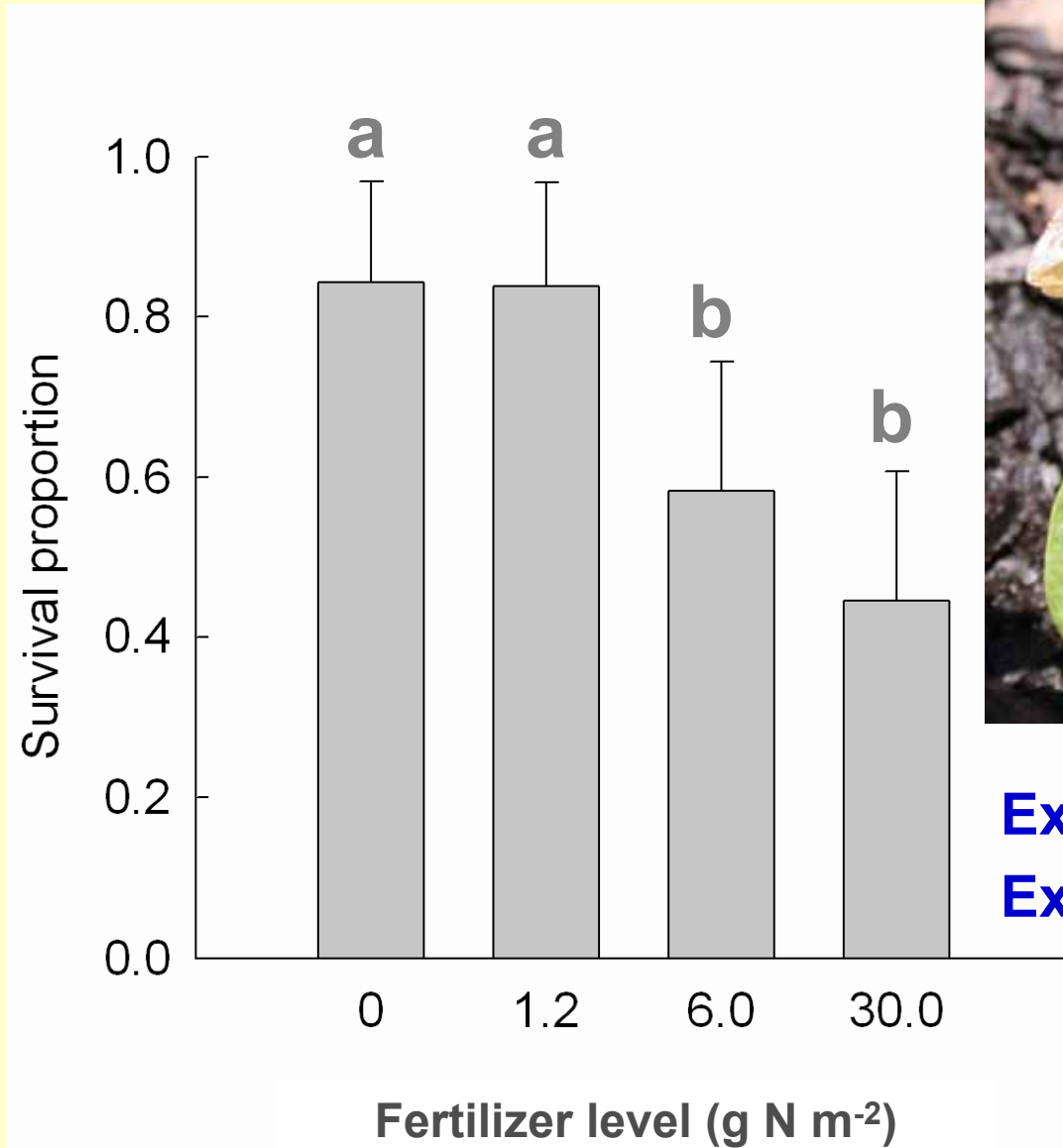
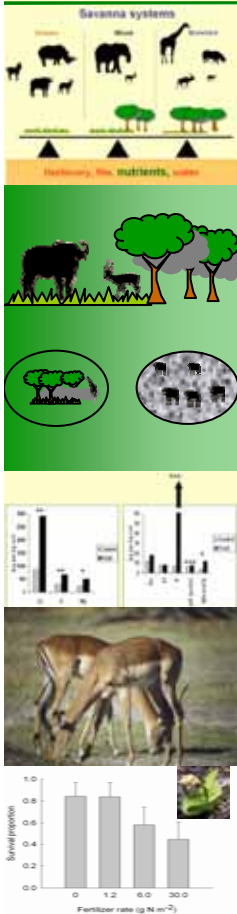
## Main findings on kraals



1. Soil nutrient status persists over time
2. Attractive to animals
3. Animals maintain nutrient status

**Why poor tree establishment on kraal sites?**

# Exp 1: Planted *C. mopane* seedlings survival in field



**Exclosures N.S.**  
**Exclosures x Fert N.S.**

# Exp 2: Pots with *C. mopane* seedlings +/- grass

Savanna systems

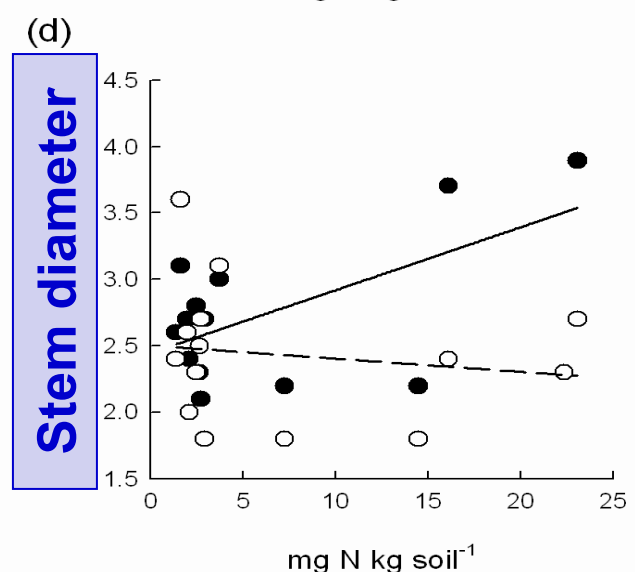
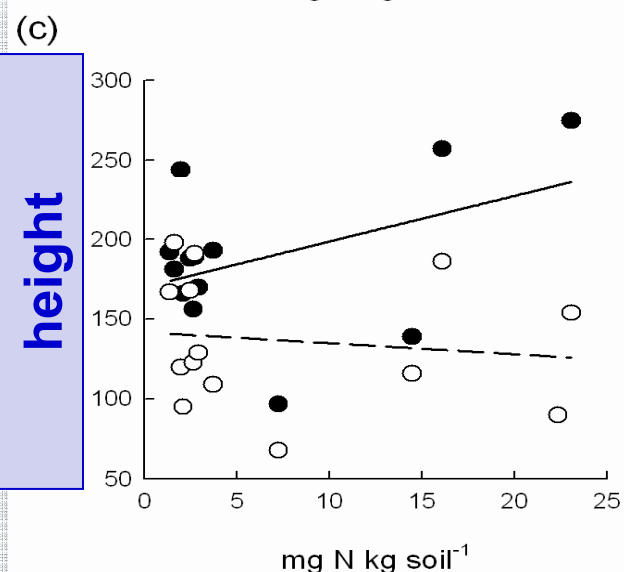
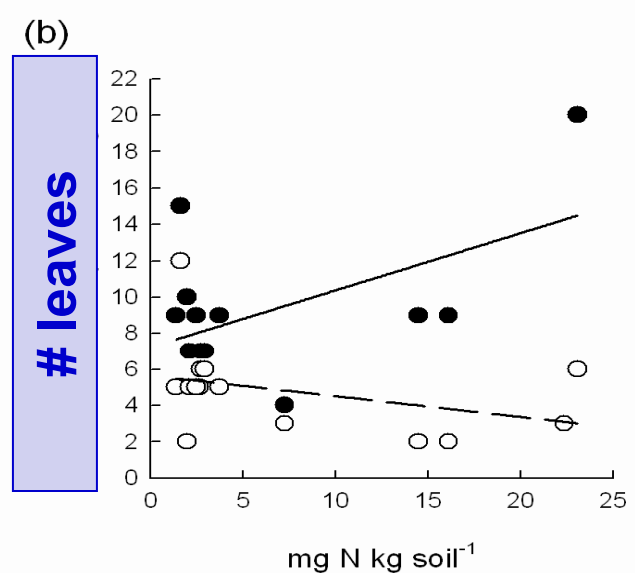
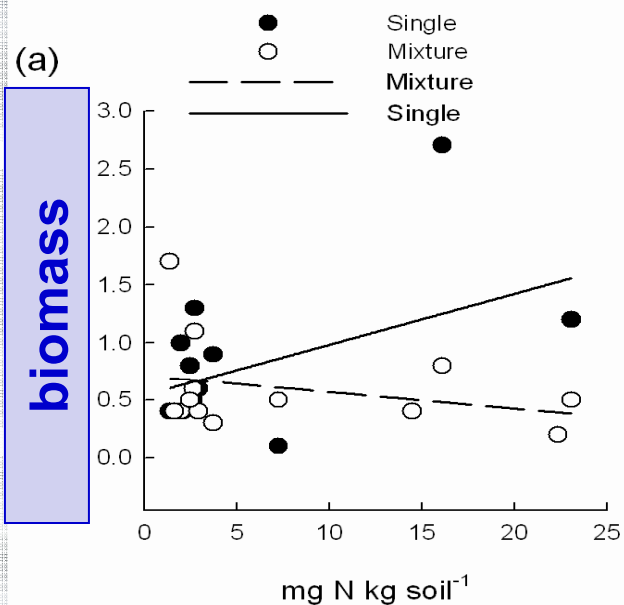
Herbivory, fire, nutrients, water

Stem elongation

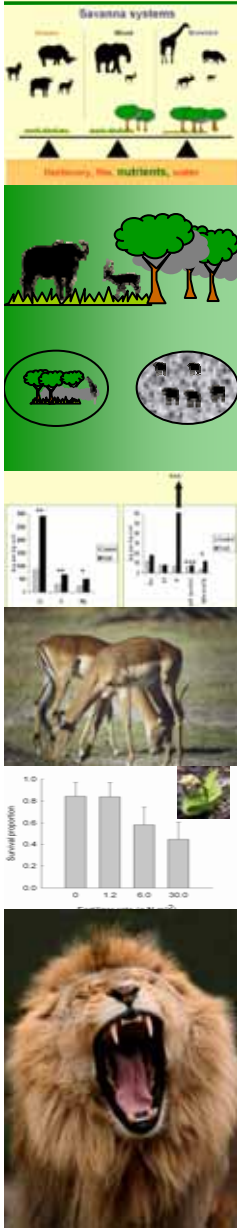
Fertilizer rate (g N m<sup>-2</sup>)

Stem elongation

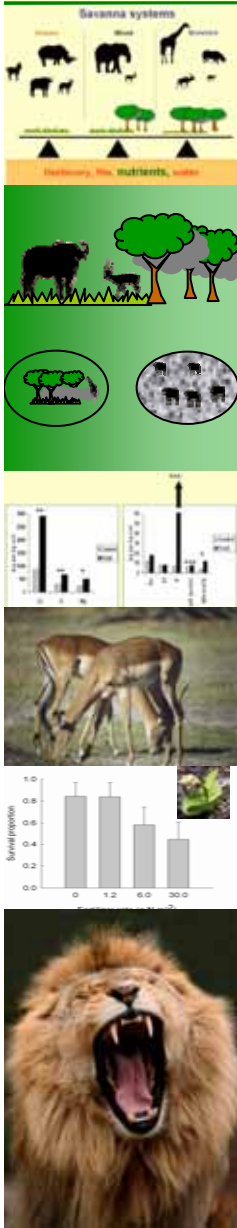
Fertilizer rate (g N m<sup>-2</sup>)



# Thus far: William barking up the wrong tree

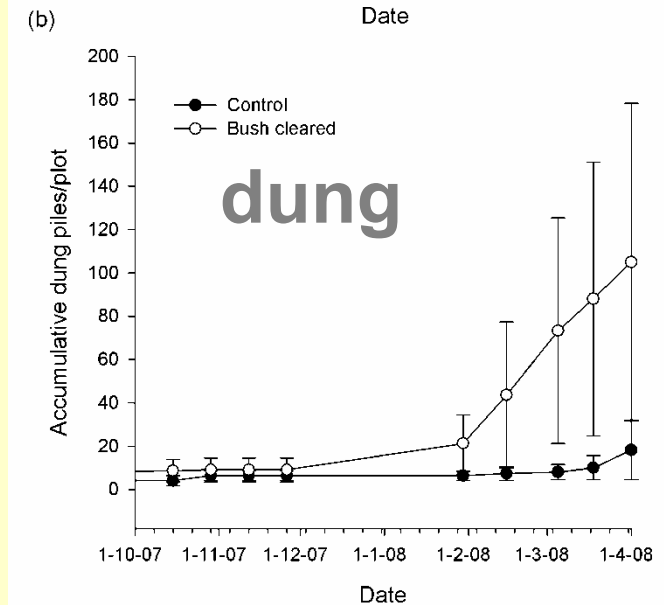
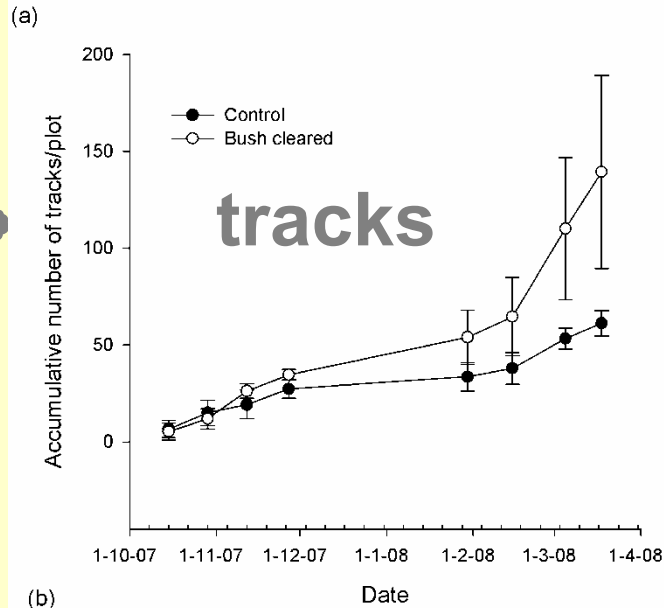
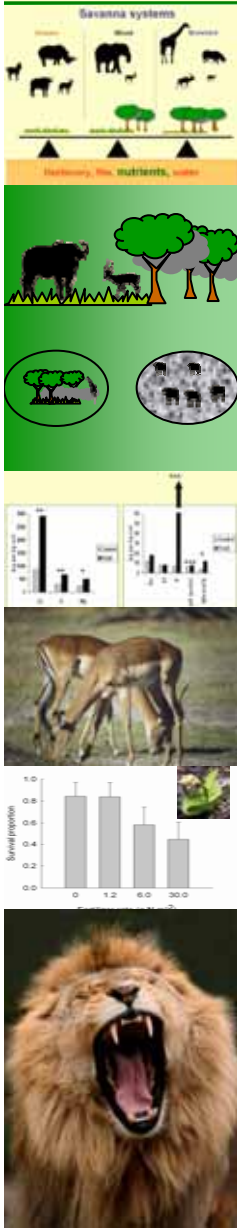


# Landscape of fear



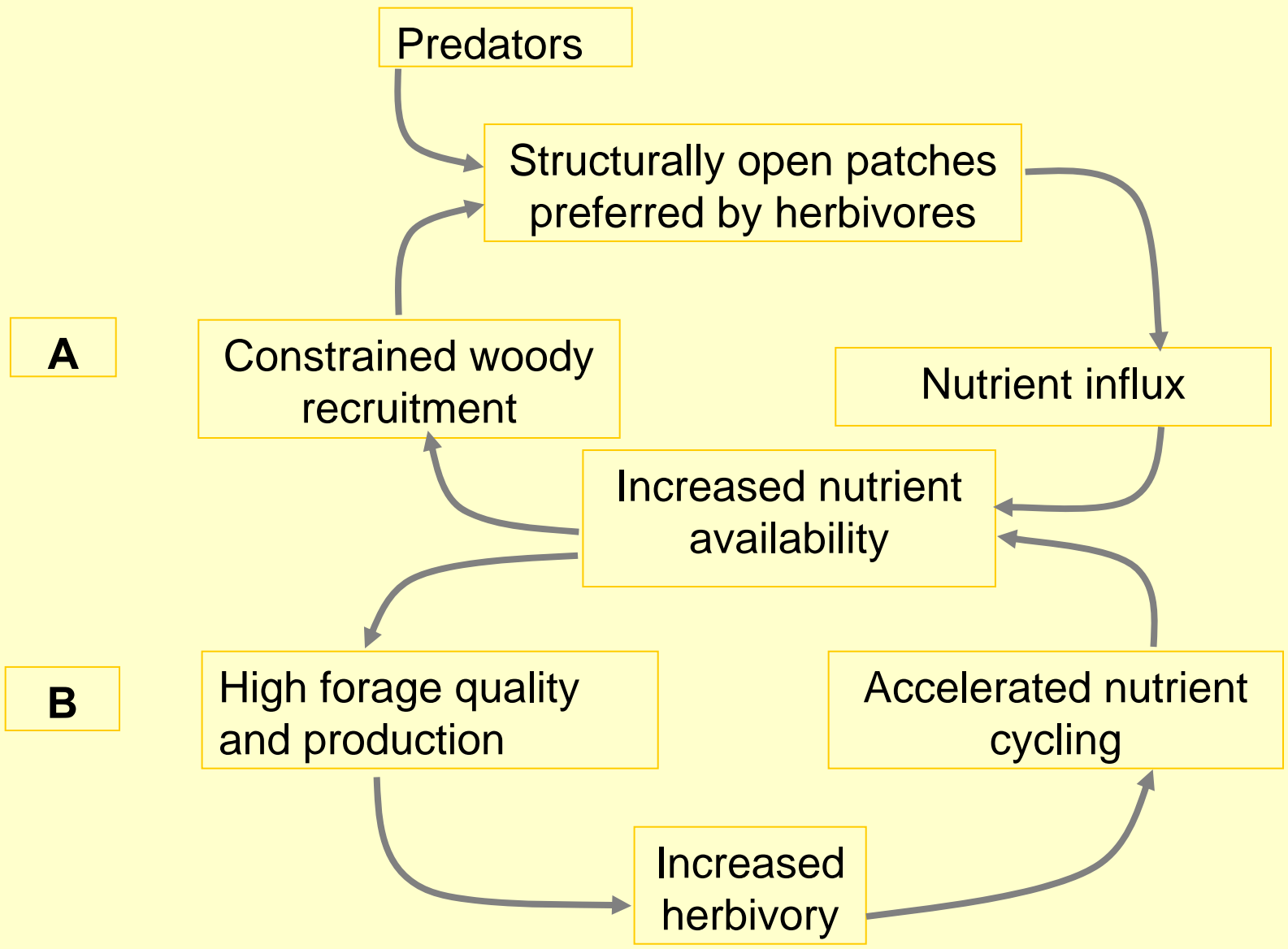
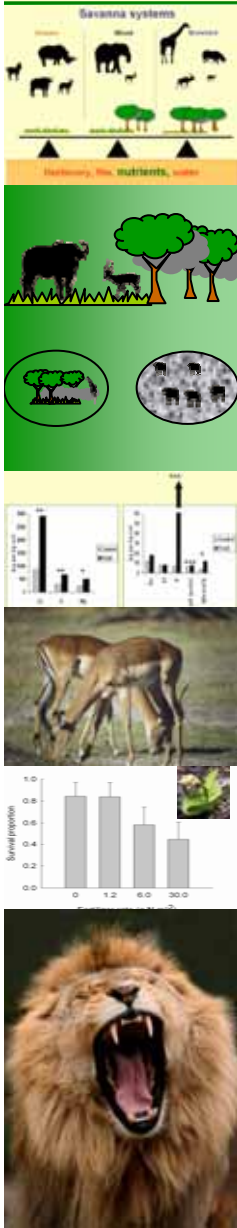
Large herbivores alter semi-arid savanna structure through soil nutrient mediation – 7th ASSNM Skukuza 2009

# Landscape of fear

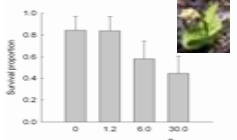
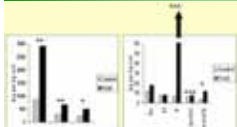
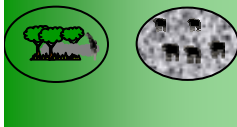
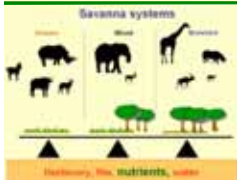


**Bush clearing patches (Ø 30 m) attract impala**

# Anti-predator behaviour of herbivores drives a positive feedback loop (A) and high soil nutrient availability (B)

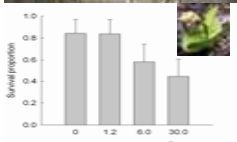
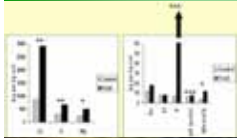
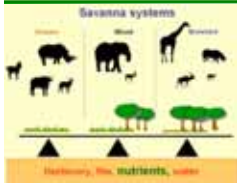


# Conclusion



1. kraal sites created, cattle → wild herbivores
2. wild herbivores fear wooded areas
3. herbivores import nutrients from elsewhere
4. grass = high quality forage
5. local nutrient cycling rates up
6. re-enforcing soil nutrient availability
7. reduced woody recruitment rates
8. open structure maintained

# Conclusion



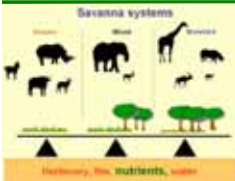
Indeed, two conditions were met:

- (1) large herbivores significantly affect local soil nutrient levels
- (2) soil nutrient levels significantly affect woody recruitment

Hence:

Large herbivores can potentially influence savanna structure through soil mediation.

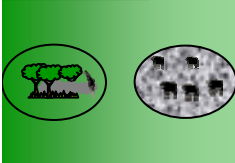
# Acknowledgements



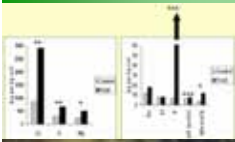
**APNR**



**Dr Marie Luttig Trust**



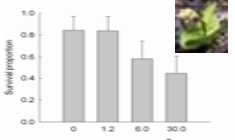
**Colin Rowes, Mrs Blatherwick, Carl van den Berg, Marius Fuls**



**Moagi Keretetse, Wim Braakhekke, Jan Bokdam, Claudius van de Vijver**



**Reis Manhique, Floris van Beest, Lemson Monareng**



**Krista Klijzing, Lizelle van der Waal, Joost van Gijn**



**Shell-SA, Omnia**

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