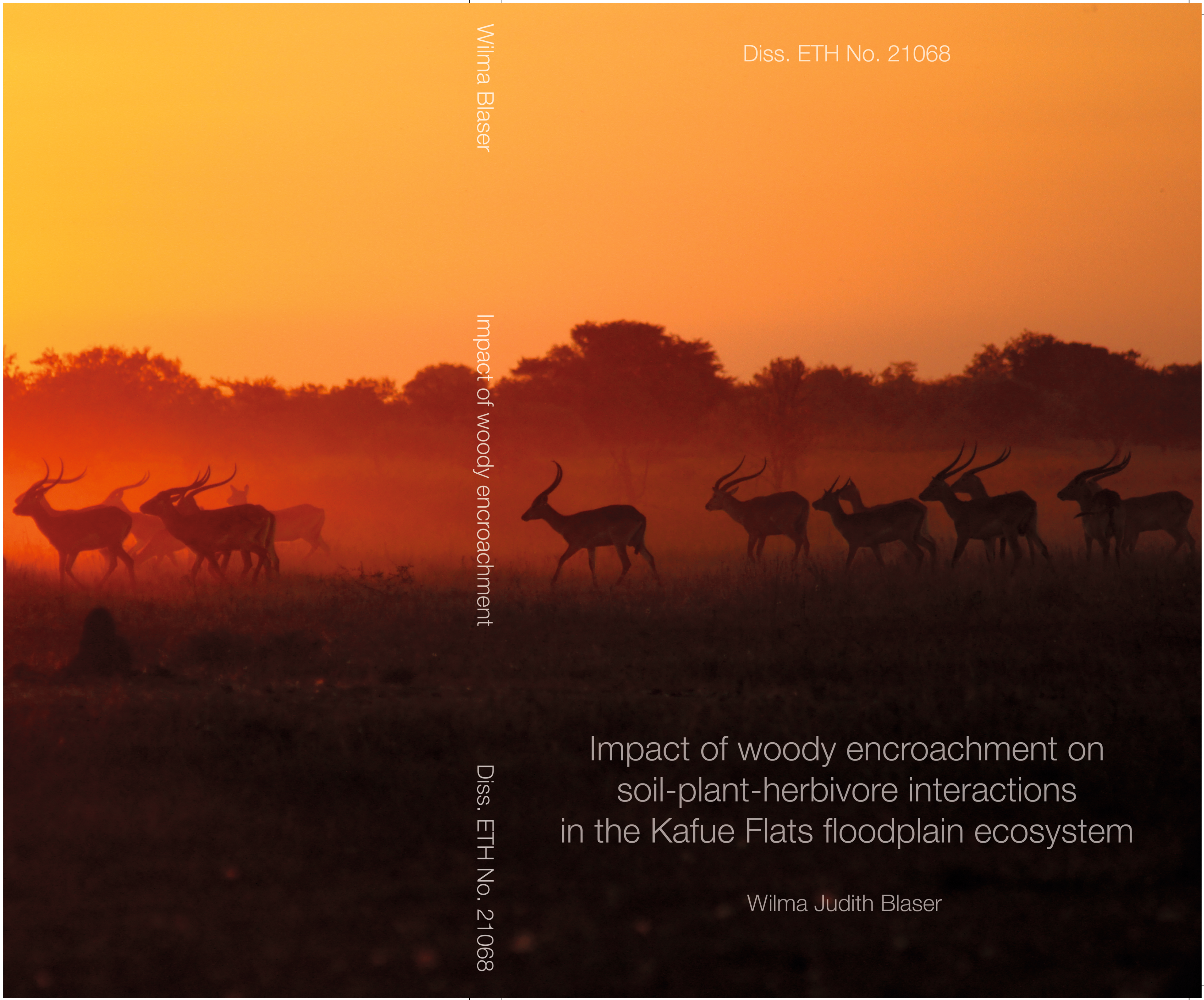

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IMPACT OF WOODY ENCROACHMENT ON SOIL-PLANT-HERBIVORE INTERACTIONS IN THE KAFUE FLATS FLOODPLAIN ECOSYSTEM

A dissertation submitted to
ETH ZURICH

for the degree of
Doctor of Sciences

presented by
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2013

Iyi nchito nimpaso kumakolo na banja langa bamene bana onesa
chidwi na chikondi chamalo yaku Kafue Flats monga ine

Contents

General introduction

Woody encroachment

During the past century, many natural grazing ecosystems including both savannas and temperate grasslands have become increasingly encroached by woody species (Archer et al. 1995, Van Auken 2000, Archer et al. 2001, Van Auken 2009). In this context, the term woody encroachment is defined as 'the increase in density, cover and biomass of woody or shrubby plants' (Van Auken 2000, 2009) and is synonymous with other terminologies such as 'bush or shrub encroachment', 'woody thickening', 'thicketization', 'woody plant proliferation', 'woody weed invasion', 'shrub invasion' and 'woody regrowth' (Burrows et al. 2002, Eldridge et al. 2011).

Woody encroachment is now common over much of the world's arid and semiarid biomes and is particularly evident in the western United States (Van Auken 2000, Knapp et al. 2008), Australia (Burrows et al. 2002, Robinson et al. 2008) and southern Africa (Trollope et al. 1989, Wigley et al. 2010, Buitenwerf et al. 2012). While great efforts have gone into understanding causes and consequences of woody encroachment in North American grassland ecosystems, much less is known about the causes and effects of encroachment on African savanna grasslands. However, in both regions encroachment seems to result from the independent and combined effects of global and local environmental changes or management regimes (Knapp et al. 2008, Eldridge et al. 2011). Possible global drivers include changing climate (Sankaran et al. 2005), atmospheric nitrogen deposition (Brown and Archer 1989) and elevated carbon dioxide concentration (Bond et al. 2003). Local drivers are mostly related to changes in management such as changes in fire and grazing regimes (i.e. overgrazing and recovery from anthropogenic disturbances from earlier societies) (Scholes and Archer 1997) but may also include hydrological changes due to dam construction and river regulation (O'Connor 2001, Dolores Bejarano et al. 2011).

Where woody plants encroach, they can modify the local environment dramatically by intercepting incoming precipitation and solar radiation and altering soil conditions, thereby creating heterogenous patches of light, water and nutrients in the grassland landscape (Breshears 2006). Because of these effects, and because they in turn induce changes in ecosystem properties (Scholes and Archer 1997, Breshears and Barnes 1999), the increase in woody cover in an ecosystem can trigger a cascade of effects on soil nutrients, understory biomass and food supply for herbivores, with multiple direct and indirect feedbacks on further woody growth (Fig. 1). Many studies have investigated the separate causal pathways shown in Fig. 1 (see references in text below), however, there is little understanding of the relative and combined importance of each of these effects within an ecosystem.

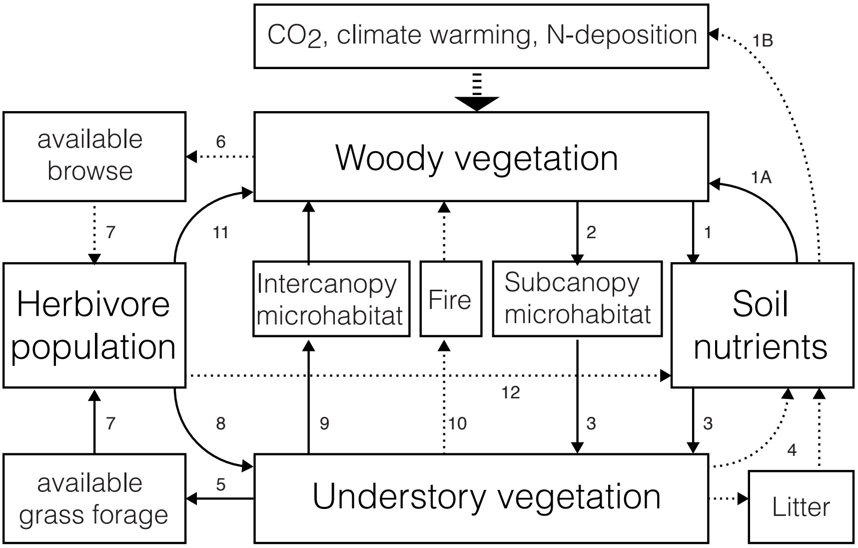


Figure 1 – Causes and consequences of shrub encroachment in grassland ecosystems via direct and indirect pathways. By altering nutrient (1) and microhabitat conditions (2) in their sub canopy woody species can facilitate or suppress the growth of understory vegetation (3), which in turn will change the food supply (5) for grazing herbivores. The understory vegetation can again have direct effects on soil nutrients but also indirectly through its effect on the litter pool (4). Changed soil nutrient pools, particularly of the growth-limiting nutrients nitrogen (N) and phosphorus (P) can induce a feedback upon the growth of woody species (1A). The shift in the dominant growth form from grasses to woody species often involves an increase in the aboveground net primary production (ANPP) in ecosystems. In combination with increased accumulation of soil carbon under woody plants (1) this can have large feedbacks to the earth-atmosphere system (1B). Increased abundance of woody species increases the food supply for browsing herbivores (6), and will affect the dominant herbivore guilds and population sizes in an ecosystem (7). Grazing herbivores (8) can promote further encroachment of shrubs by creating suitable microhabitats for further shrub encroachment (reduced competition through grasses) (9) and by reducing the fuel load for fires (10). Browsing herbivores and mixed feeders can positively affect the encroachment of shrubs by dispersing seeds outside the encroached area and increasing seed germination through ingestion (11). They may also have a negative effect upon further encroachment by browsing on shrub and tree seedlings and reducing seed production by browsing on mature plants. Dung deposition by herbivores can be an important pathway of nutrient return to the soil and will affect soil nutrients depending on the spatial heterogeneities of dung deposition (12). This thesis focuses on relations indicated with solid lines.

Nutrient accumulation below woody plants

Encroaching woody species can have complex, direct and indirect effects on nutrient dynamics of encroached grassland ecosystems. For example, many encroaching woody plants are leguminous species capable of fixing nitrogen (N) symbiotically (Scherer-Lorenzen et al. 2007, Knapp et al. 2008, Boutton and Liao 2010, Eldridge et al. 2011), and are hence responsible for a net N input from the atmosphere into the grassland ecosystem (Ludwig et al. 2004, Boutton and Liao 2010, Cech et al. 2010, Sitters et al. 2013). However, the symbiotic microorganisms responsible for N-fixation require high supplies of soil phosphorus (P) (Binkley et al. 2000, Vitousek et al. 2002), and encroaching N-fixing shrubs are therefore likely to increase the availability of soil N relative to P (Hibbard et al. 2001, Cech et al. 2008, Boutton and Liao 2010). This can potentially produce P-limiting conditions (Fig. 1, connection 1; Sitters et al. 2013). As N-fixation rates are highest under low N and high P conditions (Vitousek et al. 2002), we might expect woody species to cause a negative feedback upon their own capacity to fix N that ultimately restricts their biomass production (Fig. 1, connection 1A; Crews 1993, Pearson and Vitousek 2001, Binkley et al. 2003, Isaac et al. 2011).

Apart from changing the availability of N and P, an increase in woody cover in grasslands could have potentially important effects upon aboveground net primary production of the ecosystem (including both understory and woody biomass). This could lead to increased carbon-storage both in biomass and via increased litter inputs in the soil (Knapp et al. 2008, Barger et al. 2011). Such increased storage of carbon (C) in an ecosystem could cause feedbacks upon the earth-atmosphere system (Archer et al. 2000, Hoffmann et al. 2002, Beerling and Osborne 2006). Because of the vast extent of savanna and grassland ecosystems (25% of the global terrestrial landscape, Chapin et al. 2001) any change in patterns or controls of C inputs will be of global significance, though they have scarcely been quantified (Fig. 1, connection 1B; Knapp et al. 2008, Wigley et al. 2010). Understanding how nutrients (especially N and P) may ultimately limit woody growth, therefore, is important for assessing the potential of savanna ecosystems as C-sinks.

Modification of the microhabitat by woody plants

One of the most direct ways that woody species modify the environment is by intercepting light (Forseth et al. 2001). The proportion of light intercepted is determined by several overstory characteristics, particularly the height and density of woody plants (Barbier et al. 2008, Breshears and Ludwig 2010, Blank and Carmel 2012). Shading also influences other microclimatic and physiological properties such as air-, soil and leaf temperature, soil evaporation and plant evapotranspiration (Fig. 1, connection 2; Martens et al. 2000, Breshears 2006, Barbier et al. 2008, Breshears and Ludwig 2010). Thus, the shade cast by woody species and the resulting effect on microhabitat properties are key factors affecting plant growth and species composition in the understory (Fig. 1, connection 3; Jennings et al. 1999, Martens et al. 2000).

Effects of woody plants on herbaceous vegetation

By changing the availability of light, water and soil nutrients (described above) (Callaway 1995, Scholes and Archer 1997, Martens et al. 2000, Forseth et al. 2001, Barbier et al. 2008, Breshears and Ludwig 2010), encroaching woody species can have large effects on the dynamics of understory vegetation (Fig. 1, connection 3). Studies from many locations demonstrate that individual trees can have positive, neutral or negative effects on the species richness and productivity of herbaceous vegetation (Engle et al. 1987, Vetaas 1992, e.g. Belsky et al. 1993, Belsky 1994, Ludwig et al. 2004, Blank and Carmel 2012, Howard et al. 2012). In contrast, effects on herbage quality (tissue N and P concentrations) are generally positive (Belsky 1992, Treydte et al. 2007, Ludwig et al. 2008). The direction of the net effect of individual trees on understory productivity is often explained through the direction of resource modification and the interplay between different resources (light, water and nutrients, Vetaas 1992, Belsky 1994, Scholes and Archer 1997). By reducing evapotranspiration, for example, shading might facilitate the growth of sub-canopy plants, but the reduction in light can at the same time reduce the energy available for photosynthesis (Callaway 1995, Holmgren et al. 1997).

Many, though not all, of the studies of the effects of woody species on understory plant communities concentrate on the effects of isolated trees. However, while useful, these studies do not capture the full complexity of ecological changes associated with encroachment. Woody encroachment is usually a gradual and patchy process, shifting the vegetation from open grassland to dense woodland or thickets, with different degrees of woody densities along a continuum between these states. Properties of the understory vegetation such as productivity and species richness do not necessarily respond linearly to an increasing abundance of woody plants (Vetaas 1992, Riginos et al. 2009). Therefore there is need for studies that investigate the effects of woody encroachment along shrub or tree density gradients.

Effects of the tree-grass balance on herbivore food supply

Declining populations of many African herbivores raise concerns for the long-term existence of many species whose ranges are being reduced (Harris et al. 2009). These declines are often associated with changes in land-use, though the exact causes usually remain unclear, partly because of insufficient knowledge about processes that regulate herbivore populations (Hopcraft et al. 2010). Depending on their body size and environmental conditions, herbivore populations can be regulated either by predation (top-down) or by the abundance and quality of forage (bottom-up) (Hopcraft et al. 2010). Bottom-up regulation is common for larger herbivores (e.g. Zebra, Buffalo) and in regions where strong seasonality in the availability of food (e.g seasonal drying of grass, seasonal inundation of wetlands) causes animals to migrate (Hopcraft et al. 2010). Examples of migrations driven by seasonal changes in food supply are those of wildebeest *Connochaetes taurinus* in the Serengeti, Coke's hartebeest *Alcelaphus buselaphus* on the Athi plains of Kenya, and white-eared kob *Kobus kob*, topi *Damaliscus lunatus* and Mongalla gazelle *Eudorcas albonotata* in Sudan (Harris et al. 2009). Bottom-up control often regulates herbivore populations in a density-dependent manner due to the limited availability of forage in key resource areas during periods of food scarcity (e.g. areas utilized in the dry season; Illius and O'Connor 1999).

Herbivores can be classified into three main feeding categories based on their feeding strategy: browsing herbivores that feed on tree leaves and twigs, grazing herbivores that feed on grasses, and mixed (or intermediate) feeders that feed on a mixture of the two plant types (Gordon 2003). The tree-grass balance can thus have a strong effect on the herbivore guilds that inhabit an ecosystem, since in bottom-up regulated systems, browsers will be limited by the supply of woody plant food and grazers by the supply of grass forage (Fig. 1, connection 7; Owen-Smith 2008). Depending on the extent of the shift and the effects that the woody plants have on herbaceous biomass (Fig. 1, connection 3) and forage (Fig. 1, connection 5), encroachment may hence induce a shift in the herbivore assemblage towards more browsers and mixed feeders (Fig. 1, connections 5-7; Gordon and Prins 2008). Whether, and to what extent, such a shift occurs, however, would depend on the species of woody plants, the extent of encroachment, and the importance of the encroached habitat for herbivores, i.e. whether or not key resource areas for grazing herbivores are affected.

Effects of herbivores on the abundance of woody species

By feeding on herbaceous and woody biomass the herbivore assemblage can exert a strong influence upon the tree-grass balance in savanna, either suppressing or facilitating shrub encroachment (Du Toit and Cumming 1999, Roques et al. 2001, Augustine and McNaughton 2004). Grazing herbivores can promote further encroachment of shrubs by sustained heavy grazing (Fig. 1, connection 8) that reduces aboveground- and belowground grass biomass, producing more favourable conditions for seedling establishment (Fig. 1, connection 9; Coetzee et al. 2008). Heavy grazing also reduces the fuel load for fires, thereby reducing fire frequency and intensity, and giving young trees a greater chance of surviving to maturity (Fig. 1, connection 10; Scholes and Archer 1997, Roques et al. 2001).

The browsing of seed pods by browsing herbivores and mixed feeders, and the subsequent egestion of seeds in their dung, can promote encroachment by dispersing seeds outside the encroached area and by breaking seed dormancy (10) (Fig. 1, connection 11; Brown and Archer 1989, Vanstaden et al. 1994). On the other hand, browsing on mature trees can limit seed production and hence limit further establishment of woody plants (Goheen et al. 2007, Goheen et al. 2010).

Woody encroachment is therefore a significant ecological force that has the potential to dramatically affect grassland ecosystems. Nevertheless, although some of the links between woody encroachment and their ecosystem effects are well established, there is little understanding of the relative and combined importance of each of these effects within an ecosystem. Furthermore we still lack a unifying framework that allows easy assessment of likely effects of shrub encroachment and appropriate forms of management.

Thesis aims

The overall aim of this study was to determine the ecosystem consequences of shrub encroachment in a floodplain ecosystem with a hydrological regime that has recently been altered by the construction of dams.

Specifically, the thesis aims to:

1. quantify the effects of shrub encroachment on pools of soil carbon, nitrogen, and phosphorus and on the availability to plants of nitrogen and phosphorus, and to determine whether these changes in nutrient dynamics feed-back to influence shrub encroachment;

2. quantify the effects of shrub encroachment on the diversity and productivity of understory herbaceous plants; and

3. quantify the consequences of the shrub-induced changes in understory plant dynamics for the food supply and population dynamics of grazing herbivores.

Thesis outline

The first chapter introduces the study area and describes the hydrology and vegetation of the Kafue Flats with a special emphasis on the impact upon them of the construction of two hydroelectric dams. The chapter introduces the main encroaching shrubs in the area and reveals information upon their occurrence in relation to the hydrological regime.

The second chapter presents the results of a meta-analysis on the effects of woody plants on understory plant productivity and soil N and P pools. The effects of canopy height (i.e. the height of the lower canopy above the soil surface), the woody plants's ability to fix nitrogen and annual rainfall are used to explain why some woody species enhance the growth of understory grasses while others suppress them.

In the third chapter, effects of the leguminous shrub *Dichrostachys cinerea* on soil C, N and P pools and availabilities were measured along gradients of shrub cover and age in Lochinvar National Park in Zambia. Possible feedbacks of altered N and P pools and availabilities upon the growth of encroaching shrubs are considered in relation to C-sequestration.

The fourth chapter uses a remote sensing approach to map patterns of encroachment by *D. cinerea* and *M. pigra* in Lochinvar National Park. Attempting to understand the sequence of changes that occur during woody encroachment, the effects of these species upon the understory vegetation are investigated along two cover gradients. Data from both approaches were integrated to make predictions about how shrub encroachment may affect the food supply of grazing herbivores.

In the fifth chapter the annual spatial movement and changes in the nutritional status of the Kafue lechwe antelope are described in in relation to hydrology and food supply in the Kafue Flats floodplain ecosystem. Insights gained from previous chapters are integrated to understand how changes in hydrology, shrub encroachment and dam management have affected the lechwe population in the past three decades.

References

Archer, S., T. W. Boutton, and K. A. Hibbard. 2000. Trees in grasslands: biogeo- chemical consequences of woody plant expansion. Pages 115–137 *in* E. D. Schulze, S. P. Harrison, M. Heimann, E. A. Holland, J. Lloyd, I. C. Prentice, and D. Schimel, editors. Global Biogeochemical Cycles in the Climate System Academic Press, San Diego.

Archer, S., T. W. Boutton, and K. A. Hibbard. 2001. Trees in Grasslands: Biogeochemical Consequences of Woody Plant Expansion. Pages 115-137 *in* E. D. Schulze, M. Heimann, S. Harrison, E. Holland, J. Lloyd, I. Prentice, and D. Schimel, editors. Global Biogeochemical Cycles in the Climate System. Academic Press, San Diego.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanism of shrubland expansion: land use, climate or CO_2? Climatic Change **29**:91-99.

Augustine, D. J. and S. J. McNaughton. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. Journal of Applied Ecology **41**:45-58.

Barbier, S., F. Gosselin, and P. Balandier. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved—A critical review for temperate and boreal forests. Forest Ecology and Management **254**:1-15.

Barger, N. N., S. R. Archer, J. L. Campbell, C.-y. Huang, J. A. Morton, and A. K. Knapp. 2011. Woody plant proliferation in North American drylands: A synthesis of impacts on ecosystem carbon balance. Journal of Geophysical Research-Biogeosciences **116**: G00K07, doi:10.1029/2010JG001506.

Beerling, D. J. and C. P. Osborne. 2006. The origin of the savanna biome. Global Change Biology **12**:2023-2031.

Belsky, A. J. 1992. Effects of trees on nutritional quality of understorey gramineous forage in tropical savannas. Tropical Grasslands **26**:12-20.

Belsky, A. J. 1994. Influences of Trees on Savanna Productivity: Tests of Shade, Nutrients, and Tree-Grass Competition. Ecology **75**:922-932.

Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. Journal of Applied Ecology **30**:143-155.

Binkley, D., C. Giardina, and M. A. Bashkin. 2000. Soil phosphorus pools and supply under the influence of *Eucalyptus saligna* and nitrogen-fixing *Albizia facaltaria*. Forest Ecology and Management **128**:241-247.

Binkley, D., R. Senock, and K. Cromack. 2003. Phosphorus limitation on nitrogen fixation by Facaltaria seedlings. Forest Ecology and Management **186**:171-176.

Blank, L. and Y. Carmel. 2012. Woody vegetation patch types affect herbaceous species richness and composition in a Mediterranean ecosystem. Community Ecology **13**:72-81.

Bond, W. J., G. F. Midgley, and F. I. Woodward. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. Global Change Biology **9**:973-982.

Boutton, T. W. and J. D. Liao. 2010. Changes in soil nitrogen storage and delta15N with woody plant encroachment in a subtropical savanna parkland landscape. Journal of Geophysical Research-Biogeosciences **115**: G03019, doi:10.1029/2009JG001184.

Breshears, D. D. 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? Frontiers in Ecology and the Environment **4**:96-104.

Breshears, D. D. and F. J. Barnes. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. Landscape Ecology **14**:465-478.

Breshears, D. D. and J. A. Ludwig. 2010. Near-ground solar radiation along the grassland–forest continuum: Tall-tree canopy architecture imposes only muted trends and heterogeneity. Austral Ecology **35**:31-40.

Brown, J. R. and S. Archer. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (Prosopis glandulosa var.glandulosa) on sites differing in herbaceous biomass and grazing history. Oecologia **80**:19-26.

Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: > 50 years of data suggests CO_2 as a driver. Global Change Biology **18**:675-684.

Burrows, W. H., B. K. Henry, P. V. Back, M. B. Hoffmann, L. J. Tait, E. R. Anderson, N. Menke, T. Danaher, J. O. Carter, and G. M. McKeon. 2002. Growth and carbon stock change in eucalypt woodlands in northeast Australia: ecological and greenhouse sink implications. Global Change Biology **8**:769-784.

Callaway, R. M. 1995. Positive interactions among plants. Botanical Review **61**:306-349.

Cech, P. G., T. Kuster, P. J. Edwards, and H. Olde Venterink. 2008. Effects of herbivory, fire and N_2-fixation on nutrient limitation in a humid African savanna. Ecosystems **11**:991-1004.

Cech, P. G., H. Olde Venterink, and P. J. Edwards. 2010. N and P Cycling in Tanzanian Humid Savanna: Influence of Herbivores, Fire, and N_2-Fixation. Ecosystems **13**:1079-1096.

Chapin, F. S., III, O. E. Sala, and E. Huber-Sannwald. eds. 2001. Global biodiversity in a changing environment: Scenarios for the 21st century. Springer-Verlag, New York.

Coetzee, B. W. T., L. Tincani, Z. Wodu, and S. M. Mwasi. 2008. Overgrazing and bush encroachment by Tarchonanthus camphoratus in a semi-arid savanna. African Journal of Ecology **46**:449-451.

Crews, T. E. 1993. Phosphorus regulation of nitrogen-fixation in a traditional Mexican agroecosystem. Biogeochemistry **21**:141-166.

Dolores Bejarano, M., C. Nilsson, M. Gonzalez Del Tanago, and M. Marchamalo. 2011. Responses of riparian trees and shrubs to flow regulation along a boreal stream in northern Sweden. Freshwater Biology **56**:853-866.

Du Toit, J. T. and D. H. M. Cumming. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. Biodiversity and Conservation **8**:1643-1661.

Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters **14**:709-722.

Engle, D. M., J. F. Stritzke, and P. L. Claypool. 1987. Herbage standing crop around eastern redcedar trees. Journal of Range Management **40**:237-239.

Forseth, I. N., D. A. Wait, and B. B. Casper. 2001. Shading by shrubs in a desert system reduces the physiological and demographic performance of an associated herbaceous perennial. Journal of Ecology **89**:670-680.

Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. Journal of Animal Ecology **79**:372-382.

Goheen, J. R., T. P. Young, F. Keesing, and T. M. Palmer. 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. Journal of Ecology **95**:129-138.

Gordon, I. J. 2003. Browsing and grazing ruminants: are they different beasts? Forest Ecology and Management **181**:13-21.

Gordon, I. J. and H. H. T. Prins. 2008. Grazers and browsers in a changing world: Conclusions. Pages 309-321 *in* I. J. Gordon and H. H. T. Prins, editors. The ecology of browsing and grazing. Springer Berlin Heidelberg.

Harris, G., S. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt, and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research **7**:55-76.

Hibbard, K. A., S. Archer, D. S. Schimel, and D. W. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical Savanna. Ecology **82**:1999-2011.

Hoffmann, W. A., W. Schroeder, and R. B. Jackson. 2002. Positive feedbacks of fire, climate, and vegetation and the conversion of tropical savanna. Geophysical Research Letters **29**: NO. 22, 2052, doi:10.1029/2002GL015424

Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology **78**:1966-1975.

Hopcraft, J. G. C., H. Olff, and A. R. E. Sinclair. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends in Ecology & Evolution **25**:119-128.

Howard, K. S. C., D. J. Eldridge, and S. Soliveres. 2012. Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. Basic and Applied Ecology **13**:159-168.

Illius, A. W. and T. G. O'Connor. 1999. On the relevance of nonequilibrium concepts to arid and semiarid grazing systems. Ecological Applications **9**:798-813.

Isaac, M. E., J.-M. Harmand, D. Lesueur, and J. Lelon. 2011. Tree age and soil phosphorus conditions influence N-2-fixation rates and soil N dynamics in natural populations of Acacia senegal. Forest Ecology and Management **261**:582-588.

Jennings, S. B., N. D. Brown, and D. Sheil. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry **72**:59-73.

Knapp, A. K., J. M. Briggs, S. L. Collins, S. R. Archer, M. S. Bret-Harte, B. E. Ewers, D. P. Peters, D. R. Young, G. R. Shaver, E. Pendall, and M. B. Cleary. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Global Change Biology **14**:615-623.

Ludwig, F., H. de Kroon, F. Berendse, and H. H. T. Prins. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecology **170**:93-105.

Ludwig, F., H. De Kroon, and H. H. T. Prins. 2008. Impacts of savanna trees on forage quality for a large African herbivore. Oecologia **155**:487-496.

Martens, S. N., D. D. Breshears, and C. W. Meyer. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecological Modelling **126**:79-93.

O'Connor, T. G. 2001. Effect of small catchment dams on downstream vegetation of a seasonal river in semi-arid African savanna. Journal of Applied Ecology **38**:1314-1325.

Owen-Smith, N. 2008. The comparative population dynamics of browsing and grazing ungulates. Pages 149-177 *in* I. J. Gordon and H. H. T. Prins, editors. The ecology of browsing and grazing. Springer Berlin Heidelberg.

Pearson, H. L. and P. M. Vitousek. 2001. Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. Ecological Applications **11**:1381-1394.

Riginos, C., J. B. Grace, D. J. Augustine, and T. P. Young. 2009. Local versus landscape-scale effects of savanna trees on grasses. Journal of Ecology **97**:1337-1345.

Robinson, T. P., R. D. van Klinken, and G. Metternicht. 2008. Spatial and temporal rates and patterns of mesquite (Prosopis species) invasion in Western Australia. Journal of Arid Environments **72**:175-188.

Roques, K. G., T. G. O'Connor, and A. R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology **38**:268-280.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor, M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P. Hiernaux, H. Hrabar, K. L. Metzger, H. H. T. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden, and N. Zambatis. 2005. Determinants of woody cover in African savannas. Nature **438**:846-849.

Scherer-Lorenzen, M., H. O. Venterink, and H. Buschmann. 2007. Nitrogen enrichment and plant invasions: the importance of nitrogen-fixing plants and anthropogenic eutrophication. Pages 163-180 *in* W. Nentwig, editor. Ecological Studies.

Scholes, R. J. and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics **28**:517-544.

Sitters, J., P. J. Edwards, and H. Olde Venterink. 2013. Increases of soil C, N and P pools along an Acacia tree density gradient and their effects on trees and grasses. Ecosystems **16**: 347-357.

Treydte, A. C., I. M. A. Heitkonig, H. H. T. Prins, and F. Ludwig. 2007. Trees improve grass quality for herbivores in African savannas. Perspectives in Plant Ecology Evolution and Systematics **8**:197-205.

Trollope, W. S. W., F. O. Hobson, J. E. Danckwerts, and J. P. Van Niekerk. 1989. Encroachment and control of undesirable plants. Pages 73–89 *in* J. E. Danckwerts and W. R. Teague, editors. Veld Management in the Eastern Cape Department of Agriculture and Water Supply, Pretoria, South Africa.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics **31**:197-215.

Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management **90**:2931-2942.

Vanstaden, J., K. M. Kelly, and W. E. Bell. 1994. The role of natural agents in the removal of coat-imposed dormancy in *Dicrostachys cinerea* (L) Wight et arn seeds. Plant Growth Regulation **14**:51-59.

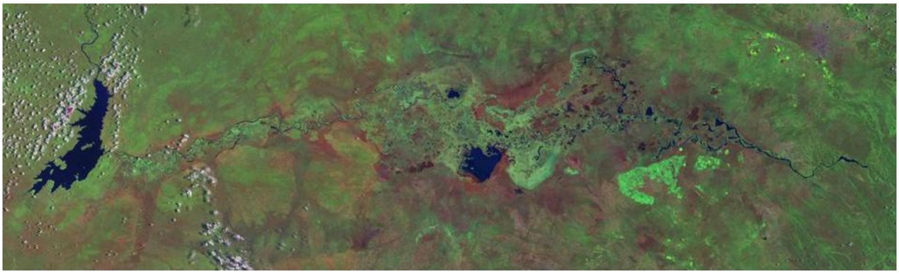
Vetaas, O. R. 1992. Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science **3**:337-344.

Vitousek, P. M., K. Cassman, C. Cleveland, T. Crews, C. B. Field, N. B. Grimm, R. W. Howarth, R. Marino, L. Martinelli, E. B. Rastetter, and J. I. Sprent. 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry **57**:1-45.

Wigley, B. J., W. J. Bond, and M. T. Hoffman. 2010. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? Global Change Biology **16**:964-976.

Chapter 1

Description of the study area: Kafue Flats and Lochinvar National Park



The Kafue Flats - an important wetland area

The Kafue Flats are an extensive seasonally inundated floodplain system in the Kafue River Basin in southern Zambia, Africa. The floodplain extends over 255 km along the course of the Kafue River, is up to 60 km wide and covers an area of approximately 6,500 km^2 (Fig. 1, Mumba and Thompson 2005). The vast area of the Kafue Flats consist of a mosaic of lagoons, marshes, and floodplain grassland surrounded by a zone dominated by termite mounds (Fig. 8) followed by munga and miombo woodlands. The one-storied munga woodlands are dominated by *Colosphermum mopane* and *Acacia spp.,* whereas miombo woodlands are two-storied and characterized by the predominant presence of *Brachystegia spp.* and scattered shrubs (Ellenbroek 1987).

The Kafue Flats are an important area for wetland conservation as the system supports many endangered and endemic species such as the endemic Kafue lechwe (*Kobus leche* ssp. *kafuensis* Haltenorth, 1963), the threatened Wattled crane (*Grus carunculatus* Gmelin, 1789), and Sitatunga (*Tragelaphus spekii* Speke, 1863) and hosts large concentrations of resident and migratory waterbirds (Fig. 2; Leonard 2005). These species are concentrated in and around two National Parks, Lochinvar and Blue Lagoon, and a multiple used buffer zone surrounding these parks (the Game Management Area), where these wildlife species are protected (Fig. 1).

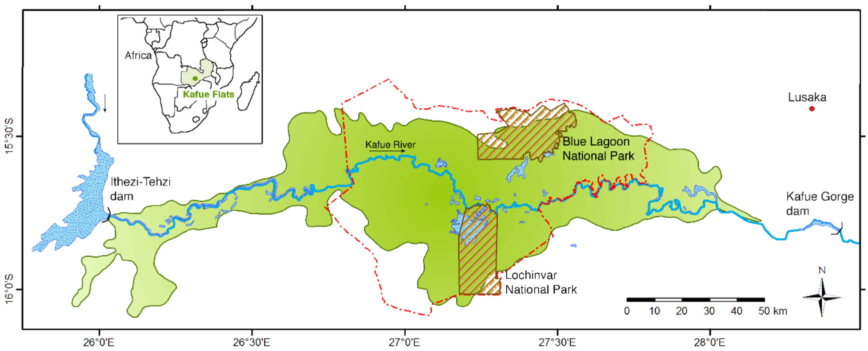


Figure 1 – The Kafue Flats in Zambia, southern Africa, between the Ithezi-Thezi dam (constructed in 1971), and the Kafue Gorge dam (constructed in 1978). The dashed red line indicates the extent of the Game Management Area, hatched areas are Blue Lagoon and Lochinvar National Park. Drawings adopted from Roland Zurbrügg (2012).

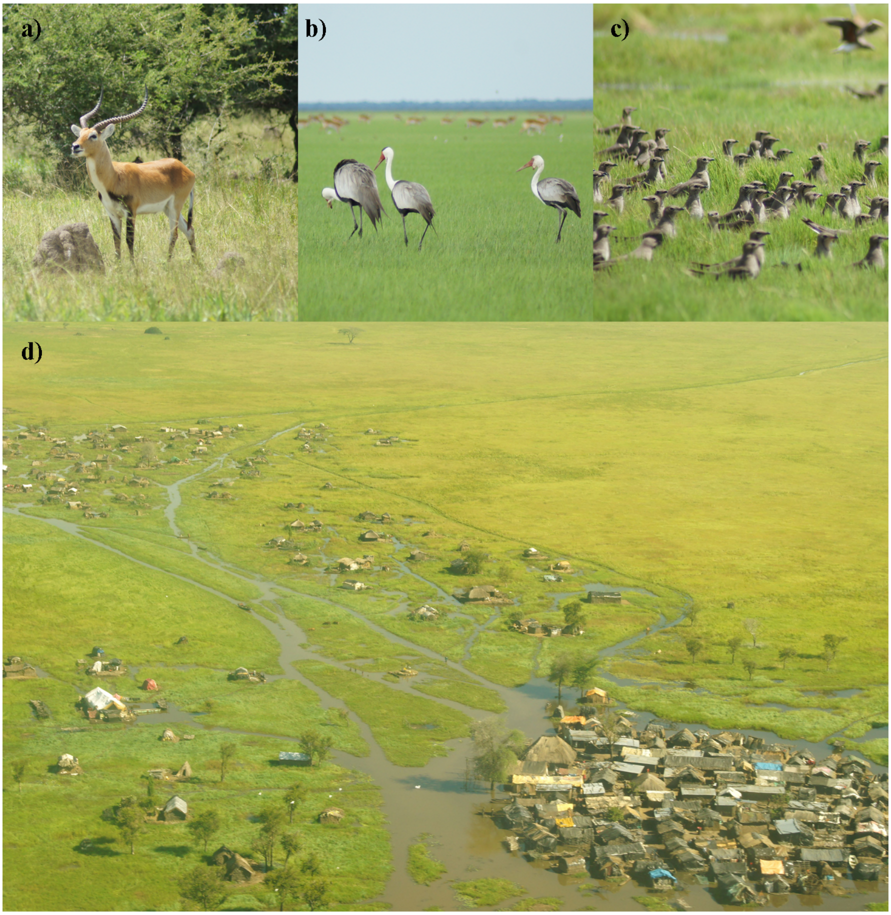


Figure 2 – Important features of the Kafue Flats: a) the endemic Kafue Lechwe (*Kobus leche* ssp. *kafuensis* Haltenorth, 1963), b) the threatened Wattled crane (*Grus carunculatus, Gmelin, 1789*), c) migratory Red-winged pratincole (*Glareola pratincola)* and d) the Namalyo fishing village.

The combined area is designated as an internationally important wetlands falling under the Ramsar Convention (Ramsar 2013) and an important Bird Area (iBA, BirdLife International; Fig. 1; Leonard 2005).

The Kafue Flats are home to 1.3 million people who are engaged in small-scale agricultural and pastoral farming as well as fishing (Fig. 2; Sheppe 1985, Mumba and Thompson 2005).

Lochinvar National Park - history and study sites

Lochinvar National Park - further called Lochinvar - is located on the southern bank of the Kafue River (Fig. 1 and 3). Covering an area of about 410 km^2, the park represents about 6.3 % of the total area of the Kafue Flats (ZAWA 2004). Lochinvar was used as a cattle ranch from the turn of the century until 1965 when it was bought by the Zambian Government. Between 1933 and 1948 the owners were sympathetic to wildlife and allowed large populations of lechwe, wildebeest, and zebras to co-exist with the cattle. However, the main land predators were shot out during the cattle-keeping period, particularly between 1948 and 1965 when Lochinvar was a commercial ranch, and, apart from a few (<10) spotted hyena (*Crocuta crocuta*), they have not returned. Since the Government took ownership cattle have been excluded from the area and Lochinvar received National Park status in 1977 (Sayer and Van Lavieren 1975, Rees 1978b, a).

Lochinvar is the best studied area in the Kafue Flats and was subject of a series of studies conducted by the Kafue Research Committee prior and around the time of dam construction in the Kafue River in the early 1970s (Handlos 1975, Williams and Howard 1977, Johnson and Roder 1979), as well as extended ecological studies by Rees (1978) and Ellenbroek (1987) in the mid 70s and early 80s, respectively.

The research presented in this thesis was largely carried out in Lochinvar where we repeated a vegetation survey at 60 sites (Fig. 3, red squares) that had been conducted by Ellenbroek (1978) in the early 1980s to quantify vegetation change.
We further followed the seasonal changes in standing biomass in 26 plots distributed over the floodplain, water-meadow and termitaria area of the Park (Fig. 3, blue dots, Chapter 5). Encroachment related research was done in two core areas that were dominated by the leguminous shrubs *Dichrostachys cinerea* and *Mimosa pigra* (Fig. 3, purple and pink squares, respectively, Chapter 3-4). The locations of the study sites are shown in Fig. 3.

Climate

The climate of the Kafue Flats is characterized by distinct seasonality and can be divided into three seasons: the cool, dry season (April to August), the hot dry season (August to November) and the warm, wet season (November to April) (Archer 1971).

The mean annual temperature is 20.6°C and mean annual precipitation is in the range of 800 mm with almost all of it falling in the warm, wet season (Ellenbroek 1987, Mumba and Thompson 2005). In the hot dry season savanna fires are common (Munyati 2000).

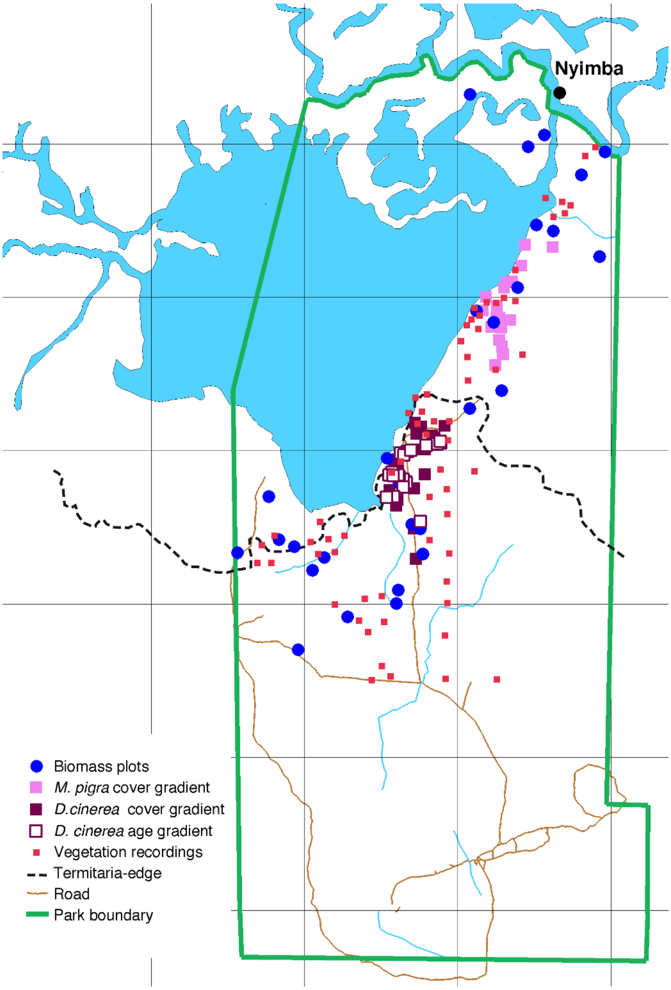


Figure 3 – Map of Lochinvar National Park in the Kafue Flats with location of the main study sites. Blue dots: sites of biomass clippings to quantify herbivore food supply (Chapter 6), pink squares: study sites in *Mimosa pigra* invaded areas (Chapter 4); purple squares: sites in *Dichrostachys cinerea* invaded areas (Chapters 4 and 5, filled symbols encroached sites along a density gradient, open symbols single standing trees along an age gradient); small red squares: sites of vegetation surveys (Chapter 1).

Hydrology

The Kafue Fats experience a distinct wet-dry cycle, with large changes in water level and large proportions of the floodplain falling dry after the flood recede (Fig. 4). Under natural conditions, before the dams were constructed, flood levels began to rise in December and the flood-peak passed slowly downstream between March and May. After the rains the floodplain dried out slowly and were dry by September (Fig. 4, Ellenbroek 1987, Leonard 2005).

In the 1970s the hydrological regime of the lower Kafue River, and in turn that of the Kafue Flats and Lochinvar, was significantly modified through the construction and operation of two dams: the downstream dam at Kafue Gorge, constructed in 1971 including a 900 MW hydropower plant and the upstream dam at Ithezi-Thezi constructed in 1978 with a 370 km^2 storage reservoir to ensure year-round power production at Kafue Gorge (Fig. 1, Mumba and Thompson 2005). The dam-induced alterations in the hydrology of the Kafue Flats are a lower maximum water level, a higher minimum level, and hence a drastic reduction in the amplitude of water level fluctuation over the year (from 5 m pre dam to 1.3 m post dam). These changes have lead to a shift in the predominant hydrological zones: the seasonally inundated area has decreased, whereas higher lying not flooded and low lying permanently inundated areas have increased (Fig. 4; Ellenbroek 1987, Leonard 2005, Mumba and Thompson 2005). Furthermore, due to management of the dams the flood level often increases well before the end of the dry season and earlier than under natural pre-dam conditions (Leonard 2005).

Vegetation

The natural vegetation in the Kafue Flats is composed of seasonally flooded, treeless grasslands within a landscape dominated by savanna woodlands (Ellenbroek 1987). Since seasonal inundation by rainwater or flooding by the Kafue River is a major environmental factor for the control of plant species distribution (cf. Spence 1982, Denny 1985, Van der Valk 1994, van Eck et al. 2003), the vegetation can be ascribed by coenoclines of inundation characteristics (depth, duration) parallel to the river.

From the main channel to the edge of the flood affected zone, the vegetation shows a gradient from (1) open water, (2) floodplain grasslands dominated by *Vossia cuspidate, Oryza longistaminata* and *Echinochloa scabra*, (3) water meadows

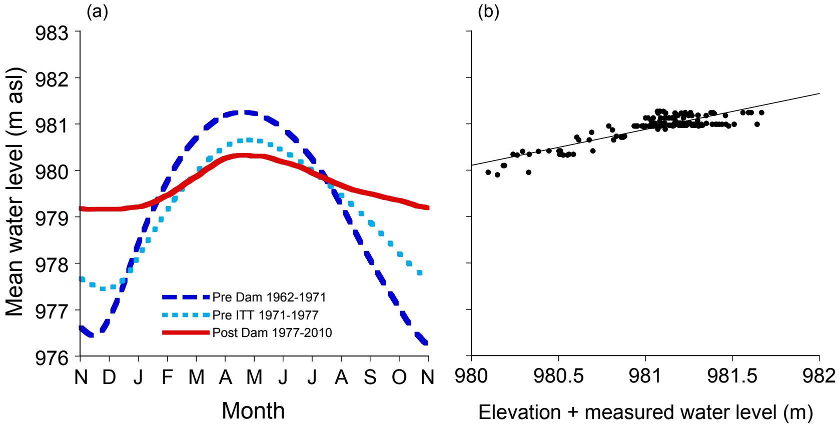


Figure 4 – (a) Mean hydrograph at Nyimba gauging station for pre-dam (1962-1971, dark blue dashed line), post Kafue Gorge and pre Ithezi-Thezi dam (1971-1977, light blue, dotted line) and post dam (1977-2010, solid red line) period. (b) Regression of daily water levels at Nyimba and measured water levels in the floodplain area in Lochinvar National park (r^2=0.74, p<0.001). Hydrological data was obtained from ZESCO hydrological gauging station at Nyimba (for detailed location see Fig. 2). Elevation measurements were obtained by means of manual land surveying with a level instrument in October 2010. Measured water levels were obtained throughout the study period (December 2009 to March 2011) in flooded sites where elevation had been assessed.

characterized by *Leersia denudata*, *Panicum repens*, *Acroceras macrum* and *Paspalidium obtusifolium*, (4) littoral zone dominated by *Cynodon dactylon*, *Vernonia glabra* and *Vetiveria nigritana*, (5) termitaria grassland characterized by the presence of many termite mounds and grass species such as *Sporobolus ioclados*, *Eragrostis inamoena*, *Digitaria milanjiana*, *Setaria spacellata* and finally (6) woodland dominated by trees, such as *Acacia*, *Albizia*, etc (Ellenbroek 1987). The occurrence of different vegetation types in the seasonally inundated areas are strongly linked to the prevailing hydrological regime of the main river channel because the flooding is strongly linked to water levels in the river (Fig. 4b).

Reported vegetation changes in the post dam period include an increase in areas covered by shrubs (Munyati 2000, Mumba and Thompson 2005, Genet 2007, Thomas 2007) along with a more subtle change in the grassland vegetation, both in the floodplain as well as in the termitaria grasslands. The main encroaching shrub species are the exotic *Mimosa pigra* as well as the native *Dichrostachys cinerea* and several *Acacia* species.

Dichrostachys cinerea *encroachment*

D. cinerea is a semi-deciduous leguminous shrub, native to southern and central Africa and one of the major encroaching species in southern African grasslands (Fig. 5, Roques et al. 2001, Hagenah et al. 2009). The key determinants for encroachment by *D. cinerea* were found to be high grazing pressure and suppression of fire frequency (Roques et al. 2001, Munyati et al. 2011). While these factors might play a role in our system field data indicates that the probability of occurrence of the species is correlated to elevation ($p<0.001$), and the species is mainly expanding its occurrence in the formerly tree less termitaria zone and littoral zone above the edge of the flooded area (Fig. 6d,e and Fig. 7). In accordance with reports that list *D. cinerea* as a species that does not support waterlogging (McGregor 1994, Orwa et al. 2009) this might indicate that a reduction in maximum flood levels might have lead to drier conditions at the edge of the floodplain, allowing woody growth of *D. cinerea* (and Acacia species) in the former waterlogged areas.

Mimosa pigra *encroachment*

M. pigra is a spiny leguminous shrub, native to South America, that has become invasive in several parts of Asia, Australia and Africa. It forms thick, impenetrable, monospecific stands that exclude other plants and most animals (Fig. 5, Lonsdale et al. 1989). The encroachment of *M. pigra* is commonly attributed to disturbance that temporarily eliminates vegetation, e.g. overgrazing and trampling (Buckley et al. 2004). In Lochinvar the species has his distribution center in the seasonally inundated floodplain (Fig 6d,e and Fig. 7). The changes in the flooding regime after dam construction might have created the disturbance needed to allow the plant to effectively establish and increase in abundance, although we have no data to proof this.

At the edge of the flooded area, in the so-called littoral zone *M. pigra* and *D. cinerea* have an area where they co-occur (Fig. 6e). The distribution of the two species in relation to elevation, and hence flooding regime, indicates that *M. pigra* might be favored in wet years with high and long floods, whereas *D. cinerea* is likely favored in drier years when the floods to not reach this zone

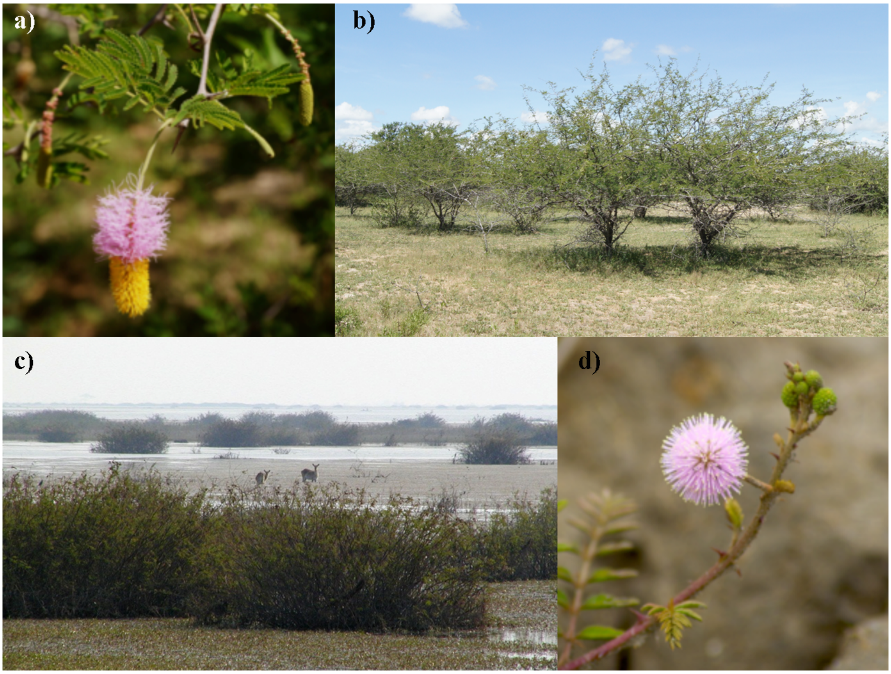


Figure 5 – Encroaching shrubs in Lochinvar National Park. *Dichrostachys cinerea* (a,b) and *Mimosa pigra* (c,d) and their respective inflorescence.

Changes in the herbaceous vegetation

We compared vegetation recordings made by Gerard Ellenbroek in Lochinvar Natonal Park in 1980 (Ellenbroek 1987), with our own re-recordings of the same sites in 2010 (60 100 m^2 sites). We assumed that the recordings in 1980 (three years after the Ithezi-Thezi was constructed) would still largely reflect situation before this dam, whereas the re-recordings in 2010 would reflect the adapted post-dam situation. This comparison showed that changes in the flooding also had an effect on the distribution of herbaceous plant species (Fig. 7). Species that were confined to the area above the high flood line shifted with the changed conditions and extended their range of occurrence to lower elevations (e.g. *Sporobolus pyramidalis, Commelina subulata, Aspilia kotschy, Hygrophila pilosa, Dichanthium insculptum, Eragrostis inamoena, Panicum novemnerve, Setaria spacellata, Cassia mimosoides, Hibiscus cannabinus, Echinochloa pyramidalis, Hygrophila auriculata, Sesbania microphilla*).

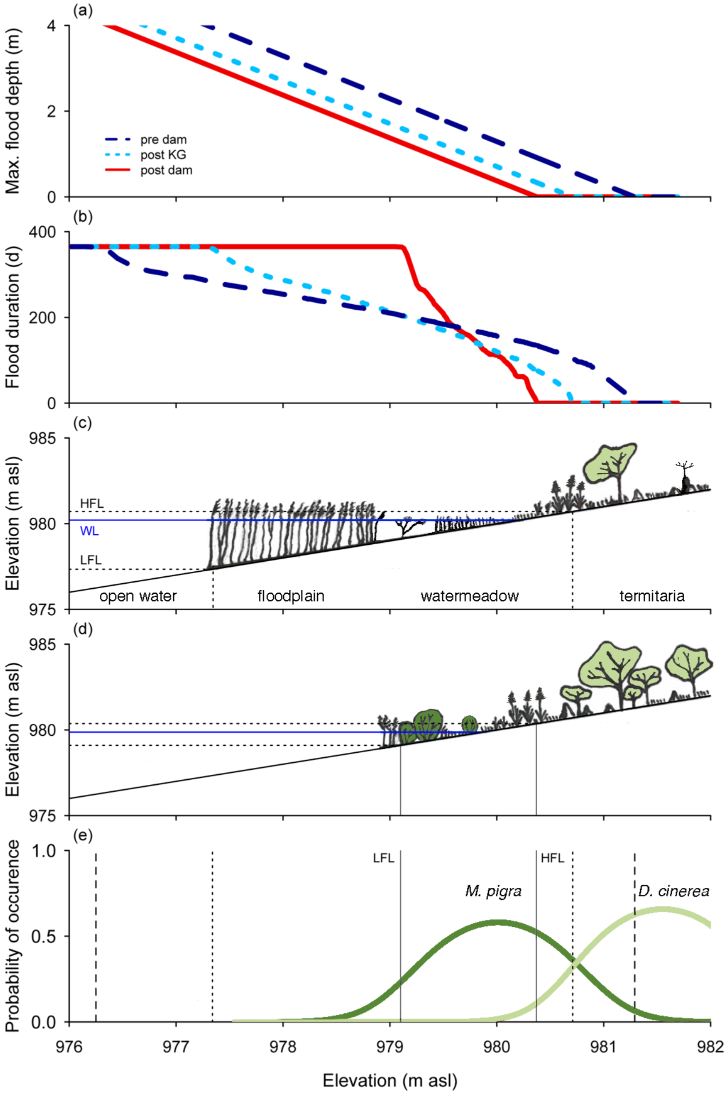


Figure 6 – Maximal flooding depth in m asl (a), flood duration in days per year (b), schematic vegetation distribution in 1980 (c) and 2010 (d) and probability of occurrence of *Mimosa pigra* and *Dichrostachys cinerea* in 2010 (d) along an elevation gradient in the Kafue Flats. Different colors and lines in (a-b) reflect the prevailing hydrological conditions in the pre dam (1962-1971, dark blue dashed line), post Kafue Gorge and pre Ithezi-Thezi dam (1971-1977, light blue, dotted line) and post dam (1977-2010, solid red line) period. High flood line (HFL) and low flood line (LFL) reflect the mean maximal and minimal waterlevels in the respective period, with line style according to the pre-or post-dam period. Hydrological data was obtained from ZESCO hydrological gauging station at Nyimba (for location see Fig. 1).

Species formerly occurring at elevations below 979.1 m asl (post-dam low flood line) were replaced by open water bodies (Fig. 6c,d), which in places now support large submerged mats of aquatic vegetation (*Lagarosiphon ilicifolius* and *Potamogeton thunbergii*) and floating invasive herbs (*Azola*, *Eichornia crassipes* and *Salvinia molesta),* as permanent inundation no longer supports the establishment and growth of floodplain grasses (cf. Sheppe 1985, Chabwela and Ellenbroek 1990, pers. observation).

Furthermore, species that are not (or rarely) consumed by herbivores (cf. Handlos et al. 1976, pers. observation) increased in abundance (e.g. *Ipomea aquatic, Aspilia kotchyi, Hygrophila pilosa, Dichanthium insculptum, Panicum novemnerve, Cassia mimosoides, Hibiscus cannabinus, Echinochloa pyramidalis, Hygrophila auriculata, Epaltes alata,* Fig. 7 and *Blepharis caloneura*, data not shown).

Herbivores

Before the construction of the two dams Lochinvar contained large herds of Kafue lechwe with an estimated population of 17,550 individuals (aerial census in 1961 of Lochinvar). In addition other species found included plain zebra (*Equus burchelli*, 2000 ind.), wildebeest (*Connochaetus taurinus,* 800 ind.) and small herds of Roan (*Hippotragus equinus,* 40 ind.), Eland (*Taurotragus oryx*, 40 ind.), Kudu (*Tragelaphus strepsiceros,* 100 ind.), Reedbuck (*Redunca arundinum*, 10 ind.), Impala (*Aepyceros melampu,* 75 ind.) and oribi (*Ourebia ourebia,* 100 ind.; data based on aerial survey report from 1961-62 by Robinett and Child 1964). Herds of roan and eland have since disappeared (possibly due to poaching) but by far the most abundant herbivore in the floodplains of Lochinvar National Park is still the Kafue lechwe with an estimated population of 18,000 individuals, followed by zebra (800 ind.). Smaller populations of wildebeest (31 ind.), oribi (150 ind.), common duiker (*Sylvicapra grimmia,* unknown population size), impala (100 ind.) and kudu (50 ind.) use the termitaria zone. In the woodland, buffalo (*Syncerus caffer,* 200-300 ind.) and bushbuck (*Tragelaphus scriptus,* unknown population size) are common (Shanungu and Blaser 2011, Ellenbroek 1987).

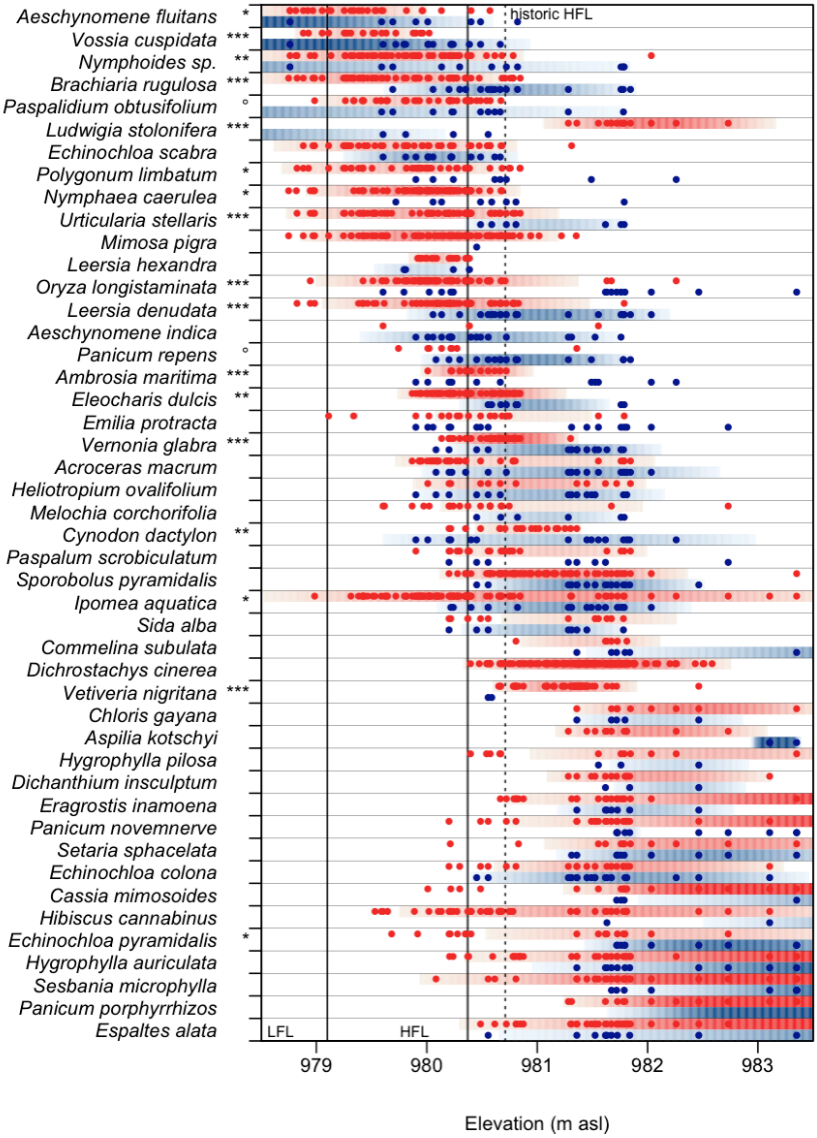


Figure 7 – Occurrence of plant species in relation to elevation above sea level in Lochinvar National Park recorded in 2010 (red color) and 1980 (blue color). Actual points represent observations in the field whereas shaded bars represent probability of occurrence above 10%. Bars were only drawn where the probability of occurrence was significantly related to flooding parameters (i.e. elevation, flooding depth or duration). Data for the 1980 are obtained from Ellenbroek (1987); the 2010 data are from re-recording of the same sites. Elevation measurements were conducted in October 2010.

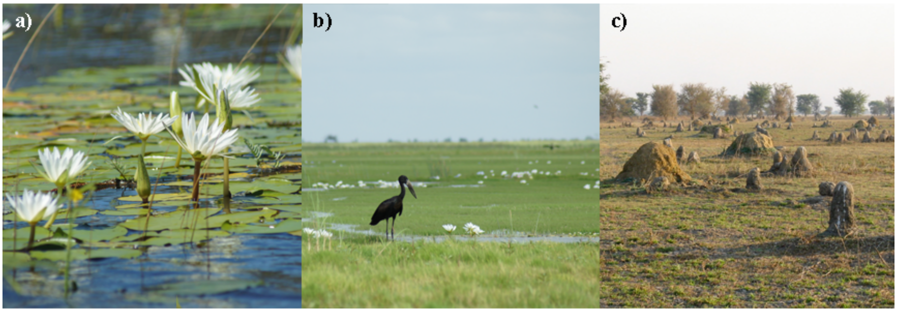


Figure 8 – Typical vegetation types in the Kafue Flats: herbaceous lagoon, floodplain grassland and termitaria.

References

Archer, D. R. 1971. Relief, drainage and geology.in D. H. Davies, editor. Zambia in Maps. University Press, London, UK, pp. 14-19.

Buckley, Y. M., M. Rees, Q. Paynter, and M. Lonsdale. 2004. Modelling integrated weed management of an invasive shrub in tropical Australia. Journal of Applied Ecology 41:547-560.

Chabwela, H. N. and G. A. Ellenbroek. 1990. The Impact of Hydro-Electric Developments on the Kafue Lechwe and its Feeding Grounds at Kafue Flats, Zambia. Pages 95-101 in D. F. Whigham, editor. Wetland Ecology and Managements: Case Studies. Kluwer Academic Publisher, Netherlands.

Denny, P. 1985. The ecology and management of African wetland vegetation-A botanical account of African swamps and swallow water bodies. Dr. W. W Junk Publishers, Netherlands.

Ellenbroek, G. A. 1987. Ecology and productivity of an African wetland system: The Kafue Flats, Zambia. PhD Thesis. Junk Publisher.

Genet, B. S. 2007. Shrub encroachment into grassland and its impact on Kafue Lechwe in Lochinvar National Park, Zambia. International Institute for Geo-information Science and Earth Observation, Enschede, The Netherlands.

Hagenah, N., H. Munkert, K. Gerhardt, and H. Olff. 2009. Interacting effects of grass height and herbivores on the establishment of an encroaching savanna shrub. Plant Ecology 201:553-566.

Handlos, D. M., W. L. Handlos, and G. W. Howard. 1976. A Study of the Diet of the Kafue Lechwe (Kobus Lechwe) by Analysis of Rumen Contents. Pages 197-211 Proceedings of the Fourth Regional Wildlife Conference for Eastern and Central Africa. National Parks & Wildlife Service, Chichele Lodge, Zambia.

Handlos, W. L. 1975. Aspects of the Kafue Basin Ecology. University papers on the Lower Kafue Basin presented by the Kafue Basin Research Committee of the University of Zambia. unpublished.

Johnson, D. S. and W. Roder. 1979. Proceedings of the National Seminar on Environment and Development. Zambia Geographical Association Lusaka.

Leonard, P. 2005. Important bird areas in Zambia: priority sites for conservation. Zambian Ornithological Society, Lusaka, Zambia.

Lonsdale, W. M., I. L. Miller, and I. W. Forno. 1989. The Ecology of Australian Weeds 20: Mimosa Pigra L. Plant Protection Quarterly 4:119-131.

McGregor, J. 1994. Woodland pattern and structure in a peasant farming area of Zimbabwe - ecological determinants and present and past use. Forest Ecology and Management 63:97-133.

Mumba, M. and J. R. Thompson. 2005. Hydrological and Ecological Impacts of Dams on the Kafue Flats Floodplain System, Southern Zambia. Physics and Chemistry of the Earth 30:442-447.

Munyati, C. 2000. Wetland change detection on the Kafue Flats, Zambia, by classification of a multitemporal remote sensing image dataset. International Journal of Remote Sensing 21:1787-1806.

Munyati, C., P. Shaker, and M. G. Phasha. 2011. Using remotely sensed imagery to monitor savanna rangeland deterioration through woody plant proliferation: a case study from communal and biodiversity conservation rangeland sites in Mokopane, South Africa. Environmental Monitoring and Assessment 176:293-311.

Orwa, C., A. Mutua, R. Kindt, R. Jamnadass, and A. Simons. 2009. Agroforestree database: a tree species reference and selection guide version 4.0 World Agroforestry Centre ICRAF, Nairobi, Kenya.

Ramsar. 2013. Ramsar Sites in order of their addition to the Ramsar List of Wetlands of International Importance.

Rees, W. A. 1978. The ecology of the Kafue lechwe: The food supply. The Journal of Applied Ecology 15:177-191.

Roques, K. G., T. G. O'Connor, and A. R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology 38:268-280.

Sayer, J. A. and L. P. Van Lavieren. 1975. The ecology of the Kafue lechwe population of Zambia before the operation of hydro electric dams on the Kafue River. East African Wildlife Journal 13:9-38.

Shanungu, G. K., and Blaser W.J. (2011). Lochinvar National Park: Distribution and population estimates of Large Mammals and the Status of Mimosa pigra invasion. Technical Report. Department of Research, Zambia Wildlife Authority, Chilanga

Sheppe, W. A. 1985. Effects of humn activities on Zambia Kafue Flats Ecosystems. Environmental Conservation 12:49-57.

Spence, D. H. N. 1982. The zonation of plants in fresh-water lakes. Advances in Ecological Research 12:37-125.

Thomas, I. J. 2007. Mapping and Modeling of Mimosa pigra Expansion in Lochinvar National Park, Zambia. International Institute for Geo-information Science and Earth Observation, Enschede, The Netherlands.

Van der Valk, A. G. 1994. Effects of prolonged flooding on the distribution and biomass of emergent species along a fresh-water wetland coenocine Vegetatio 110:185-196.

van Eck, W., J. P. M. Lenssen, H. M. van de Steeg, C. Blom, and H. de Kroon. 2003. Seasonal dependent effects of flooding on plant species survival and zonation: a comparative study of 10 terrestrial grassland species. Pages 59-69. Springer, Nijmegen, Netherlands.

Williams, G. J. and G. W. Howard. 1977. Development and Ecology in the Lower Kafue Basin in the Nineteen Seventies. 2nd edition edition. Papers from the Kafue Basin Research Committee of the University of Zambia, Lusaka.

ZAWA. 2004. Lochinvar National Park General Management Plan. Zambian Wildlife Authority Chilanga, Zambia.

Chapter 2

Facilitative or competitive effects of woody plants on understory vegetation depend on N-fixation, canopy shape and rainfall

Wilma J. Blaser, Judith Sitters, Simon P. Hart, Peter J. Edwards and Harry Olde Venterink

Forum paper in Journal of Ecology (in press, doi: 10.1111/1365-2745.12142)

Abstract

A recent meta-analysis suggested that differences in rainfall are a cause of variation in tree-grass interactions in savannas, with trees facilitating growth of understorey grasses in low-rainfall areas, but competing with them under higher rainfall. We hypothesized that this effect of rainfall upon understorey productivity is modified by differences in the growth form of the woody plants (i.e. the height of the lower canopy) or by their capacity to fix nitrogen.

We performed a meta-analysis of the effects of woody plants on understorey productivity, incorporating canopy height and N-fixation, and their interaction with rainfall.

N-fixing woody plants enhanced understorey productivity whereas non-fixers had a neutral or negative effect, depending on high or low canopy, respectively. We found a strong negative correlation between rainfall and the degree to which trees enhanced understorey productivity, but only for trees with a high canopy.

Synthesis. The effect of woody plants on understorey productivity depends not only on rainfall, but also on their growth form and their capacity to fix N. Facilitation occurs mostly when woody plants ameliorate both water and nitrogen conditions. However, a low canopy suppresses understorey vegetation by competing for light, regardless of water and nutrient relations

Introduction

Woody encroachment can have positive (i.e. facilitative), neutral, or negative (i.e. competitive) net effects on the understorey productivity of grazing ecosystems (i.e. savannas and temperate grasslands; Vetaas 1992, Scholes and Archer 1997). Understanding the reasons for these contrasting outcomes is important for predicting how encroachment will affect a grazing ecosystem. In a recent meta-analysis, Dohn *et al*. (2013) showed that net facilitative or competitive effects of trees on understorey grasses were related to annual rainfall, with trees facilitating understorey growth where water was limited, but suppressing growth where the water supply was adequate. These results, which are consistent with the stress-gradient hypothesis (Bertness and Callaway 1994, Callaway et al. 2002), represent a substantial advance in our understanding of large-scale patterns of tree-grass relations. However, we argue that their predictive capacity could be substantially improved by explicitly including those functional traits of woody plants most likely to mediate the outcome of tree-grass interactions (Mordelet and Menaut 1995, Scholes and Archer 1997). For example, facilitation of understorey species is only likely when the benefits accrued from improved water relations outweigh the disadvantage of canopy shading (Holmgren et al. 1997). Therefore, the differential ability of woody species to shade understorey species should strongly influence the transition from net competition to net facilitation across a rainfall gradient. Furthermore, although Dohn *et al.* (2013) show that woody species increase soil nutrient status generally; we hypothesize that these effects will depend on the tree’s capacity to fix nitrogen.

In this paper, we expand upon the approach of Dohn *et al.* (2013) to include plant functional traits known to mediate tree-grass interactions across resource gradients. We hypothesize that the understorey growth is more vigorous beneath trees with an elevated canopy than one reaching to ground level, since the former only casts significant shade when the sun is directly overhead whereas most light will not reach the subcanopy independently of the sun under a canopy reaching to ground level (Fig. S1 in Supporting Information). We also hypothesize that nitrogen-fixing species have a stronger facilitative effect on the understorey growth than non-fixers, since nitrogen-fixing species increase soil nitrogen availability, which is expected to positively affect understorey vegetation (Ludwig et al. 2008, Eldridge et al. 2011, Sitters et al. 2013). We test these hypotheses using data from a meta-analysis of the effects of woody plants on understorey productivity. In summary, we consider whether the observed effects of rainfall on tree-grass interactions (Dohn et al. 2013) can be further explained by variation in canopy shape and the capacity of trees to fix nitrogen.

Methods

To identify studies reporting effects of woody species on understorey productivity we searched the ISI Web of Knowledge database (1945-2012) using a combination of the keywords: “tree”, “woody”, “shrub”, “bush”, “encroachment”, “thickening”, “biomass”, “productivity” and “dry matter”. We also considered any studies cited in references, including those cited in Dohn *et al.* (2013) and Mordelet & Menaut (1995) that reported direct measurements of herbaceous production or peak biomass in both subcanopy areas and open grasslands and also contained information about the woody species. We followed the same selection criteria as Dohn *et al.* (2013). Any studies reporting heavy grazing in the study area were excluded from the meta-analysis, unless the grass production measurements had been made within exclosures. As we were interested in the general effects of woody species on the understorey, we included data from both natural and man-made grazing ecosystems (e.g. dehesa or montado systems) in our analysis. With these selection criteria, our final meta-analysis was based on 36 studies, including 113 independent measurements of understorey peak biomass production from 32 species. Data reported at the same site but for different tree species were included as separate data points.

We determined whether the various woody species were nitrogen fixers, using Sprent (2009) as the main source of information. We also classified mature plants according to their canopy shape, using photographs of the species growing in natural settings (many of them obtained from the internet). We distinguished between ‘High Canopy’ species, which have their lowest foliage raised well above the ground, and ‘Low Canopy’ species, which have foliage reaching to ground level (Fig. S1). If studies reported results from mixed woody communities, we determined the canopy height and N-fixing ability of each species, but only assigned the woody community to a shape category if all species were of the same type. In our database we then assigned the mixed community effect as an effect of the most dominant species in the community.

Following Dohn *et al.* (2013), we classified all sites as either ‘tropical’ (N=46) or ‘temperate’ (N=67). For rainfall, we used either the information given in the original studies, if reported, or else a long-term mean annual precipitation (MAP) for the location.

We quantified the effect of woody species by comparing understorey production in the presence (subcanopy) and absence (open grassland) of woody species. Following Dohn *et al.* (2013), we calculated normalized tree-effect ratios (y) of subcanopy (s) to open grassland (g) herbaceous production, where $y = \frac{(s-g)}{(s+g)}$. The normalized effect ratio responds linearly to proportional changes in the two components and has the advantage of reducing differences among studies due to varying sampling procedures (cf. Dohn et al. 2013).

To quantify the effect of woody species on total soil nutrient pools, we also calculated normalized tree-effect ratios for soil nitrogen (N) and phosphorus (P) measurements, where these data were available in the source literature. We also extended the dataset with total soil N and P nutrient data of paired encroached and un-encroached plots from an extensive literature review by Eldridge *et al.* (2012). As for herbaceous production, the nutrient data were normalized using the ratio of subcanopy to open-grassland nutrient concentrations.

We used ANCOVA to determine effects of the plant traits ‘canopy shape’ (high/low) and ‘nitrogen fixing capacity’ (yes/no) of woody species on understorey biomass, as well as that of the continuous variable ‘annual rainfall’ and interactions among these variables (full model). It was not possible to include the factor ‘Region’ (temperate vs tropical sites) in the complete ANCOVA model because there were too few observations for some trait-region combinations. Instead, we followed a stepwise analysis approach and computed two ANCOVA models incorporating, besides annual rainfall and climate, either canopy shape or nitrogen fixing ability. To test for consistency in patterns both within and across climatic regions, we also analysed the temperate data separately. Separate ANCOVA’s similar to the full model were calculated for the effects of woody plants on soil N and P pools.

Type-II Sums of Squares were used in all analyses to account for unequal numbers of replicates. Models were subsequently simplified via stepwise deletion, with non-significant interactions and factors being removed until no further simplification was justified ($\alpha<0.25$). Linear regression analysis was used to assess and visualize the relationship between tree-effect ratios and annual rainfall. All statistical analyses were conducted using R version 2.15.2 (R Foundation for Statistical Computing 2009).

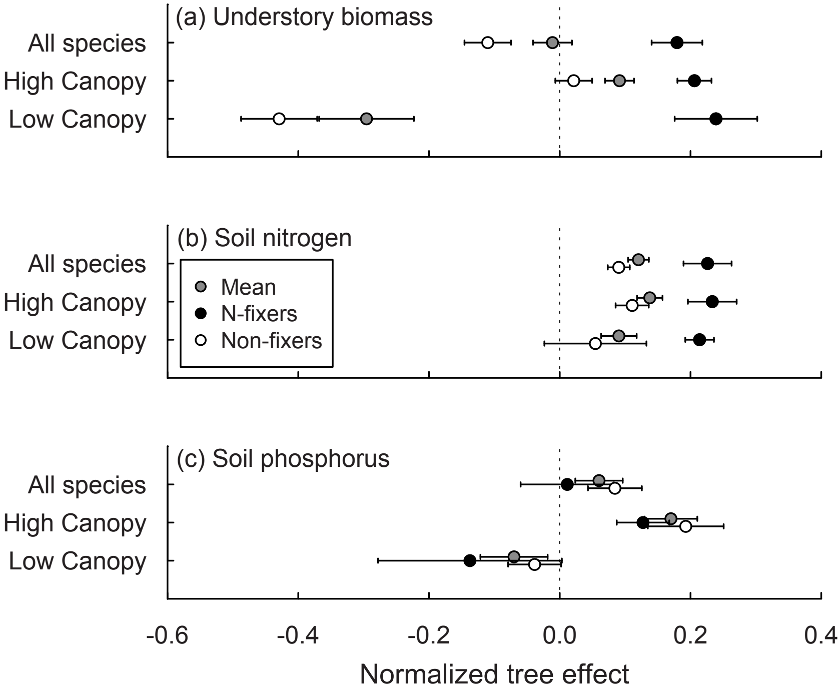


Figure 1 – Effect of woody plants on understorey biomass (a), soil total-nitrogen (b), and total-phosphorus (c) concentrations, taking into account the canopy shape of the woody plants and their capacity to fix nitrogen. Data are presented as normalized tree-effect ratios of subcanopy to reference open grassland plots. A value of 0 indicates no difference between subcanopy and open grassland, positive values represent a positive effect, negative values a negative effect. Species with foliage reaching all the way to the ground were classified as "Low Canopy" species; species where the height of the lowest foliage was elevated above the ground were classified as "High Canopy" species (cf. Fig. S1). Error bars displayed for mean values indicate plus or minus one standard error. The overview of all included species in panel a is given in Fig. S1.

Results

On average, N-fixing woody plants increased understorey biomass by 18% compared with open grassland, while non-fixers reduced it by 11% (Fig. 1a). This effect of N-fixers was highly significant (Table 1). Further analysis revealed that the negative effect of the non-fixers on understorey biomass was mainly due to the shape of the canopy (N-fixation × Shape interaction in Table 1). Thus, non-fixers with a low canopy reduced understorey productivity by 43%, whereas non-fixers with a high canopy had no effect (Fig. 2).

Consistent with Dohn *et al.* (2013), the influence of trees upon understorey biomass changed across the rainfall gradient, indicating a shift from net facilitation of understorey biomass in arid climates towards net competition in mesic climates (Fig. 2 and Table 1). However, the effect of rainfall depended largely upon the canopy shape (significant Rainfall × Shape interaction in Table 1); while 'High Canopy' species showed this pattern, 'Low Canopy' species didn't (Fig. 2).

Although, N-fixing high-canopy species appeared to respond stronger to rainfall than non-fixing high-canopy species (steeper slope in Fig. 2a), this interaction between rainfall and N-fixation was not significant (Table 1). Nevertheless, regression analysis suggested that N-fixers started to facilitate understorey productivity at higher rainfall than non-fixers (compare the crossing points of the regression lines with the zero-effect line in Fig. 2a).

Table 1 – Effects of the plant traits 'canopy shape (shape)' and 'nitrogen fixing capacity (N-fixation)' of woody plants, as well as annual rainfall, on understorey biomass, soil N and soil P pools (ANCOVA with Type II test for unbalanced data). For understorey biomass, the 3-way interaction was not significant and left out of the analysis. Adjusted R^2 values: 0.62, 0.09 and 0.39 for understorey biomass, soil N and soil P respectively

	Understorey biomass		**Soil N**		**Soil P**	
Source of variation	F-value	*P*-value	F-value	*P* -value	F-value	*P* -value
N-fixation	41.9	<0.001	12.1	<0.001	1.5	0.221
Shape	66.1	<0.001	1.7	0.190	17.8	<0.001
Rainfall	6.6	0.012	6.5	0.012	1.4	0.237
N-fixation × Shape	25.0	<0.001	0.1	0.786	0.2	0.673
N-fixation × Rainfall	1.9	0.173	0.2	0.66	0.9	0.359
Shape × Rainfall	7.7	0.007	0.0	0.892	7.1	0.011
N-fix × Shape x Rainfall			2.4	0.120	2.4	0.126

On average all woody plants increased soil N, but this effect was significantly higher under N-fixing than under non-fixing species (Fig. 1b and Table 1). Effects were independent of canopy shape but increased with rainfall (Table 1). Total soil P was significantly affected by canopy shape, with increased concentrations beneath ‘High Canopy’ species compared with the surrounding grassland, and reduced concentrations beneath ‘Low Canopy’ species (Fig. 1c and Table 1). Soil P was not significantly related to either rainfall or a tree’s capacity to fix N (Table 1), and the significant Rainfall × Canopy Shape interaction (Table 1) was be driven by a single site.

Discussion

Previous work has shown that woody plants can both increase and decrease understorey productivity in savanna ecosystems. We demonstrate that, in addition to the effects of rainfall, these contrasting effects (facilitative vs. competitive) are closely linked with important functional characteristics of the woody plants, namely their capacity to fix N and the shape of their canopy (Fig. 2). Although previous studies have pointed to such influences in particular cases (Belsky et al. 1993, Mordelet and Menaut 1995, Rivest et al. 2011, Soliveres et al. 2012), this is the first analysis to demonstrate their general importance across a broad range of grazing ecosystems.

It is widely accepted that plants may facilitate the growth of other plants when they increase the availability of a limiting resource, but negatively affect their growth when they compete for it (Callaway 1995, Holmgren et al. 1997). Dohn *et al.* (2013) concluded that woody plants facilitate understorey productivity under conditions of water stress, but outcompete them under wet conditions. Such an effect, which would be consistent with the stress-gradient hypothesis SGH (Bertness and Callaway 1994, Callaway et al. 2002), could arise if woody plants improved water conditions for understorey plants, for example through hydraulic lift or by reducing understorey evapotranspiration (Breshears et al. 1998, Ludwig et al. 2004a, b). Our results go one step further, showing that facilitation under more arid conditions does not apply for all woody plants but only for shrubs and trees with an elevated canopy (High canopy species in Fig. 2). Presumably, any amelioration of moisture conditions by low canopy species is overridden by the much denser shade that they cast. This interaction between effects of rainfall and canopy shape supports Maestre *et al.* (2009), who argued that a refinement of the SGH is needed by incorporating plant traits in predictive models.

The facilitative effect under dry conditions was greatest for N-fixing trees, suggesting that these plants improve both soil moisture conditions and N availability (cf. Eldridge et al. 2011, Sitters et al. 2013). Non-fixing tall canopy trees also enhanced understorey growth, but the shift from net facilitation to net competition occurred at a lower rainfall than for N-fixing species (Fig. 2a). Hence, trees are most likely to promote understorey growth when they ameliorate the supply of multiple resources (in this case, water and soil nitrogen) without excessively reducing light.

The analysis of Dohn *et al.* (2013) also revealed that woody plants tended to increase soil N and P concentrations beneath the canopy. We evaluated whether these effects were stronger for N-fixers than for non-fixers (including the data of Eldridge et al. 2012) as one would expect based on Fig. 1a. Our analyses revealed that this was the case for N but not for P, providing a further indication of how High Canopy N-fixing species facilitate understorey vegetation (Fig. 1b).

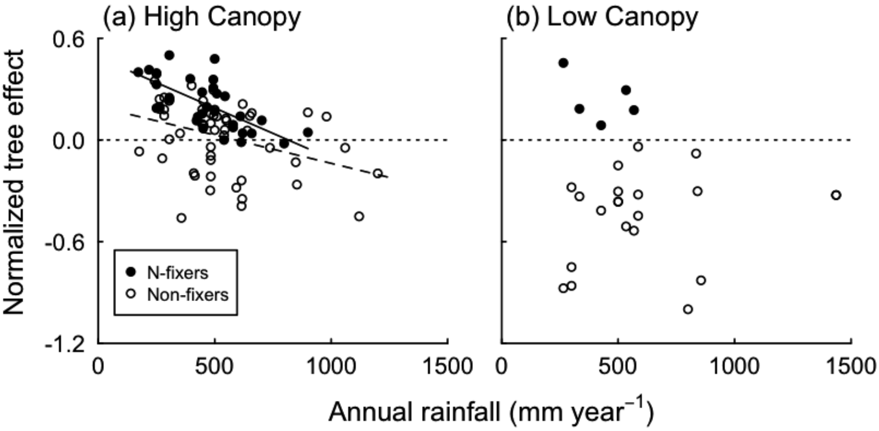


Figure 2 – Effect of woody plants on understorey biomass, expressed as normalized ratios of subcanopy to open grassland herbaceous production along a gradient of annual rainfall for (a) High Canopy species and (b) Low Canopy species (cf. Fig. S1). A value of 0 indicates no difference between subcanopy and open grassland, positive values represent a positive effect, negative values a negative effect on understorey biomass. Regression lines were only drawn if significant ($P < 0.05$); solid line for 'High Canopy', N-fixers (R^2=0.49, $P < 0.001$), dashed line for 'High canopy', Non-fixers (R^2=0.13, $P = 0.009$).

A low canopy of trees (i.e., a canopy that touches the soil surface) almost always reduced understorey growth, regardless of rainfall. The only exception was the leguminous shrub *Retama sphaerocarpa* (see Fig. S1), suggesting that N-fixation can sometimes override the effect of a low canopy - as indicated by a significant interaction between nitrogen fixing ability and canopy shape (Table 1). We note, however, that this interaction is entirely driven by a single species and that the canopy of this species was not easy to classify. Data for more low canopy N-fixing species would be needed to confirm this possible overriding effect. Nevertheless, our classification (High vs. Low Canopy) clearly separated species with an overall negative effect from those with a neutral to positive effect on understorey productivity (cf. the non-fixing species in Fig. 1a and Fig. S1). The negative effect of low canopy species on understorey vegetation is probably due to a strong negative effect of shading on photosynthesis that overrides any positive effects on water stress (Holmgren et al. 1997), or protection from grazing through associational resistance (Smit et al. 2007). Moreover, a comparison of our results using canopy shape with those obtained using canopy diameter (Dohn et al. 2013) suggests that canopy shape reflects understorey light conditions better, since canopy diameter is also influenced by the age of trees. Further studies are needed to determine the absolute or relative canopy height above the ground at which net effects of woody species change from net competitive to net facilitative. These studies could also evaluate how canopy height above soil surface depends on the absolute canopy height, since recently the latter was shown to affect facilitation-competition patterns of trees on understorey vegetation, as well (Moustakas et al. 2013).

From their statistical analysis, Dohn *et al.* (2013) concluded that the processes of facilitation and competition operate at different scales in African and North-American savannas, and suggested that this perhaps might be due to differences in climatic conditions (e.g. annual temperature, seasonality in rain). As functional groups were unevenly distributed across the two regions in our dataset, we were unable to statistically evaluate in one overall ANCOVA (including Region as fourth factor) whether the effects of region shown by Dohn *at al.* (2013) were driven by plant traits. Calculating several ANCOVAs with fewer factors, we obtained significant differences between regions (Fig. S3), but consistent effects of canopy shape and capacity to fix N (Table S1). Since there were more N-fixers (59% vs. 16%) and fewer Low Canopy species (9% vs. 33%) in the tropical than in the temperate sub-dataset (Fig. S4), we speculate that the regional differences reported by Dohn *et al.* (2013) were due to differences in the proportions of these functional types in the data set. However, it cannot be concluded that this reflects a general difference between temperate and tropical regions, since the tree species were not randomly sampled.

We conclude that the facilitation effect of woody plants upon understorey depends upon the interaction between abiotic conditions and plant traits (i.e. canopy shape and N-fixation capacity). Trees facilitate understorey growth mainly if they ameliorate both water and nitrogen availabilities, while allowing enough light to penetrate to the soil surface. These conditions are most likely to occur beneath N-fixing trees with a high canopy, such as many *Acacia* species. The interplay of water and nitrogen is most important where both these factors are potentially growth-limiting, which is the case in many savanna ecosystems (cf. Olff et al. 2002, Cech et al. 2008). This insight contributes to our understanding of fundamental processes of facilitation and competition among woody and herbaceous plants and emphasizes the importance of plant traits in mitigating these effects along stress gradients.

Acknowledgements

We thank Sabine Güsewell for her help with statistical analysis. This work was made possible through funding provided by the Competence Center for Environment and Sustainability (CCES) at the ETH domain.

References

Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. Journal of Applied Ecology **30**:143-155.

Bertness, M. D. and R. Callaway. 1994. Positive interactions in communities. Trends in Ecology & Evolution **9**:191-193.

Blank, L. and Y. Carmel. 2012. Woody vegetation patch types affect herbaceous species richness and composition in a Mediterranean ecosystem. Community Ecology **13**:72-81.

Breshears, D. D. and J. A. Ludwig. 2010. Near-ground solar radiation along the grassland–forest continuum: Tall-tree canopy architecture imposes only muted trends and heterogeneity. Austral Ecology **35**:31-40.

Breshears, D. D., J. W. Nyhan, C. E. Heil, and B. P. Wilcox. 1998. Effects of woody plants on microclimate in a semiarid woodland: Soil temperature and evaporation in canopy and intercanopy patches. International Journal of Plant Sciences **159**:1010-1017.

Callaway, R. M. 1995. Positive interactions among plants. Botanical Review **61**:306-349.

Callaway, R. M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortie, R. Michalet, L. Paolini, F. I. Pugnaire, B. Newingham, E. T. Aschehoug, C. Armas, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature **417**:844-848.

Cech, P. G., T. Kuster, P. J. Edwards, and H. Olde Venterink. 2008. Effects of herbivory, fire and N_2-fixation on nutrient limitation in a humid African savanna. Ecosystems **11**:991-1004.

Dohn, J., F. Dembélé, M. Karembé, A. Moustakas, K. A. Amévor, and N. P. Hanan. 2013. Tree effects on grass growth in savannas: competition, facilitation and the stress-gradient hypothesis. Journal of Ecology **101**:202-209.

Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters **14**:709-722.

Eldridge, D. J., F. T. Maestre, S. Maltez-Mouro, and M. A. Bowker. 2012. A global database of shrub encroachment effects on ecosystem structure and functioning. Ecology **93**:2499-2499.

Holmgren, M., M. Scheffer, and M. A. Huston. 1997. The interplay of facilitation and competition in plant communities. Ecology **78**:1966-1975.

Ludwig, F., T. E. Dawson, H. H. T. Prins, F. Berendse, and H. de Kroon. 2004a. Below-ground competition between trees and grasses may overwhelm the facilitative effects of hydraulic lift. Ecology Letters **7**:623-631.

Ludwig, F., H. de Kroon, F. Berendse, and H. H. T. Prins. 2004b. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecology **170**:93-105.

Ludwig, F., H. De Kroon, and H. H. T. Prins. 2008. Impacts of savanna trees on forage quality for a large African herbivore. Oecologia **155**:487-496.

Maestre, F. T., R. M. Callaway, F. Valladares, and C. J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. Journal of Ecology **97**:199-205.

Mordelet, P. and J.-C. Menaut. 1995. Influence of trees on above-ground production dynamics of grasses in a humid savanna. Journal of Vegetation Science **6**:223-228.

Moustakas, A., W. E. Kunin, T. C. Cameron, and M. Sankaran. 2013. Facilitation or competition? Tree effects on grass biomass across a precipitation gradient. Plos One **8**:e57025.

Olff, H., M. E. Ritchie, and H. H. T. Prins. 2002. Global environmental controls of diversity in large herbivores. Nature **415**:901-904.

Rivest, D., V. Rolo, L. Lopez-Diaz, and G. Moreno. 2011. Shrub encroachment in Mediterranean silvopastoral systems: *Retama sphaerocarpa* and *Cistus ladanifer* induce contrasting effects on pasture and *Quercus ilex* production. Agriculture Ecosystems & Environment **141**:447-454.

Scholes, R. J. and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics **28**:517-544.

Sitters, J., P. J. Edwards, and H. O. Venterink. 2013. Increases of soil C, N, and P pools along an *Acacia* tree density gradient and their effects on trees and grasses. Ecosystems **16**:347-357.

Smit, C., C. Vandenberghe, J. den Ouden, and H. Mueller-Schaerer. 2007. Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. Oecologia **152**:265-273.

Soliveres, S., D. J. Eldridge, F. Hemmings, and F. T. Maestre. 2012. Nurse plant effects on plant species richness in drylands: The role of grazing, rainfall and species specificity. Perspectives in Plant Ecology Evolution and Systematics **14**:402-410.

Sprent, J. I. 2009. Legume Nodulation: A Global Perspective. Wiley-Blackwell, Oxford, UK.

Vetaas, O. R. 1992. Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science **3**:337-344.

Supporting information

Table S1 ANCOVA results of regional analysis

Figure S1 Schematic presentation of the effect of lower canopy height on photosynthetically active radiation (PAR) reaching the subcanopy.

Figure S2 Effects of functional and morphological groups on understorey biomass production. Differences between species.

Figure S3 Normalized ratio of subcanopy to open grassland herbaceous biomass along a gradient of annual rainfall. Differences between tropical and temperate Savannas.

Figure S4 Normalized ratio of subcanopy to open grassland herbaceous biomass along a gradient of annual rainfall. Differences between functional groups across tropical and temperate savannas.

Table S1 – ANCOVA results of regional analysis.

Effects of the plant traits 'canopy shape' (shape) and 'nitrogen fixing ability (N-fixation) of woody plants as well as annual rainfall and climatic region (region) on understory biomass. ANCOVA with Type II test for unbalanced data. Table a) results for the temperate sub-dataset with N-fixation, shape and rainfall as factors b) full data model with N-fixation, region and rainfall as factors c) full data model with canopy shape, region and rainfall as factors. Non significant interactions ($\alpha<0.25$) were excluded from the models for simplification.

	Source of variation	**F-value**	***P*-value**
a)	N-fixation	32.9	<0.001
	Shape	36.9	<0.001
	Rainfall	1.59	0.225
	N-fixation × Shape	15.0	<0.001
	N-fixation × Rainfall	1.4	0.248
	Shape × Rainfall	8.3	0.005
	Adj. R^2 of model	R^2=0.58, *P*<0.001	
b)	N-fixation	17.5	<0.001
	Rainfall	10.2	0.002
	Region	6.0	0.016
	N-fixation × Rainfall	1.4	0.237
	N-fixation × Region	2.2	0.142
	Adj. R^2 of model	R^2=0.33, *P*<0.001	
c)	Shape	37.9	<0.001
	Rainfall	13.8	<0.001
	Region	10.6	0.001
	Shape × Rainfall	4.5	0.036
	Shape × Region	1.4	0.245
	Adj. R^2 of model	R^2=0.42, *P*<0.001	

Figure S1 – Schematic presentation of the effect of lower canopy height on photosynthetically active radiation (PAR) reaching the subcanopy.

Under tall, single-stemmed trees with elevated lower canopies (High Canopy, e.g *Acacia xanthophloea* (c)), a large proportion of PAR will reach the sub canopy in the morning (a) and afternoon but light is largely intercepted over noon (b). Under short, multi-stemmed shrubs with lower canopies adjacent to the ground (Low Canopy, e.g. *Mimosa pigra* (f)), most PAR will not reach the subcanopy independent of the angle of the sun (d,e). Drawings were adopted from Blank and Carmel (2012) under consideration of Breshears and Ludwig (2010).

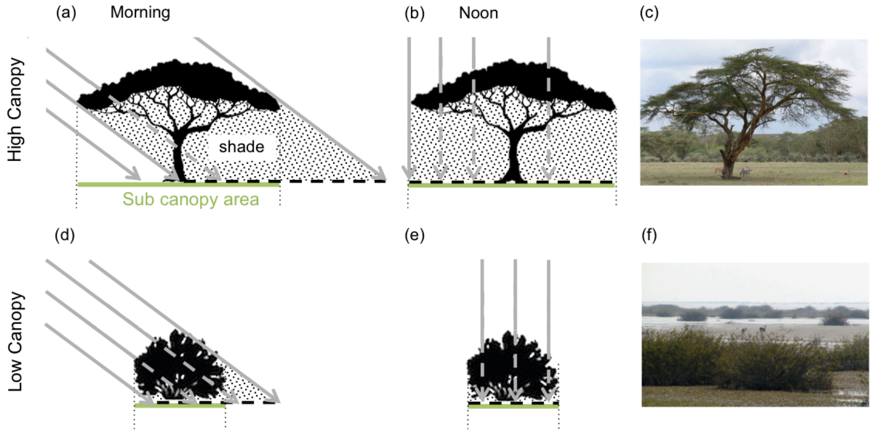


Figure S2 – Effects of functional and morphological groups on understorey biomass production. Differences between species.

Effect of woody plants on understory biomass, taking into account the canopy shape of the woody plants and their capacity to fix nitrogen. Data are presented as normalized tree-effect ratios of subcanopy to reference open grassland plots. A value of 0 indicates no difference between subcanopy and open grassland, positive values represent a positive effect, negative values a negative effect. Species with foliage reaching all the way to the ground were classified as "Low Canopy" species; species where the height of the lowest foliage was elevated above the ground were classified as "High Canopy" species (cf. Fig. S1).

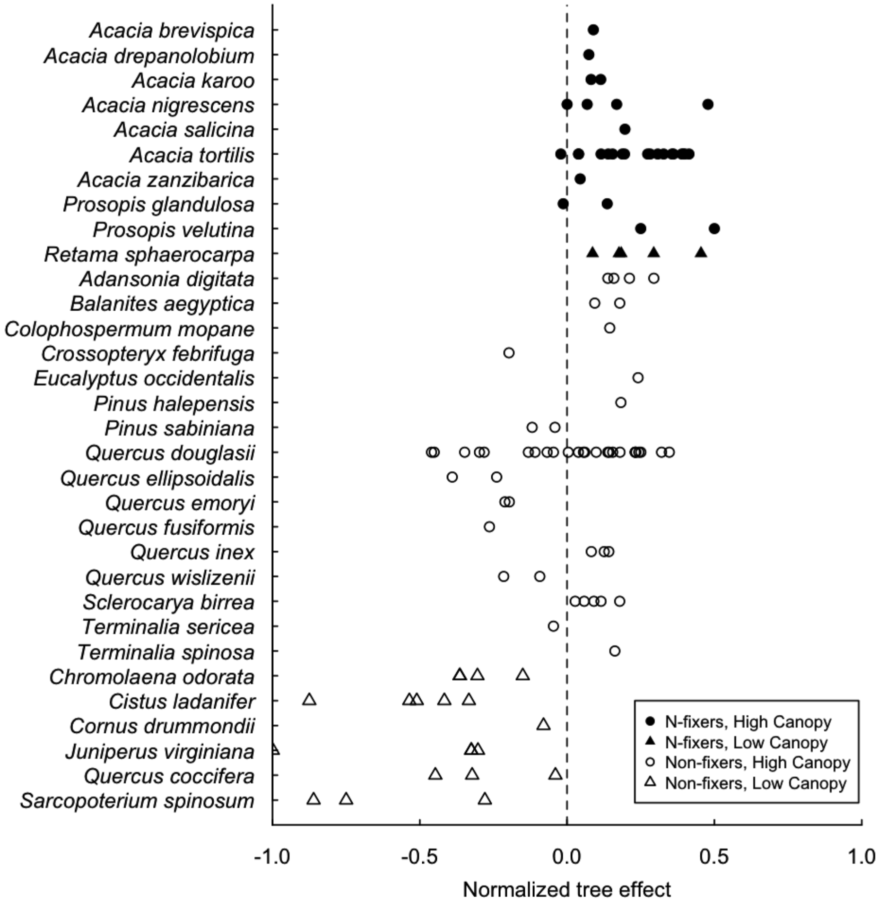


Figure S3 – Normalized ratio of subcanopy to open grassland herbaceous biomass along a gradient of annual rainfall. Differences between tropical and temperate Savannas.

Effect of woody plants on understory biomass, expressed as normalized ratios of subcanopy to reference open grassland herbaceous production along a gradient of annual rainfall for temperate and tropical savannas. A value of 0 indicates no difference between subcanopy and open grassland, positive values represent a positive effect, negative values a negative effect on understory production. Lines represent significant relationships. There was no significant difference in the effect of rainfall between regions (region x rainfall interaction), but there was a significant main effect of region. Statistical analysis is shown in Table S1 (b,c).

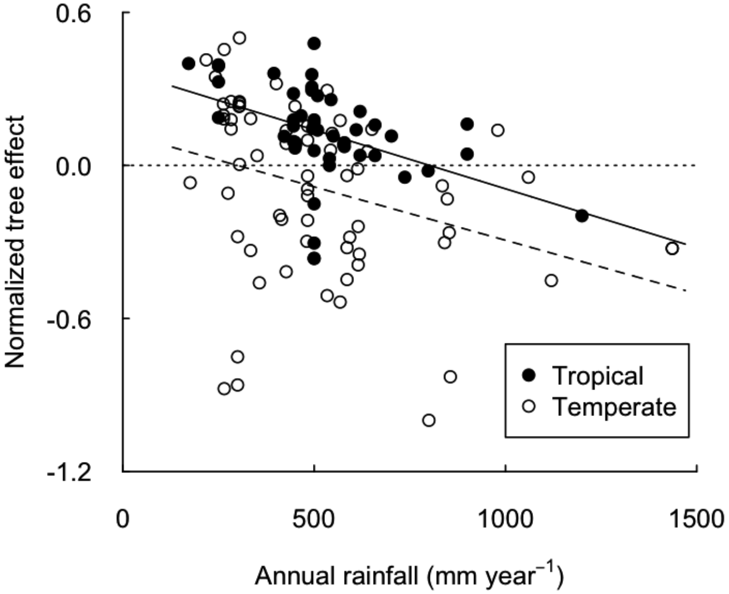
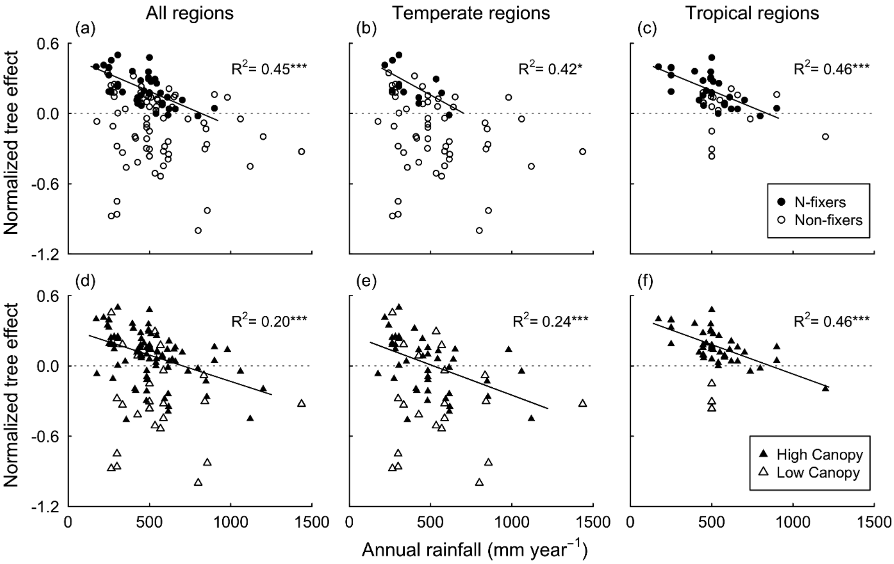


Figure S4 – Normalized ratio of subcanopy to open grassland herbaceous biomass along a gradient of annual rainfall. Differences between functional groups across tropical and temperate savannas.

Effect of woody plants on understorey biomass, presented as normalized ratios of subcanopy to reference open grassland plots along a gradient of annual rainfall for (a, d) all regions, (b, e) temperate regions and (c, f) tropical regions. The different subplots take the capacity to fix nitrogen (a, b, c) and canopy shape of the woody plants (d,e, f) into account. A value of 0 indicates no difference between subcanopy and open grassland, positive values represent a positive effect, negative values a negative effect on understory production. Regression lines were only drawn if significant ($P < 0.05$); solid lines represent significant relationships of a functional (N-fixers) or morphological group (High Canopy) and the respective R^2-values are displayed in the panels with significant codes $P < 0.5$ *, $P > 0.01$ **, $P > 0.001$ ***. The relationship for Low Canopy or Non-fixers was not significant and is hence not displayed.



Chapter 3

Woody encroachment reduces nutrient limitation and promotes soil carbon sequestration

Wilma J. Blaser, Griffin K. Shanungu, Peter J. Edwards and Harry Olde Venterink

Abstract

During the past century, grassland and savanna ecosystems throughout the world have been increasingly encroached by woody species. Since many of these species fix nitrogen symbiotically, they have the potential to influence the availabilities of nitrogen (N) and phosphorus (P), and also pools of soil N, P and carbon (C).

We quantified the effects of encroachment by the N-fixing shrub *Dichrostachys cinerea* on soil N, P and C pools and availabilities in a mesic African savanna in Zambia. We also evaluated whether these effects can potentially induce feedbacks upon the growth of understory vegetation and encroaching shrubs.

D. cinerea shrubs increased total N and P pools, as well as resin-adsorbed N and soil extractable P in the top 10-cm soil. Shrubs and understory grasses differed in their foliar N and P concentrations along gradients of increasing encroachment, suggesting that they use differing sources of these nutrients. For example, the shrubs can fix N_2 from the atmosphere, and probably also obtain some of their P from deeper soil layers than grasses. The storage of soil C increased significantly under *D. cinerea* and was apparently not limited by shortage of soil N or P.

We conclude that the shrub *D. cinerea* does not create a negative feedback loop by inducing P-limiting conditions, probably because it can obtain P from deeper soil layers. Furthermore, C-sequestration is not limited by a shortage of N, so that mesic savanna encroached by this species could represent a C-sink for several decades.

Introduction

During the past century, many savannas and other grass-dominated ecosystems around the world have been affected by the spread of woody plants (Archer et al. 1995, Van Auken 2000, 2009). Drivers for such shrub encroachment include changes in climate and atmospheric CO_2-enrichment, herbivory and fire regime, with the relative importance of these factors varying among ecoregions (Archer et al. 1995, Van Auken 2009, Buitenwerf et al. 2012).

Many encroaching species are capable of fixing nitrogen (N) symbiotically (Knapp et al. 2008, Boutton and Liao 2010, Eldridge et al. 2011), which brings N to the ecosystem (Ludwig et al. 2004, Boutton and Liao 2010, Cech et al. 2010) but requires high supplies of soil P (Binkley et al. 2000, Vitousek et al. 2002). Thus, encroaching N-fixing shrubs may increase the availability of soil N relative to P (Hibbard et al. 2001, Cech et al. 2008, Boutton and Liao 2010), which can potentially produce P-limiting conditions. This, in turn, could cause a negative feedback upon the woody species's capacity to fix N (Crews 1993, Pearson and Vitousek 2001, Binkley et al. 2003, Isaac et al. 2011), as well as reducing growth of understory vegetation (Riginos et al. 2009, Van Auken 2009, Sitters et al. 2013). However, such effects are not inevitable, and field studies show that far from depleting soil P, N-fixing woody species - especially those with a high canopy - may even increase P pools in the top soil (e.g. Geesing et al. 2000, Ludwig et al. 2004, Sitters et al. 2013, Chapter 3). The source of this additional P is not known, though it could potentially come from deeper soil layers, either taken up by deep roots or transported to the upper soil by hydraulic lift (Scholes and Archer 1997, Ludwig et al. 2004, McCulley et al. 2004, Sitters et al. 2013), or through widely spreading lateral roots from the surface soil (Belsky et al. 1989, Scholes and Archer 1997). In addition, many leguminous plants have a high root phosphatase activity, which may give them an advantage over other plants in acquiring P present in the soil in an organic form (Houlton et al. 2008, Olde Venterink 2011).

While great efforts have gone into understanding consequences of woody encroachment in North American grassland ecosystems, much less is known about African savanna grasslands (Table 1). However, simulations for Africa semi-arid and mesic savannas predict that woody C3 plants will have an increasing competitive advantage over C4 grasses as atmospheric CO_2 concentrations increase (Bond et al.

2003). The widespread replacement of grasses by woody plants could have potentially important effects upon both the structure of the vegetation and its aboveground net primary production (ANPP) (Knapp et al. 2008, Barger et al. 2011). Apart from light and water availability, ANPP mainly depends on the availability of the growth limiting nutrients N and P (Schimel et al. 1996, Cech et al. 2008). If the growth of N-fixing shrubs is affected by a negative feedback due to declining P availability, then their dominance might be of short duration; however, if encroaching N-fixing shrubs do not induce a negative feedback they might remain abundant, which would have profound consequences for savanna ecosystems. One potentially beneficial effect is that the tree-dominated ecosystems might continue to sequester C and act as a buffer for increased CO_2 levels. Indeed, since grasslands and savanna ecosystems account for 30-35% of the global terrestrial net primary production (Field et al. 1998), an increase in C input through shrub encroachment and subsequent changes in C storage could have global implication for the earth-atmosphere system (Knapp et al. 2008).

The aim of this study was to quantify the effect of shrub encroachment on soil N, P and C pools and availabilities in a mesic African savanna, and to evaluate whether these effects induce feedbacks upon the growth of encroaching shrubs. For this purpose, we studied effects of the N-fixing shrub *Dichrostachys cinerea* on soil N, P and C pools and availabilities along gradients of shrub cover and shrub age in the Kafue Flats, Zambia. This species only began to spread about 30 years ago (Shanungu et al. unpublished), and the previous conditions have been described in detail (Douthwaite and Van Lavieren 1977, Ellenbroek 1987). We predicted that encroachment would be associated with increases in soil N and C pools, as has been documented in other studies (Eldridge et al. 2011, Sitters et al. 2013, Chapter 3). Following the recent demonstration that leguminous shrubs with a high canopy tend to accumulate soil P (Chapter 2), we also predicted that soil P availability beneath *D. cinerea* would be higher than in surrounding grassland. Assuming this proved correct, we aimed to determine whether the additional P was derived from deeper soil layers, from surface soil through lateral roots, or from increased root phosphatase activity.

Table 1 – A survey of studies reporting C, N and P accretion rates in the topsoil after woody encroachment.

Region	MAP* (mm yr-1)	Encroaching Species	Stand Age (yr)	Soil depth (cm)	C-accretion (g m-2 yr-1)	N-accretion (g m-2 yr-1)	P-accretion (g m-2 yr-1)	Reference
N-fixing shrubs								
Texas, USA	230	*Prosopis glandulosa*	40	0-100	17	1.2	-	Jackson et al. (2002)
Arizona, USA	370	*Prosopis velutina*	~100	0-20	10		-	Throop & Archer (2008)
Arizona, USA	330-430	*Prosopis velutina*	~100	0-20	6 to 12	0.6 to 1.3	-	Wheeler et al. (2007)
Texas, USA	660	*Prosopis glandulosa*	30	0-100	-25	-3.3	-	Jackson et al. (2002)
Texas, USA	715	*Prosopis glandulosa*	0-130	0-15	-	0.8 to 1.1	-	Boutton et al. (2010)
Texas, USA	645-850	*Prosopis glandulosa*	50-120	0-20	4 to 9	0.9 to 2.2	0.003 to 0.007	Geesing et al. (2000)
Texas, USA	710	*Acacia farnesiana*	5-50	0-10	239		-	Bush (2008)
Texas, USA	716	*Prosopis glandulosa*	14-86	0-15	16		-	Creamer et al. (2011)
Texas, USA	716	*Prosopis glandulosa*	10-130	0-15	10 to 30	1 to 3	-	Liao et al. (2006)
Texas, USA	720	*Prosopis glandulosa*		0-20	12 to 22	1.9 to 2.7	-	Archer et al. (2001, 2004)
Texas, USA	720	*Prosopis glandulosa*	50-77	0-10	8 to 23	0.9 to 2.0	-	Hibbard et al.(2001)
Zambia, Africa	753	*Dichrostachys cinerea*	30-Jul	0-10	12 to 16	1.3 to 2.0	-0.16 to 0.09	This study
Texas, USA	840	*Prosopis glandulosa*	75-100	0-100	-61 to 82	-3.8 to -5.7	-	Jackson et al. (2002)
Washington, USA	888	*Cytisus scoparius*	10-15'	0-10	15 to 23	1.8 to 2.8	-	Haubensak & Parker (2004)
Iberian peninsula	700-1250	*Cytisus balansae*	19	0-15	42	6.6	-	Montané et al. (2007)
Non-fixing shrubs								
Texas, USA	277	*Larrea tridentate*	>50	0-100	4	-0.3	-	Jackson et al. (2002)
Texas, USA	322	*Atriplex canescens*	>50	0-100	26	-5.8	-	Jackson et al. (2002)
Utah, USA	360	*Artemisia tridentata*	0-400	0-10	30	1	-	Neff et al. (2009)
North Dakota, USA	400	*Several shrub species†*	17-42	0-15	18	1.7	-	Springsteen et al. (2010)
Texas, USA	835	*Juniperus virginiana*	35-75	0-10	3 to 16	0.2 to 1.2	-	McKinley & Blair (2008)
Iberian peninsula	700-1250	*Juniperus comunis*	32	0-15	28	2.8	-	Montané et al. (2007)
Texas, USA	1070	*Juniperus spp*	40	0-100	-81	-6	-	Jackson et al. (2002)

*Mean annual precipitation; †Amelanchier alnifolia, Shepherdia argentea, Rhamnus cathartica, Symphoricarpos occidentalis

Materials and methods

Study site and selected shrub cover and age gradients

The study was conducted in Lochinvar National Park (LNP, ~ 410 km^2) in Central Zambia (15°52'S, 27°14'E), which is located within a vast floodplain ecosystem known as the Kafue Flats. The park is a former cattle ranch in which larger carnivores were systematically exterminated in the first part of the 20th century but wild herbivores were protected. By far the most abundant of these is the endemic Kafue lechwe, *Kobus leche kafuensis* Gray 1850 (Ellenbroek 1987). Annual precipitation is 753 mm (2000-2011 mean) and is highly seasonal, with almost all rain falling in the wet season (November to April). The mean annual temperature is 20.6°C (Ellenbroek 1987, Mumba and Thompson 2005).

The vegetation of the area can be divided into three main zones, which are strongly related to the flooding regime: seasonally inundated floodplain grasslands, the termitaria zone above the high flood line, and woodlands (Ellenbroek 1987). In the past 30 years the termitaria and floodplain grasslands of LNP have experienced a significant increase in woodland and shrub cover - by the exotic *Mimosa pigra* in relatively wet zones of the floodplain, and by the native *D. cinerea* and several native *Acacia* species in drier areas (Chabwela and Mumba 1998, Mumba and Thompson 2005, Genet 2007, Shanungu et al. unpublished). These changes may be related, at least in part, to the construction of two dams in the Kafue River, which significantly altered the hydrological regime of the Kafue Flats from about 1980 onwards (Chapter 1).

In the area encroached by *D. cinerea*, we selected 20 sites (10×10m) representing a gradient from open grassland (0% cover) to dense thicket (100% cover). We also selected 20 sites along a gradient of shrub age that ranged from seven to 30 years (see determination of age below). Each site along the age gradient consisted of two paired plots, one located under an isolated shrub and the other a reference plot located in grassland 7 m away from the *D. cinerea* stem. All sites along both gradients had similar soil and hydrological conditions. There was no obvious spatial pattern in age and cover of *D. cinerea*, and no other woody species were present.

Determination of shrub age

At the end of the study, all shrubs along the age gradient were cut, and sample discs were taken at approximately 10 cm above ground in early April 2011. Slices were dried and polished on a belt sander with four grades of grit, to a high standard of clarity. We measured the basal diameter of the slices and examined them under a light microscope. *D. cinerea* does not have well defined annual rings. However, for *Acacia* species growing in climatic zones with a single wet season, the number of parenchyma bands has been shown to approximate the age of the tree (Gourlay and Kanowski 1991). According to Neumann et al. (2001), the anatomy of *D. cinerea* wood is similar, and can hence be included in the *Acacia* type. We therefore counted the number of continuous marginal parenchyma bands in our samples, and treated this number as the shrub age, Linear regressions showed that the age of each shrub was positively related to the basal diameter (Fig. 1).

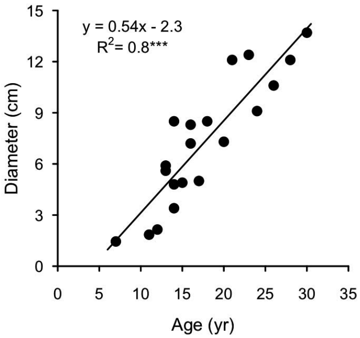


Figure 1 – Linear relationship between *D. cinerea* tree age, based on number of tree rings, and basal diameter, in a mesic savanna in Zambia.

Soil nutrient pools and availabilities

Surface soils of all sites (5.0 cm diameter cores, top 10-cm soil) were sampled during two periods in the early and mid-growing season (December 2010 and February 2011). We only sampled the topsoil layer as this layer is highly influenced by plant growth and nutrients that are considered most limiting to plant growth are strongly cycled in this layer (Jobbagy and Jackson 2001). Along the cover gradients, we collected three soil samples at 2-m from the center of each plot. Along the age gradient we sampled three cores 20cm away from the *D. cinerea* stem, as well as three cores 1-m away from a central point in the paired open site.

The three cores per plot or subplot were pooled and root fragments were removed by hand. Samples were weighed to calculate bulk density, and a subsample was dried to constant weight to determine water content. The dried soil samples were then ground and sieved through a 0.5-mm sieve. Total C and N concentrations were determined using a dry combustion analyzer (CN-2000, LECO Corp., St Joseph, Minesota USA). Total P concentrations were measured colorimetrically after Kjeldahl digestion using an auto-analyzer (AutoAnalyzer 3HR, Seal Analytical). To calculate soil nutrient pool (volumetric measure) for each site, we multiplied values of soil bulk density with nutrient concentrations (gravimetric measure). The δ^{13}C and δ^{15}N values of soil were determined for all plots using a Carlo-Erba elemental analyzer (NCS-2500, Carlo Erba) coupled in continuous flow to an isotope ratio mass spectrometer (Optima, Micro-Mass).

The relative proportion of soil organic matter derived from C_4 (grass) and C_3 (shrub) photosynthetic pathway sources were estimated with mass balance equations:

$$F_{C4} = \frac{\delta^{13}C_{soil} - \delta^{13}C_{C3}}{\delta^{13}C_{C4} - \delta^{13}C_{C3}},$$

where F_{C4} is the carbon fraction derived from C_4 sources, $\delta^{13}C_{soil}$ is the measured $\delta^{13}C$ of the soil sample, $\delta^{13}C_{C4}$ is the mean $\delta^{13}C$ of C_4 sources, and F_{C3} is the carbon fraction derived from C_3 inputs (Balesdent and Mariotti 1996). We assumed that the grass C_4 source had a $\delta^{13}C$ value of -14.6 ‰ and that the *D.cinerea* added organic matter with a $\delta^{13}C$ value of -27.4 ‰ (means of $\delta^{13}C$ values measured in foliar samples collected along the gradient, n=20 and 19, respectively).

In December 2010 and in February 2011, we measured N and P release rates in the soil at all sites using ion-exchange resin (IER) bags. The 5×5 cm bags were made of a fine nylon fabric (60 µM mesh width, Sefar Nitex 03- 60/35, Sefar AG, Thal, Switzerland) and contained 2 ± 0.002g mixed-bed ion-exchange resin (Amberlite IRN 150, H^+- and OH^--form, Sigma-Aldrich, Switzerland). To saturate exchange sites with K^+ and Cl^- ions before use, the bags were shaken for 2 hours in 2 M KCl and thoroughly rinsed with distilled water.

In the field, each bag was inserted in the soil at 5cm depth in a 45% slant incision made with a knife and closed carefully thereafter. Four bags were set out at each site. The bags set out in December were removed after 50 days, while those set out in February were removed after 28 days. On removal, all bags were cleaned with distilled water, dried, and stored in zip-bags until extraction. Resin bags were extracted for 1 hour in 30 ml 1 M KCL solution. The extraction solution was then analyzed colorimetrically for PO_4^{2-}, NO_3^- and NH_4^+ using a continuous flow analyzer (AutoAnalyzer 3HR, Seal Analytical). Mean daily N and P adsorption rates were calculated per site.

To estimate net N mineralization and the inorganic P pool, we collected three pairs of soil cores per plot along the *D. cinerea* cover and age gradient (5.0-cm diameter cores, top 10-cm soil) in February 2011. One core of each pair was taken for extraction and drying while the other was incubated to measure nitrogen mineralization. *In situ* incubations were not possible because of high risk of flooding in some sites along the gradients. The tubes containing the cores were therefore closed with plastic lids and incubated for 28 days in soil of an *ex situ* termitaria plot;

holes in the tubes above the soil enabled gas exchange with the air. Inorganic N pool (NH_4^+ and NO_3^-) was determined by extracting a fresh equivalent of 5 g dry soil with 50 ml of 0.2 M KCl for 1 hour. Inorganic P pool was determined by extracting a fresh equivalent of 5 g dry soil with 50 ml Bray-II extraction solution for 1 hour (Bray and Kurtz 1945). All extractions were done within 12 hours of collection of the soil cores and extracts were stored frozen until further analysis. Concentrations of NH_4^+, NO_3^- and PO_4^{2-} in the extracts were measured colorimetrically using a continuous flow injection analyzer (AutoAnalyzer 3HR, Seal Analytical). Soil pH was determined in the KCl extracts. Net N mineralization was calculated as the difference between extractable N at the start and at the end of the incubation period (Olff et al. 1994).

Foliar nutrient contents and plant traits

Nutrient concentrations as well as $\delta^{13}C$ and $\delta^{15}N$ values in *D. cinerea* biomass and the aboveground grass biomass were determined along the *D. cinerea* cover gradient in the 2011-2012 growing season. To avoid possible sampling bias, we collected 10 fully expanded *D. cinerea* leaves from several heights in the canopy. We clipped the herbaceous biomass in a 50×50 cm square at ground level. Herbs and dead grass biomass was removed and biomass samples were dried until constant weight. Dry samples were ground to powder, and after Kjeldahl digestion analyzed for total N and P contents by means of a continuous flow injection analyzer (AutoAnalyzer 3HR, Seal Analytical). $\delta^{13}C$ and $\delta^{15}N$ values were determined as described above for soil samples.

We used the ^{15}N natural abundance method to estimate the activity of symbiotic N_2-fixation of *D. cinerea*. The percentage of N derived from the atmosphere (*NdfA*) was estimated following Amarger et al. (1979):

$$NdfA = \frac{\delta^{15}N_{ref} - \delta^{15}N_{leg}}{\delta^{15}N_{ref} - B},$$

where $\delta^{15}N_{leg}$ is the measured ^{15}N abundance in the N_2-fixing legume species, $\delta^{15}N_{ref}$ is the mean $\delta^{15}N$ value measured in non- N_2-fixing reference species growing in the same location, and B is the abundance of ^{15}N in a legume individual that obtains all its nitrogen from N_2-fixation. As our sites had been chosen to contain no woody species other than *D. cinerea*, the leaf material for these analyses (leaves of *D. cinerea* as well as those of other leguminous and non-leguminous reference trees or shrubs) was collected from other sites. The samples were collected in March 2011. *D. cinerea* had significant lower foliar δ^{15}N values than the most common non-fixing reference species *Combretum imberbe* (pairwise t-test , t = -7.582, df = 3, p = 0.005) and *Diospyros senensis* (pairwise t-test , t = -6.915, df = 4, p = 0.002), which is the essential basis for determining N_2-fixation by the natural abundance method (Boddey et al. 2001). We used the mean value of both reference species (4.85 ± 0.51‰) to calculate *NdfA* for *D. cinerea*. The parameter B was set to the lowest detected δ^{15}N value of a legume (-0.0269 ‰ in *D. cinerea*), following Hansen and Vinther (2001) and Cech et al. (2010).

In March 2011, we measured the root phosphomonoesterase (PME) activity of *D. cinerea* and 10 other plant species that commonly occur with *D. cinerea* - four legumes, four grasses and two forbs (Fig. 6). The root samples were collected in 10 sites containing small *D. cinerea* shrubs (~5 years old) and located in the same general study area as the plots used in the main study. Plant roots were dug out and washed gently to remove soil. Within 12 h after sampling, three analytical replicates of cleaned root pieces (100 mg) were incubated in reaction tubes with 5 ml of a 5 mM *p*-nitrophenyl phosphate (pNPP) solution buffered at pH 6 (Tabatabai and Bremner 1969, Olde Venterink 2011). After one hour of shaking at room temperature, the reaction was stopped by adding 0.5 ml of each test solution to 6.5 ml of 2 N NaOH. The absorbance of the solution was measured at 410 nm using a spectrophotometer (HACH, USA) and converted into the amount of *p*-nitrophenol (pNP) released from the substrate. PME activity was then expressed as µmol *p*-nitrophenol produced per g fresh root mass and hour, and hence as µmol pNPP cleaved.

Calculations and statistical analysis

All plant and soil variables along the gradients were analyzed using linear regression with shrub cover and shrub age as the independent variable. For analyzing the age gradient data, we used both the absolute values around the shrubs, and also relative values represented by the difference between encroached site (20 cm around the shrub trunk) and the paired open reference site (referred to here as the “shrub effect”). In calculations using total C, N and P pools, we used the mean values of both measurement periods (December 2010 and February 2011) were used.

One of the IER bags yielded an exceptionally high value for resin-adsorbed P (> mean + X-STD), and this was omitted in calculating the mean site value. We also excluded this site from the extractable P regression analysis as the data were unusually high, probably due to dung or urine deposition from herbivore. Another site was completely omitted from the analyses, since a hippopotamus died and decomposed there during our study, and hence the measured soil variable could no longer be ascribed to the effect of the tree.

Comparisons between species for PME activity were computed using one-way ANOVA. Differences in N-fixation of *D. cinerea* compared to non-fixing reference plants were analyzed using paired t-tests. When necessary, data were log-transformed to fulfill assumptions of normality and homogeneity of variance. All statistical analyses were conducted using R version 2.10.1 (R Foundation for Statistical Computing 2009).

Results

Soil nutrient pools and availabilities

The total soil N pool increased significantly along the cover gradient, with the regression line rising from 47.8 g m^{-2} in the absence of D. cinerea to 98.2 g m^{-2} at a cover of 100%(Fig. 2a; Table 2). In contrast, the N pool was not significantly related to shrub age (Fig. 2b; Table 2). However, the 'shrub effect' (i.e. the difference in soil N pool beneath a tree and in adjacent grassland; Fig. 2c) did increase along the age gradient, yielding an average accretion rate of 1.6 (1.3-2.0) g N m^{-2} yr^{-1}. In the non-encroached reference sites along the age gradient, total N pools tended to decrease along the age gradient, through the result was only marginally significant (Fig. 2b). Resin adsorbed-N increased significantly with shrub cover and age, but there was no significant age effect when comparing encroached with adjacent grassland sites (Fig. 2d,e,f). Net N-mineralization showed a quadratic relationship with shrub cover and age, with rates being lowest at intermediate values (Table 2). We found no significant patterns for extractable N and δ^{15}N values along either gradient (Table 2).

Total P and extractable P pools increased along the shrub cover gradient (Fig. 2g,j). There was also a significant positive effect of age upon extractable P beneath shrubs relative to that in reference plots (i.e. shrub effect; Fig. 2l). P-adsorption to resin marginally increased along the age gradient, but not along the shrub cover gradient (data not shown, Table 2).

The total soil C pool increased significantly along the cover gradient, but not with age (Fig. 2m,n). However, the shrub effect data (i.e. the difference between encroached with reference sites) did show a marginally significant increase with age, which was equivalent to an accretion rate of 14 (12-16) g C m^{-2} yr^{-1} (Fig. 2o, Appendix A). In the non-encroached reference sites along the age gradient, total C pools tended to decrease along the age gradient (Fig. 2n). $\delta^{13}C$ values decreased with both cover and age (Fig. 3a,b,c, Table 2), and showed that the proportion of C derived from C_3-plant increased with shrub age in the encroached but not in the adjacent reference sites (Fig. 3b). Based upon the isotopic mixing model, we calculated that the proportion of soil C derived from C_3 plants was <42% under dense *D. cinerea* and <50% under 30-year-old shrubs.

The N:P ratio for soil pools increased with shrub age, and the equivalent C:N ratio decreased with shrub cover, both trends being marginally significant (data not shown, Table 2). None of the other ratios (N:P, C:P and C:N) showed any significant patterns along either gradient (data not shown, Table 2).

Soil bulk density did not vary significantly with shrub cover, but decreased with age, leading to significant larger differences between encroached and reference plots with increasing age (data not shown, Table 2).

Plots did not differ in soil moisture. Soil pH did not vary with cover and age for plots around trees. However, pH in adjacent grassland plots increased in one measurement period, leading to larger (negative) differences between encroached and reference plots with increasing age (Table 2).

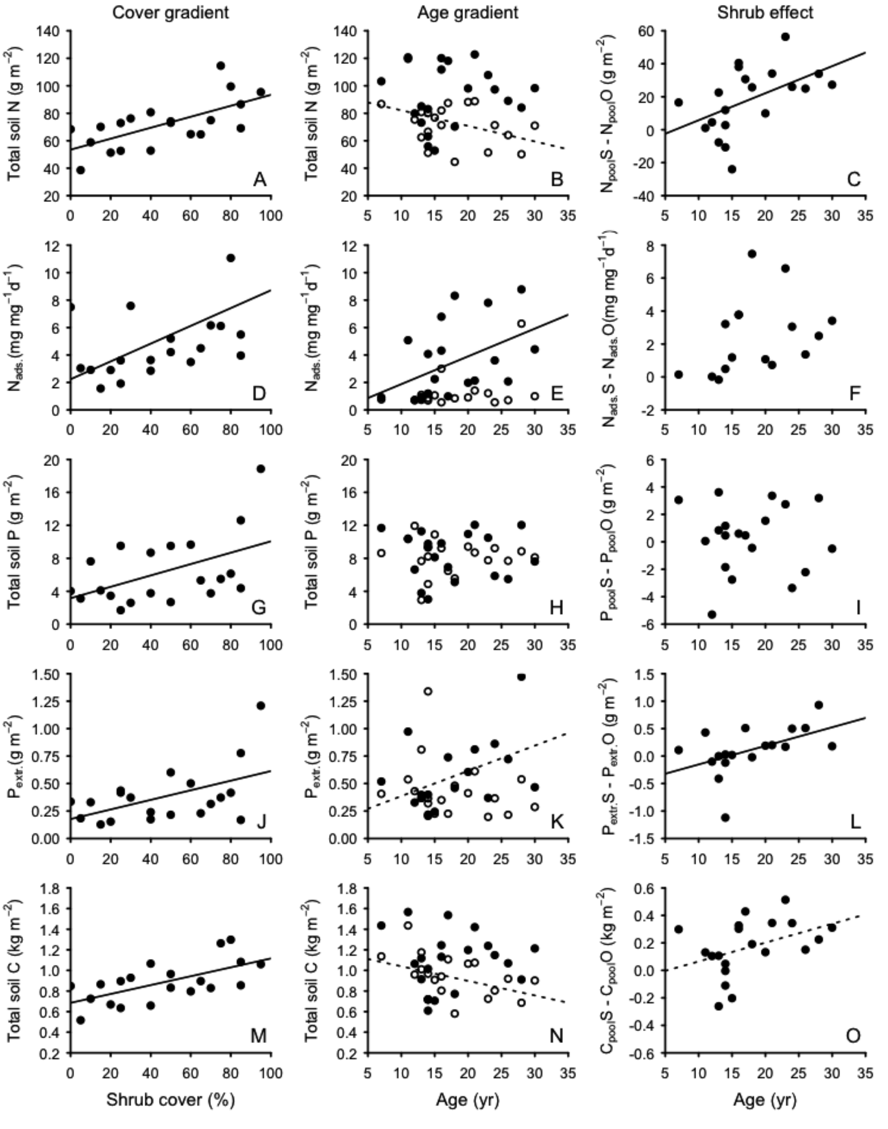


Figure 2 – Soil N, P and C pools, N adsorption to resin, and soil extractable P along gradients of *D. cinerea* shrub cover or age in a mesic savanna in Zambia. Data points in the first two columns of graphs (cover gradient and age gradient) represent absolute amounts. In the age gradient: solid symbols are sites under the shrub canopy, open symbols are the paired reference sites outside the canopy. Data points in the third column (shrub effect) represent the difference in soil variables of encroached sites from the age gradient compared to adjacent reference sites. Soil samples were taken from the top 10-cm soil in December 2010, except for soil extractable P in February 2011. Solid lines represent significant linear regressions ($p<0.05$), dotted lines represent a marginal significant trend ($0.05<p<0.1$).

Foliar nutrients and $\delta^{15}N$ values of D. cinerea *and understory grass biomass*

N and P concentrations and N:P ratios of *D. cinerea* foliage showed quadratic relationships with shrub cover, with N and P values being lowest and N:P ratios peaking at intermediate shrub cover (Fig. 4 a,b,c, Table 2). Foliar N and P concentrations in understory grass biomass (living material) increased significantly along the shrub cover gradient, while the N:P ratio decreased (Fig. 4d,e, f, Table 2).

Foliar $\delta^{15}N$ values increased and *NdfA* of *D. cinerea* shrubs decreased along the cover gradient (Fig. 5a,b). However, foliar $\delta^{15}N$ values of the understory grasses followed a quadratic relationship with lowest values occurring at intermediate shrub cover (Fig. 5c).

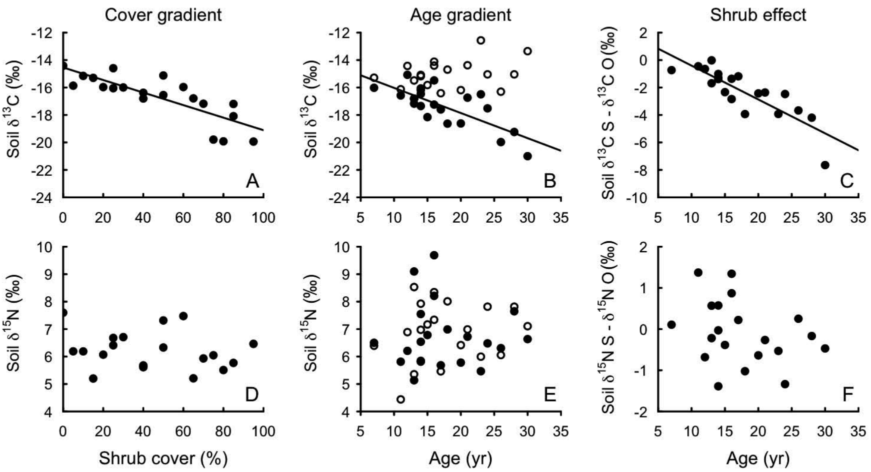


Figure 3 – Soil δ^{13}C and δ^{15}N values along gradients of *D. cinerea* shrub cover or age in a mesic savanna in Zambia. Data points in the first two columns of graphs (cover gradient and age gradient) represent absolute amounts. In the age gradient: solid symbols are sites under the shrub canopy, open symbols are the paired reference sites outside the canopy. Data points in the third column (shrub effect) represent the difference in soil variables of encroached sites from the age gradient compared to adjacent reference sites. Soil samples were taken from the top 10-cm soil in December 2010. Solid lines represent significant linear regressions ($p<0.05$).

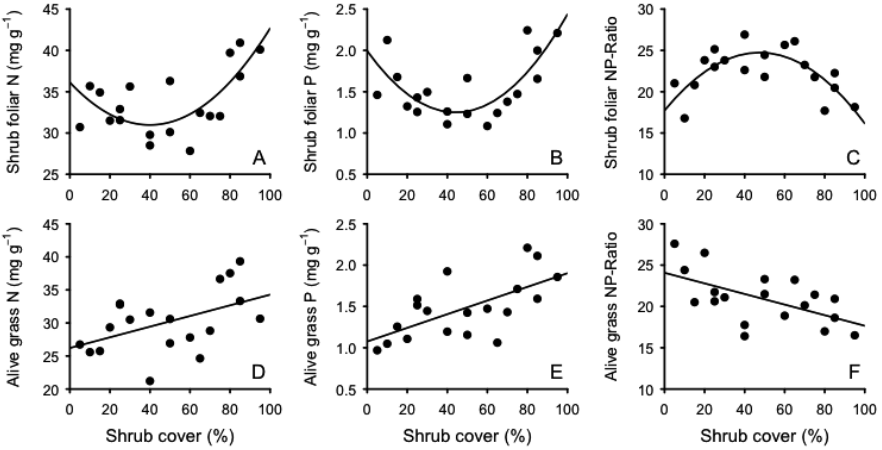


Figure 4 – Foliar N and P concentrations, and N:P ratios, of the shrub *D. cinerea* and of understory alive grass biomass, along a *D. cinerea* cover gradient in a mesic savanna in Zambia, in January 2012. Quadratic and linear regressions are significant (p<0.05).

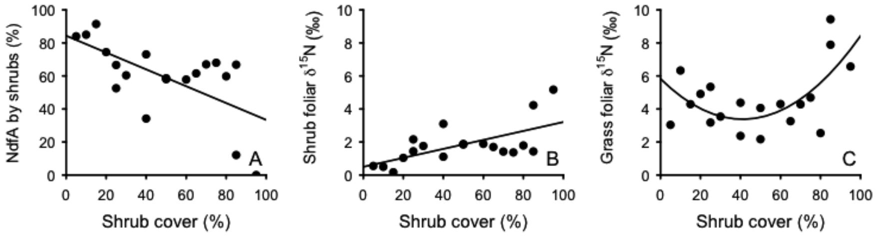


Figure 5 – *D. cinerea* and grass foliar δ^{15}N and % N derived from atmosphere (*Ndfa*) along a cover gradient of *D. cinerea* shrubs. Quadratic and linear regressions are significant (p<0.05).

Root phosphomonoesterase (PME) activity

As a group, the legumes had significantly higher PME activity than either grasses or forbs (ANOVA, p< 0.001, F= 36.4). However, in comparisons among individual species, PME activity of *D. cinerea* did not differ significantly from the values for any other species except *Hygrophila auriculata* and *Dichanthium insculptum*, which were lower (Fig. 6).

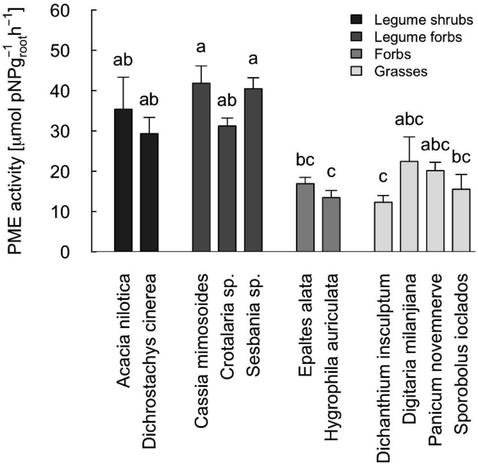


Figure 6 – Root phosphomonoesterase (PME) activity of 11 plant species from a in a mesic savanna in Zambia. Error bars show standard errors of 4-12 samples. Species not connected by same letter are significantly different (Tukey HSD test).

Table 2 – Results of linear regressions (R^2 values and significance levels) for several soil variables in top 10-cm soils against gradients of *D. cinerea* shrub cover or age. The "shrub effect" represents the difference in soil variables of encroached sites compared to adjacent reference plots. If two values are shown, the first is for the December 2010 and the second for the February 2011 measurement period. For total C, N and P as well as total nutrient ratios mean values of the December 2010 and February 2011 measurements were used. N= 20 for all variables apart for adsorbed N and P along the age gradient n=16-20 and for total P and extractable P along the age gradient n=19.

	Cover gradient	Age gradient		
		Absolute values		Shrub effect
Soil variables		Shub	Grass	
Total N (g m^{-2})	0.44**	n.s.	0.16†	0.26*
Extractable N (g m^{-2})	n.s.	n.s.	n.s.	n.s.
Adsorbed N (mg g^{-1} d^{-1})	0.30*/0.33**	0.27*	n.s.	n.s.
Net. N min. (g m^{-2} d^{-1})	0.30*^{a}	0.46†^{a}	0.18†	0.46*^{a}
δ15N (‰)	n.s.	n.s.	n.s.	n.s.
Total P (g m^{-2})	0.24*	n.s.	n.s.	n.s.
Extractable P (g m^{-2})	0.26*	0.21†	n.s.	0.25*
Adsorbed P (mg g^{-1} d^{-1})	n.s./n.s.	0.17†	n.s.	n.s.
Total C (kg m^{-2})	0.40**	n.s.	0.18†	0.17†
δ13C (‰)	0.66***	0.56***	n.s.	0.72***
Total N:P	n.s.	n.s.	n.s.	0.15†
Extractable N:P	n.s.	n.s.	n.s.	n.s.
Adsorbed N:P	n.s./n.s.	n.s.	n.s.	n.s.
Total C:N	n.s.	0.15†	n.s.	n.s.
Total C:P	n.s .	n.s.	n.s.	n.s.
pH	n.s./n.s.	n.s./n.s.	n.s./0.20*	n.s./0.29*
Moisture (%)	n.s./n.s.	n.s./n.s.	n.s./n.s.	n.s./n.s.
Bulk density (g cm^{-3})	n.s.	0.21*	n.s.	0.20†
Foliar variables				
D.cinerea N (mg g^{-1})	0.50**^{a}	–	–	–
D.cinerea P (mg g^{-1})	0.56**^{a}	–	–	–
D.cinerea N:P	0.53**^{a}	–	–	–
D.cinerea δ^{15}N (‰)	0.40**	–	–	–
D.cinerea Ndfa (%)	0.40**	–	–	–
Alive grass N (mg g^{-1})	0.24*	–	–	–
Alive grass P (mg g^{-1})	0.41**	–	–	–
Alive grass N:P	0.34**	–	–	–
Alive grass δ^{15}N (‰)	0.38*^{a}	–	–	–

[a] quadratic regression; † $p<0.1$, * $p<0.05$, ** $p<0.01$ *** $p<0.001$, n.s. non significant results

Discussion

Increases in soil N and P pools under the encroaching shrubs

Encroachment of the N-fixing shrub *D. cinerea* in our Zambian mesic savanna increased top-soil pools of both N and P. This finding is consistent with results from other African savanna ecosystems, where sites encroached by individual trees have been compared with open grassland (Ludwig et al. 2004, Hagos and Smit 2005). The difference in soil N pools between paired sites with and without *D. cinerea* increased with shrub age, indicating that the net nutrient accumulation was induced by the encroaching shrub species (Fig. 2c). Furthermore, the rates of nutrient accretion (1.3-2.0 g N m^{-2} yr^{-1}) correspond well with those reported elsewhere, although these are only for a few species, mainly from sites in the USA (Table 1).

The finding that P accumulates in the topsoil along our gradients is also consistent with similar studies of N-fixing woody species in other African savannas (Ludwig et al. 2004, Sitters et al. 2013). Thus, our study contributes to a growing body of evidence that N-fixing woody plants obtain P from sources not available to grasses. Despite having a higher P requirement than grasses (Binkley et al. 2000, Vitousek et al. 2002), therefore, they may not suffer from P limitation induced by their own growth (i.e. there is no negative feedback).

In a recent meta-analysis, Blaser et al (Chapter 3) showed that N-fixing woody plants increase soil N more than other woody plants. In this study, the increase in soil N under *D. cinerea* is probably due to shrubs producing more biomass than competing grasses and to their N-fixing capacity. Although we did not measure litter production, foliage production by *D. cinerea* was almost three times that of grasses (658±117 g m^{-2} mean of six 14-20 year old *D. cinerea* trees *versus* 237.6±50 g m^{-2} for similar sized grassland plots, Blaser et al unpublished data). Furthermore, the fact that roots of seedlings and young shrubs contained nodules, while foliar $\delta^{15}N$ values were significantly lower than for non-fixing shrubs, are clear indications that the trees were fixing atmospheric N_2. On the other hand, soil $\delta^{15}N$ values did not decrease along the gradient as might be expected if the source of the increase in soil N pools was N-fixation (Fig. 3, Boutton and Liao 2010). However, this effect might have been neutralised by other processes affecting the ^{15}N concentration, such as N pumping from deeper soil layers and isotope fractionation during litter decomposition (Hobbie and Ouimette 2009, Boutton and Liao 2010) and denitrification (Robinson 2001, Garten et al. 2008). As our sites were inundated for several weeks each year denitrification may have been a significant process, with higher rates under denser stands of *D. cinerea* where N concentrations were higher (Fig. 2d,m) (Davidson and Swank 1986, Seitzinger 1994, Olde Venterink et al. 2002).

The increases in both total-P and extractable-P in the topsoil of encroached areas were probably not due to lateral transport in widely spreading roots, since we found no evidence of depletion of either total or extractable P in the non-encroached reference sites (Fig. 2h,k). This conclusion is consistent with results obtained along a gradient of increasing *Acacia zanzibarica* density in moist savanna in Tanzania, where trees were found not to deplete extractable P pools in topsoil beyond the canopy (Sitters et al. 2013). An alternative explanation could be a higher root phosphatase activity of this leguminous species compared to other plants (Houlton et al. 2008, Olde Venterink 2011). However, despite generally higher levels of PME activity in leguminous species, the differences between *D. cinerea* and other species were mainly not significant. This leads us to conclude that the increases in both total-P and extractable-P were mainly due to *D. cinerea* having deeper roots than the competing grasses, enabling shrubs to take up P from lower soil layers. This additional P is initially incorporated into plant tissues, but becomes available in the top soil as litter falls to the ground and decomposes (Marsh et al. 2000, Jobbagy and Jackson 2001, Jackson et al. 2002, McCulley et al. 2004).

In the non-encroached reference sites, total N and C pools tended to decrease along the age gradient, though the result was only marginally significant (Fig. 2b,n). One reason for these unexpected trends could be that shrubs were in some way altering soil conditions at a distance. However, this seems unlikely, given that we observed no lateral accumulation of P (see above), while N and C contents in soil of open sites were highly correlated ($F=86.4$, $p>0.001$, $R^2 = 0.83$), which indicates that the N originated from organic matter. A second possibility is that the temporal spread of shrubs was confounded with a spatial pattern in soil conditions, with more recently colonized sites containing more organic matter. This pattern could have reflected small differences in topography, with the soil in moister depressions having a higher organic content (Gregorich et al. 1998), though we have no data to test this possibility. Such a confounding pattern could explain why we found no absolute increase in soil nutrients with age, as has been reported in other studies (e.g. Geesing et al. 2000, Ludwig et al. 2004, Throop and Archer 2008). However, because we used a paired plot approach, we are confident that possible heterogeneities in site conditions do not affect our main conclusions.

Plant soil feedback

Two important results emerge from the foliar analyses of shrubs and grasses. First, the analyses of *D. cinerea* show highly significant unimodal patterns in N and P concentrations, which are lowest at intermediate shrub cover, while the N:P ratio peaks at intermediate cover (Fig. 4a,b,c). These patterns suggest a temporal negative feedback at intermediate shrub cover, and a positive feedback when shrubs reach a certain density or age (because denser plots often contained older trees, age and cover are positively correlated; $R^2 = 0.42$ $p = 0.002$). Second, N and P concentrations in grass samples increase along the cover gradient (Fig. 4d,e), suggesting that shrubs in some way improve nutrient availabilities for understory plants. To explain these patterns, we suggest that a shrub colonizing a grass-dominated site initially has a good P supply, perhaps because it rapidly establishes a deep root system or because it can utilize organic forms of P better than competing grasses (or both, Sitters et al. 2013). With increasing shrub age and density, the easily accessible P fractions become depleted, which negatively affects P uptake and consequently also N-fixation (Almeida et al. 2000). As a deep root system continues to develop, however, and as litter is returned to the soil surface, the supply of organic P and N in the topsoil increases (Sitters et al. 2013), while competition from understory grasses is reduced through shading (Shanungu et al. unpublished). Through these processes, the P supply for shrubs improves once the shrub cover has reached about 50%. Meanwhile, N availability also increases again. However, since foliar $\delta^{15}N$ indicate reduced N_2-fixation rates in plots with a dense shrub cover, we suppose this effect is mostly due to increased production and accumulation of organic matter (Fig. 5a,b). Thus, of the two main factors known to control N-fixation - soil N and P availability; (Vitousek et al. 2002, Pons et al. 2007) - the reduction under high cover is probably due to increased soil N availability rather than to reduced P availability (cf. Fig. 2). Plants in the understory also benefit from the increased nutrient supply under high shrub cover, although their growth becomes increasingly limited by factors such as shortage of water or light (Shanungu et al unpublished data). Moreover, the decreasing N:P ratio in the grasses with increasing cover indicates that N becomes relatively more limiting than P in the denser sites (Cech et al. 2008).

Overall, we found no evidence that *D. cinerea* negatively affects its own nutrient supply, and also no indication that encroachment is part of a cyclical process that will eventually return the ecosystem to grassland. In the altered hydrological conditions of the Kafue Flats, however, *D. cinerea* might gradually be replaced by non-fixing trees, converting the former grasslands into woodland communities, as has occurred in other savanna ecosystems (Archer et al. 1988).

Effects on carbon sequestration

The question of how the carbon balance of an ecosystem is affected by shrub encroachment has proved to be difficult to answer, and the evidence remains controversial. Jackson et al. (2002) found that woody encroachment in grasslands increased soil C and N stocks in drier regions, but decreased them in regions with mean annual precipitation (MAP) greater than c. 500 mm yr^{-1} (Table 1). However, Barger et al. (2011) tested the robustness of the pattern with MAP and concluded that while changes in soil C pools with tree encroachment were inversely related to MAP, responses to shrub encroachment were highly variable and unrelated to MAP. This conclusion was supported by a recent meta-analysis (Eldridge et al. 2011), which confirmed that effects of encroachment (by both trees and shrubs) on soil C pools were not rainfall dependent. Moreover, we found 15 studies with data from 21 different locations that could be used to calculate soil C accretion rates (Table 1). In this sample, the rates ranged from losses of -80 g C m^{-2} yr^{-1} to accumulations of 239 g C m^{-2} yr^{-1} (mean 21 g C m^{-2} yr^{-1}), and were unrelated to MAP (Table 1). The results presented in our study also indicate that encroachment in mesic savanna ecosystems can be associated with positive soil C and N balances. Furthermore, we only studied the top 10-cm soil, and C sequestration likely takes place in deeper soil layers as well (Jackson 2002), perhaps serving as a C sink for centuries (Jobbagy and Jackson 2000).

A second, related problem concerns how the capacity of ecosystems to sequester C may be affected by rising concentrations of atmospheric CO_2. Based upon a meta-analysis, Van Groenigen et al. (2006) concluded that C storage in the soil could only increase if N inputs were to rise substantially above present levels (< 30 kg N ha^{-1} yr^{-1} in the US and Europe). However, in encroached soils we recorded an increase of 1.3 to 2.0 g C m^{-2} yr^{-1} with no external addition of N, suggesting that N-fixing species such as *D. cinerea* have the potential to overcome this particular constraint upon carbon accumulation (Hungate et al. 2003). Furthermore, P-limitation is also unlikely to become a constraint, in our study system at least, because of the species' ability to mobilize P from deeper soil layers. Thus, as shrub encroachment in mesic savannas has increased, and is predicted to further increase by 70% with CO_2 concentrations doubling (Bond et al. 2003), this ecoregion might continue to act as a carbon sink for many decades.

Acknowledgements

We thank Benjamin Wishikoti, Osten Mwiimbwe, Michael Sinjote, Chris Nchimunya, Rodger and Event Ngandu, Chrispin 'Palaman' Mulimbika, Kenrod Chipeka, Philippe Blaser and Aud Halbritter for their assistance during fieldwork. Britta Jahn-Humphrey, Marilyn Gaschen, Stefan Bernasconi and Veronique Ringwald supported laboratory analyses. Helpful comments by Judith Sitters significantly improved the manuscript. Research was conducted with permission and support given by the Zambia Wildlife Authority (ZAWA). Funding for this study came from the Competence Center for Environment and Sustainability (CCES) at the ETH domain.

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References

Almeida, J. P. F., U. A. Hartwig, M. Frehner, J. Nosberger, and A. Luscher. 2000. Evidence that P deficiency induces N feedback regulation of symbiotic N-2 fixation in white clover (Trifolium repens L.). Journal of Experimental Botany **51**:1289-1297.

Amarger, N., A. Mariotti, F. Mariotti, J. C. Durr, C. Bourguignon, and B. Lagacherie. 1979. Estimate of symbiotically fixed nitrogen in field-grown soybeans using variations in ^{15}N natural abundance. Plant and Soil **52**:269-280.

Archer, S., T. W. Boutton, and K. A. Hibbard. 2001. Trees in Grasslands: Biogeochemical Consequences of Woody Plant Expansion. Pages 115-137 *in* E. D. Schulze, M. Heimann, S. Harrison, E. Holland, J. Lloyd, I. Prentice, and D. Schimel, editors. Global Biogeochemical Cycles in the Climate System. Academic Press, San Diego.

Archer, S., T. W. Boutton, and C. R. McMurtry. 2004. Carbon and nitrogen accumulation in a savanna landscape: field and modeling perspectives. Pages 359-373 *in* M. Shiyomi, H. Kawahata, A. Tsuda, and Y. Awaya, editors. Global Environmental Change in the Oceans and on Lands. Terra Scientific Publishing, Tokyo.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanism of shrubland expansion: land use, climate or CO_2? Climatic Change **29**:91-99.

Archer, S., C. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a sub-tropical savanna - conversion of grassland to thorn woodland. Ecological Monographs **58**:111-127.

Balesdent, J. and A. Mariotti. 1996. Measurement of soil organic matter turnover using ^{13}C natural abundance. . Pages 83-111 *in* T. W. Boutton and S. I. Yamasaki, editors. Mass spectrometry of soils. Marcel Dekker New York, USA.

Barger, N. N., S. R. Archer, J. L. Campbell, C.-y. Huang, J. A. Morton, and A. K. Knapp. 2011. Woody plant proliferation in North American drylands: A synthesis of impacts on ecosystem carbon balance. Journal of Geophysical Research-Biogeosciences **116**.

Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology **26**:1005-1024.

Binkley, D., C. Giardina, and M. A. Bashkin. 2000. Soil phosphorus pools and supply under the influence of *Eucalyptus saligna* and nitrogen-fixing *Albizia facaltaria*. Forest Ecology and Management **128**:241-247.

Binkley, D., R. Senock, and K. Cromack. 2003. Phosphorus limitation on nitrogen fixation by Facaltaria seedlings. Forest Ecology and Management **186**:171-176.

Boddey, R. M., J. C. Polidoro, A. S. Resende, B. J. R. Alves, and S. Urquiaga. 2001. Use of the (15)N natural abundance technique for the quantification of the contribution of N(2) fixation to sugar cane and other grasses. Australian Journal of Plant Physiology **28**:889-895.

Bond, W. J., G. F. Midgley, and F. I. Woodward. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. Global Change Biology **9**:973-982.

Boutton, T. W. and J. D. Liao. 2010. Changes in soil nitrogen storage and delta^{15}N with woody plant encroachment in a subtropical savanna parkland landscape. Journal of Geophysical Research-Biogeosciences **115**:G03019.

Bray, R. H. and L. T. Kurtz. 1945. Determination of total, organic and available phosphorus in soils. Soil Science **59**:39-45.

Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: > 50 years of data suggests CO_2 as a driver. Global Change Biology **18**:675-684.

Bush, J. K. 2008. Soil nitrogen and carbon after twenty years of riparian forest development. Soil Science Society of America Journal **72**:815-822.

Cech, P. G., T. Kuster, P. J. Edwards, and H. Olde Venterink. 2008. Effects of herbivory, fire and N_2-fixation on nutrient limitation in a humid African savanna. Ecosystems **11**:991-1004.

Cech, P. G., H. Olde Venterink, and P. J. Edwards. 2010. N and P Cycling in Tanzanian Humid Savanna: Influence of Herbivores, Fire, and N_2-Fixation. Ecosystems **13**:1079-1096.

Chabwela, H. N. W. and W. Mumba. 1998. Case Study: Zambia. Integrating Water Conservation and Population. Strategies on the Kafue Flats

Creamer, C. A., T. R. Filley, T. W. Boutton, S. Oleynik, and I. B. Kantola. 2011. Controls on soil carbon accumulation during woody plant encroachment: Evidence from physical fractionation, soil respiration, and delta^{13}C of respired CO_2. Soil Biology & Biochemistry **43**:1678-1687.

Crews, T. E. 1993. Phosphorus regulation of nitrogen-fixation in a traditional Mexican agroecosystem. Biogeochemistry **21**:141-166.

Davidson, E. A. and W. T. Swank. 1986. Environmental parameters regulating gaseous nitrogen losses from two forested ecosystems via nitrification and denitrification. Applied and Environmental Microbiology **52**:1287-1292.

Douthwaite, R. J. and L. P. Van Lavieren. 1977. A Description of the vegetation of Lochinvar National Park, Zambia. Technical Report 34. National Council for Scientific Research, Lusaka, Zambia.

Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters **14**:709-722.

Ellenbroek, G. A. 1987. Ecology and productivity of an African wetland system: The Kafue Flats, Zambia. PhD Thesis. Junk Publisher.

Field, C. B., M. J. Behrenfeld, J. T. Randerson, and P. Falkowski. 1998. Primary production of the biosphere: Integrating terrestrial and oceanic components. Science **281**:237-240.

Garten, C. T., P. J. Hanson, D. E. Todd, B. B. Lu, and D. J. Brice. 2008. Natural 15N- and 13C-Abundance as Indicators of Forest Nitrogen Status and Soil Carbon Dynamics. Pages 61-82 Stable Isotopes in Ecology and Environmental Science. Blackwell Publishing Ltd.

Geesing, D., P. Felker, and R. L. Bingham. 2000. Influence of mesquite (*Prosopis glandulosa*) on soil nitrogen and carbon development: Implications for global carbon sequestration. Journal of Arid Environments **46**:157-180.

Genet, B. S. 2007. Shrub encroachment into grassland and its impact on Kafue Lechwe in Lochinvar National Park, Zambia. International Institute for Geo-information Science and Earth Observation, Enschede, The Netherlands.

Gourlay, I. D. and P. J. Kanowski. 1991. Marginal parenchyma bands and crystalliferous chains as indicators of age in African Acacia species. Iawa Bulletin **12**:187-194.

Gregorich, E. G., K. J. Greer, D. W. Anderson, and B. C. Liang. 1998. Carbon distribution and losses: erosion and deposition effects. Soil & Tillage Research **47**:291-302.

Hagos, M. G. and G. N. Smit. 2005. Soil enrichment by *Acacia mellifera* subsp detinens on nutrient poor sandy soil in a semi-arid southern African savanna. Journal of Arid Environments **61**:47-59.

Hansen, J. P. and F. P. Vinther. 2001. Spatial variability of symbiotic N_2 fixation in grass-white clover pastures estimated by the ^{15}N isotope dilution method and the natural ^{15}N abundance method. Plant and Soil **230**:257-266.

Haubensak, K. A. and I. M. Parker. 2004. Soil changes accompanying invasion of the exotic shrub *Cytisus scoparius* in glacial outwash prairies of western Washington USA. Plant Ecology **175**:71-79.

Hibbard, K. A., S. Archer, D. S. Schimel, and D. W. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical Savanna. Ecology **82**:1999-2011.

Hobbie, E. A. and A. P. Ouimette. 2009. Controls of nitrogen isotope patterns in soil profiles. Biogeochemistry **95**:355-371.

Houlton, B. Z., Y. P. Wang, P. M. Vitousek, and C. B. Field. 2008. A unifying framework for dinitrogen fixation in the terrestrial biosphere. Nature **454**:327-U334.

Hungate, B. A., J. S. Dukes, M. R. Shaw, Y. Q. Luo, and C. B. Field. 2003. Nitrogen and climate change. Science **302**:1512-1513.

Isaac, M. E., J.-M. Harmand, D. Lesueur, and J. Lelon. 2011. Tree age and soil phosphorus conditions influence N-2-fixation rates and soil N dynamics in natural populations of Acacia senegal. Forest Ecology and Management **261**:582-588.

Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature **418**:623-626.

Jobbagy, E. G. and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications **10**:423-436.

Jobbagy, E. G. and R. B. Jackson. 2001. The distribution of soil nutrients with depth: Global patterns and the imprint of plants. Biogeochemistry **53**:51-77.

Knapp, A. K., J. M. Briggs, S. L. Collins, S. R. Archer, M. S. Bret-Harte, B. E. Ewers, D. P. Peters, D. R. Young, G. R. Shaver, E. Pendall, and M. B. Cleary. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Global Change Biology **14**:615-623.

Liao, J. D., T. W. Boutton, and J. D. Jastrow. 2006. Storage and dynamics of carbon and nitrogen in soil physical fractions following woody plant invasion of grassland. Soil Biology & Biochemistry **38**:3184-3196.

Ludwig, F., H. de Kroon, F. Berendse, and H. H. T. Prins. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecology **170**:93-105.

Marsh, A. S., J. A. Arnone, B. T. Bormann, and J. C. Gordon. 2000. The role of *Equisetum* in nutrient cycling in an Alaskan shrub wetland. Journal of Ecology **88**:999-1011.

McCulley, R. L., E. G. Jobbagy, W. T. Pockman, and R. B. Jackson. 2004. Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. Oecologia **141**:620-628.

McKinley, D. C. and J. M. Blair. 2008. Woody plant encroachment by *Juniperus virginiana* in a mesic native grassland promotes rapid carbon and nitrogen accrual. Ecosystems **11**:454-468.

Montane, F., P. Rovira, and P. Casals. 2007. Shrub encroachment into mesic mountain grasslands in the Iberian peninsula: Effects of plant quality and temperature on soil C and N stocks. Global Biogeochemical Cycles **21**:GB4016.

Mumba, M. and J. R. Thompson. 2005. Hydrological and ecological impacts of dams on the Kafue Flats floodplain system, Southern Zambia. Physics and Chemistry of the Earth **30**:442-447.

Neff, J. C., N. N. Barger, W. T. Baisden, D. P. Fernandez, and G. P. Asner. 2009. Soil carbon storage responses to expanding pinyon-juniper populations in southern Utah. Ecological Applications **19**:1405-1416.

Neumann, K., W. Schoch, P. Détienne, and F. H. Schweingruber. 2001. Woods of the Sahara and the Sahel. Haupt, Bern, Stuttgart, Wien.

Olde Venterink, H. 2011. Legumes have a higher root phosphatase activity than other forbs, particularly under low inorganic P and N supply. Plant and Soil **347**:137-146.

Olde Venterink, H., T. E. Davidsson, K. Kiehl, and L. Leonardson. 2002. Impact of drying and re-wetting on N, P and K dynamics in a wetland soil. Plant and Soil **243**:119-130.

Olff, H., F. Berendse, and W. Devisser. 1994. Changes in nitrogen mineralization, tissue nutrient concentrations and biomass compartmentation after cessation of fertilizer application to mown grassland. Journal of Ecology **82**:611-620.

Pearson, H. L. and P. M. Vitousek. 2001. Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. Ecological Applications **11**:1381-1394.

Pons, T. L., K. Perreijn, C. van Kessel, and M. J. A. Werger. 2007. Symbiotic nitrogen fixation in a tropical rainforest: N-15 natural abundance measurements supported by experimental isotopic enrichment. New Phytologist **173**:154-167.

Riginos, C., J. B. Grace, D. J. Augustine, and T. P. Young. 2009. Local versus landscape-scale effects of savanna trees on grasses. Journal of Ecology **97**:1337-1345.

Robinson, D. 2001. delta^{15}N as an integrator of the nitrogen cycle. Trends in Ecology & Evolution **16**:153-162.

Schimel, D. S., B. H. Braswell, R. McKeown, D. S. Ojima, W. J. Parton, and W. Pulliam. 1996. Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. Global Biogeochemical Cycles **10**:677-692.

Scholes, R. J. and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics **28**:517-544.

Seitzinger, S. P. 1994. Linkages between organic matter mineralization and denitrification in eight riparian wetlands. Biogeochemistry **25**:19-39.

Sitters, J., P. J. Edwards, and H. O. Venterink. 2013. Increases of soil C, N, and P pools along an *Acacia* tree density gradient and their effects on trees and grasses. Ecosystems **16**:347-357.

Springsteen, A., W. Loya, M. Liebig, and J. Hendrickson. 2010. Soil carbon and nitrogen across a chronosequence of woody plant expansion in North Dakota. Plant and Soil **328**:369-379.

Tabatabai, M. A. and J. M. Bremner. 1969. Use of p-nitrophenyl phosphate for assay of soil phosphatase activity. Soil Biology and Biochemistry **1**:301-307.

Throop, H. L. and S. R. Archer. 2008. Shrub (Prosopis velutina) encroachment in a semidesert grassland: spatial-temporal changes in soil organic carbon and nitrogen pools. Global Change Biology **14**:2420-2431.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics **31**:197-215.

Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management **90**:2931-2942.

van Groenigen, K. J., J. Six, B. A. Hungate, M. A. de Graaff, N. van Breemen, and C. van Kessel. 2006. Element interactions limit soil carbon storage. Proceedings of the National Academy of Sciences of the United States of America **103**:6571-6574.

Vitousek, P. M., K. Cassman, C. Cleveland, T. Crews, C. B. Field, N. B. Grimm, R. W. Howarth, R. Marino, L. Martinelli, E. B. Rastetter, and J. I. Sprent. 2002. Towards an ecological understanding of biological nitrogen fixation. Biogeochemistry **57**:1-45.

Wheeler, C. W., S. R. Archer, G. P. Asner, and C. R. McMurtry. 2007. Climatic/edaphic controls on soil carbon/nitrogen response to shrub encroachment in desert grassland. Ecological Applications **17**:1911-1928.

Chapter 4

Impact of shrub encroachment on the understory vegetation differs among shrub species in the Kafue Flats, Zambia

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Abstract

Woody encroachment has become a widespread phenomenon in grassland ecosystems throughout the world. Encroachment is often a gradual process, making it important to consider the extent of woody cover when assessing its influence on the understory vegetation. We used remote sensing to map patterns of encroachment by *Dichrostachys cinerea* and *Mimosa pigra* in Lochinvar National Park, Zambia. Results revealed that woody cover increased from 26 to 45% while open areas decreased from 50 to 33% of the park area between 1986 and 2010. In the field, we recorded the effects of encroaching shrubs on the growth and species composition of understory vegetation. *D. cinerea* led to a more than doubling of herbage quality (N and P concentrations), while *M. pigra* density had no net effect on herbage quality. Both species reduced the available herbaceous biomass. *M. pigra* linearly decreased richness and grass cover with increasing cover, whereas species richness and grass cover followed a unimodal relation with *D. cinerea* and only decreased at shrub cover above 40%. We conclude that there is no general pattern for encroaching woody species along cover gradients, and that the canopy architecture and level of encroachment have to be taken into account when assessing potential effects. However, all encroachment ultimately leads to reduced biomass and richness at dense covers.

Introduction

Over the past century, many grazing systems such as savannas and grasslands have experienced woody thickening or encroachment (Archer et al. 1995, Van Auken 2000, Archer et al. 2001, Van Auken 2009). This spread of tree and shrub species has been variously ascribed to global or regional environmental changes (e.g. climate warming, CO_2 enrichment, N deposition) and to local effects related to management (e.g. changes in fire and grazing regimes) (Van Auken 2000, Bond et al. 2003, Van Auken 2009, Eldridge et al. 2011, Buitenwerf et al. 2012). Woody encroachment profoundly changes the structure of grassland ecosystems, with consequences for the productivity, composition and species richness of the understory vegetation (Lett and Knapp 2005) and ultimately the food supply for herbivores (Riginos et al. 2009). To understand these consequences, many aspects of the encroachment process need to be considered, including: 1) how woody plants expand on a spatial and temporal scale, 2) how the encroachment of wood plants alters important environmental conditions such as light penetration to the sub canopy, and 3) how the encroachment of woody plants affects productivity, quality and composition of the understory vegetation.

Effects of woody encroachment on understory vegetation have mainly been studied under isolated trees or shrubs or in paired open and encroached plots. These studies have shown that isolated woody species have the ability to modify their local understory environment, which may have positive, neutral, or negative effects on herbaceous productivity and richness (Engle et al. 1987, Vetaas 1992, Belsky et al. 1993, Belsky 1994, Ludwig et al. 2004, Blank and Carmel 2012, Howard et al. 2012), but generally positive effects on herbage quality (tissue N and P concentrations; Belsky 1992, Treydte et al. 2007, Ludwig et al. 2008). However, these studies do not take into account the gradual nature of encroachment, and the fact that the understory does not necessarily respond linearly to an increasing abundance of woody plants (Vetaas 1992, Riginos et al. 2009). Hence there is need for further studies that investigate the characteristics of the understory vegetation along shrub or tree density gradients.

The aim of this study is to assess the spatio-temporal spread of woody plants, as well as their effects on productivity, quality and composition of the understory vegetation. By investigating these effects along shrub density gradients we attempt to understand the sequence of changes that occur during encroachment.

The work was performed in Lochinvar National Park in the Kafue Flats, Zambia, where two leguminous shrubs *Dichrostachys cinerea* and *Mimosa pigra* have spread rapidly in recent years. The first species is indigenous to the area (Roques et al. 2001), while the second is a native of South America that has become invasive in many tropical regions (Shanungu 2009). Both species have become much more abundant on the Kafue Flats since the late 1980s, which may be at least partly related to the construction of dams on the Kafue River (Mumba and Thompson 2005). However, there are few quantitative data of the rate of spread of these shrubs and their effects on the understory vegetation.

Methods

Study area

Field sampling was conducted in Lochinvar National Park, located in the seasonally inundated Kafue Flats, a floodplain of the Kafue River in central Zambia (15°52'S, 27°14'E). The vegetation of the area can be divided into three main vegetation zones which are influenced by their elevation relative to the Kafue river: the seasonally inundated floodplain grasslands, the termitaria grassland above the high flood line characterized by the abundant presence of termite mounds, and the woodland (Ellenbroek 1987). The park is a former cattle ranch in which larger carnivores were systematically exterminated but wild herbivores were protected and are still found in large herds. By far the most abundant herbivore in the floodplain and termitaria zones is the Kafue Lechwe (*Kobus leche kafuensis* Haltenorth, 1963), followed by zebra (*Equus burchelli*). Smaller populations of wildebeest (*Connochaetus taurinus*), oribi (*Ourebia ourebia*), common duiker (*Sylvicapra grimmia*), impala (*Aepyceros melampus*) and kudu (*Tragelaphus strepsiceros*) use the termitaria zone. In the woodland, buffalo (*Syncerus caffer*) and bushbuck (*Tragelaphus scriptus*) are common (Ellenbroek 1987). Annual precipitation is 753 mm (2000-2011 mean) and is highly seasonal, with almost all rain falling in the wet season from November to April. The mean annual temperature is 20.6°C (Ellenbroek 1987, Mumba and Thompson 2005).

Since the early 1980s, Lochinvar National Park has experienced a significant increase in woodland and shrub cover by the exotic *Mimosa pigra*, as well as the native *Dichrostachys cinerea* and several native *Acacia* species (Chabwela and

Mumba 1998, Mumba and Thompson 2005, Genet 2007). *M. pigra* is a highly invasive, spiny leguminous shrub, that forms dense monospecific stands that exclude other plants and most animals (Lonsdale, 1989, Paynter et al, 2000). *D. cinerea* is a native leguminous shrub or tree, but one of the major encroaching species in grasslands in southern Africa (Roques et al. 2001, Hagenah et al. 2009).

Remote sensing

We mapped spatial changes in shrub cover using a temporal sequence of Landsat TM scenes downloaded from the free online archive (http://glovis.usgs.gov). In selecting the images, we aimed to have cloud-free coverage from both the wet and dry season, so that multi-temporal analyses within individual years were possible. We selected the following three periods (containing 2-3 images):

- 1986 (based on May 25 1986 and Nov 17 1986)
- 1994-1995 (based on Dec 9 1994 and Mar 31 1995)
- 2008-2010 (based on Sept 26 2008, May 24 2009 and Jan 19 2010)

Images where reprojected to WGS_1984_UTM_Zone_35S. All bands (with exception of thermal band 6) from one period were then stacked (using Erdas Imagine 9.2) and clipped to include the Lochinvar Park. A supervised maximum likelihood classification algorithm was used within Erdas Imagine 9.2. We classified ten major vegetation types: 1. *Mimosa pigra* (areas dominated by *M. pigra* > 30% shrub cover); 2. *Dichrostachys cinerea* (areas dominated by *D. cinerea* > 30% shrub cover); 3. *Acacia sp*. (areas dominated by several *Acacia* species, i.e. *A. sieberana, A. seyal, A. nilotica*); 4. Mixed shrub termitaria (grasslands above the high flood line, dotted with termite mounds and with abundant growth of mixed shrubs on largely all as well as in-between termite mounds (e.g. *Combretum imberbe, Diospyros senensis, Albizia harveyi*); 5. Woodland (open, one story woodlands dominated by *Albizia harveyi* and several *Acacia* and *Combretum* species); 6. Open floodplain grassland (seasonally inundated grasslands dominated by *Vossia cuspidata*, *Oryza longistaminata*, *Echinochloa scabra*, *Paspalidium obtusifolium, Panicum repens*, *Leersia denudata*, and *Acroceras macrum*); 7. Open termitaria grassland (open grasslands above the high flood line, dotted with termite mounds and occasional trees on termite mounds); 8. *Vetiveria nigritana* grassland (tree-less areas dominated by the large tussock grass *V. nigritana* and dotted with termite mounds); 9. Swamp areas (permanently flooded areas dominated by *Typha domingensis* and *Cyperus papyrus sp.*); 10. Open water areas.

The training samples for the 2008-2010 period were created based on 859 ground-truthing sites, which were located throughout the park and recorded in September 2010. Patch sizes of the different classes (included within the data) were used to create a buffer file around each ground-truth point. In half of these buffer rings, training areas were created based on visual interpretation of similar signal within the buffer, leaving the other half to assess the accuracy of the classified image. Training samples for 1986 were created using field data collected in the 1970s (Douthwaite and Van Lavieren 1977). In addition, we selected a sample of points from the 2010 data for which, according to local expert knowledge, the vegetation class had not changed in the past few decades. Training samples for the 1994-1995 period were created using a combination of the early field data and the 2010 data (excluding points from 2010 and including points from the 1970s data based on expert knowledge).

To enhance the classification of the 1994-1995 image, we performed some post-classification processing. For this, we first calculated a cross-matrix of the 1994-1995 and 2008-2010 data using Erdas' utility "Matrix". The resulting image was then reclassified based on ecological assumptions of likelihood of changes in classes between the 1994-1995 and 2008-2010 data sets (Supporting information Table S1). In cases where changes between classes from the 1994-1995 and 2008-2010 classified images were unlikely to have occurred we replaced the 1994-1995 class with the 2008-2010 class. In all other cases the classes of the 1994-1995 classified image were preserved. This was done based on the assumption that the 2008-2010 classified image was more reliable (higher accuracy, more ground truth available, recent expert knowledge and field observations).

Accuracy assessment was performed in Erdas Imagine 9.2. For the 1994-1995 and 2008-2010 images, half of the buffer areas (described above) were used to generate 500 random points that were used as reference data; for the 1980s image, half of the training points were used. Producers/users accuracies were generated for the overall classification of the images as well as for individual classes. These values were later corrected for the area of cover of the represented class resulting in "area weighted producers/users accuracies" (Table S2, Congalton 1991).

Field study

To investigate the impacts of *M. pigra* and *D. cinerea* on the understory vegetation, we carried out a field study along cover gradients of these shrubs. We located 36 sites (10×10m^2) in the *D. cinerea* and 23 sites in the *M. pigra* area, representing in both cases a shrub cover gradient from open to densely covered plots. Shrub cover and species composition of the vegetation were recorded at each site in April to May 2010, the time when the largest number of plant species was flowering. The cover of all species was visually estimated. Nomenclature followed Flora Zambeziaca and Ellenbroek (1987).

For a selection of 12 plots along both the *M. pigra* and *D. cinerea* gradients, we measured standing biomass and biomass production of the herbaceous vegetation using the movable cage method (McNaughton 1979, 1996). In November 2010, before the onset of the rains, we placed a movable cage (1×1m^2) at each site to protect the biomass from grazing and selected two reference plots (1×1m^2) within the site with the same vegetation and ground cover. Biomass was clipped to ground level in a 50×50cm^2 quadrat in one of the two reference plots. After 6 weeks (late December 2011) the biomass in the movable cages, as well as in the second reference plots, were cut in a 50×50 cm^2 quadrat. Cut material was initially separated into grasses, forbs and shrub seedlings, and then further into living and dead biomass, all fractions being separately dried and weighed. Subsamples of living grass material from the reference plots were ground, and after Kjeldahl digestion, total N and P concentrations were determined in an auto-analyzer (Seal, Analytical). N and P concentrations were then multiplied by the living grass biomass to estimate herbaceous N and P mass.

In each site we estimated grass production between November and late December from the difference in biomass under the cage in December and the biomass cut in the reference plot in November. In *D. cinerea* sites biomass for the entire 100 m^2 was estimated by extrapolating from the 0.25 m^2 plots. In the dense *M. pigra* sites, it was not possible to place the cages evenly as *M. pigra* forms thick impenetrable thickets and biomass could only be measured in the open spaces between the shrubs. The biomass for the entire site was therefore calculated by up-scaling measurements from the clipped 0.25 m^2 plot to the grass covered area only (100 m^2 – shrub covered area). This approach assumes that where *M. pigra* grows, all other forms of vegetation are excluded, which is supported by field observations.

In March 2011, when the new foliage was fully expanded, photosynthetically active radiation (PAR) was measured with a light sensor (Sensor - JYP 1000, SDEC France) in 20 out of the 36 sites along the *D. cinerea* gradient. These measurements were made at nine positions along two transects spanning diagonally through each site and at heights of 0 cm, 20 cm, 60 cm and 1m. PAR was also measured at a nearby open site, and these values were used to calculate the percentage of full light penetration for each canopy layer and site. Light measurements under *M. pigra* were performed in three dense and three young stands at 30 cm above soil surface and expressed as percentage of an open reference, as walking transects through the sites were not possible. All light measurements were carried out on cloudless days between 11:00 and 13:00.

Statistical analysis

Linear and quadratic regression analysis was used to assess the relationships between the shrub canopy cover and recorded vegetation variables. If assumptions of normality and homogeneity of variance were not fulfilled, data were log transformed. All statistical analysis was conducted using R version 2.10.1 (R Foundation for Statistical Computing 2009).

Results

Shrub encroachment in time

Woody cover (*M. pigra*, *D. cinerea*, *Acacia* spp, Mixed shrub termitaria and Woodland classes) increased from 26 to 45% of the park area between 1986 and 2010, whereas open areas (Floodplain grassland, Open termitaria and Vetiveria nigritana classes) decreased from 50 to 33% (Fig. 1, Table 1). *Dichrostachys cinerea* and native *Acacia* species encroached in drier zones of the termitaria and at the edge of the former floodplain. The spread of *M. pigra* was limited to relatively wetter zones of the floodplain area (Fig. 1).

The area-weighted accuracies of the classified images varied between 75% (for the 1986 period) to 80% (for the 1994-1995 period). Although this is considerably lower than the suggested 85% (Congalton, 1991), producers/users accuracies of individual classes reached much higher values (Table. S2).

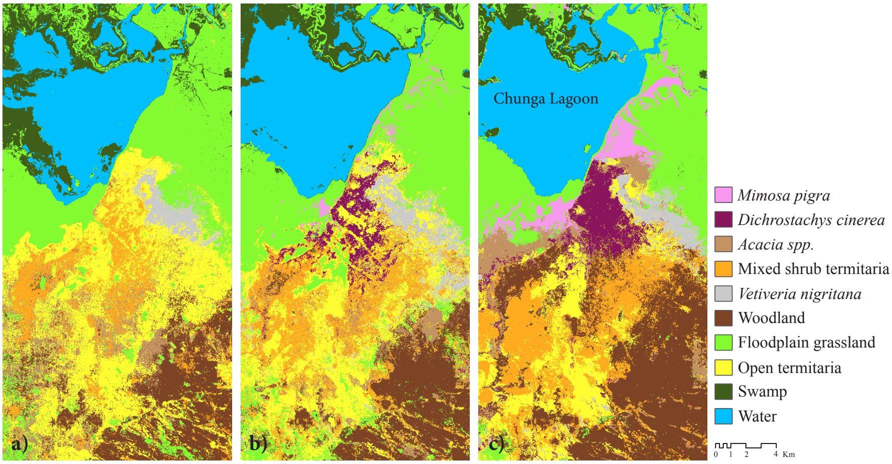


Figure 1 – Vegetation maps of Lochinvar national park in a) 1986 b) 1994-1995 and c) 2008-2010, generated through supervised classification of multitemporal, hyperspectral Landsat TMimages.

Table 1 – Abundance of the major vegetation types in Lochinvar National Park, expressed as percent of total park area (45000 ha). Furthermore, rate of change between the three moments in time and absolute changes in cover between 1986 and 2010 are shown. Data is based on the vegetation maps in Fig. 1. Vegetation types are described in the methods section.

Vegetation type	**1986**	**1995**	**2010**	**Rate of change (ha yr^{-1})**		**Change 1986 -2010**	
	%	**%**	**%**	**1986 - 1995**	**1995-2010**	**%**	**ha**
Mimosa pigra	0	0.9	3.8	+44.6	+86.1	+8.0	+1693
Dichrostachys cinerea	0	2.9	4.2	+144.8	+40.6	+4.2	+1912
Acacia spp.	7.4	4.2	5.2	-161.7	+31.6	-2.2	-982
Mixed shrub termitaria	7.8	11.1	13	+167.5	+58.2	+5.3	+2381
Woodland	11.1	10.8	19.1	-14.8	+249.5	+3.8	+3610
Floodplain grass	24.7	25.4	19.6	+31.2	-171.3	-5.1	-2289
Open termitaria	23.8	17.4	10.8	-321.5	-199.0	-13.0	-5879
Vetiveria nigritana	1.9	3.7	2.6	+88.0	-33.5	+0.6	+289
Swamp/Bare ground	8.3	4.8	3	-175.0	-55.2	-5.3	-2403
Water	15.1	18.8	18.8	+181.9	+2.0	+3.7	+1668

Herbaceous biomass and herbage quality

Total standing biomass, as well as the fractions of living biomass and grass biomass, decreased significantly along both *D. cinerea* and *M. pigra* cover gradients (Fig. 2, Table 2). Also, the production of living biomass decreased with increasing shrub cover along both gradients, though the patterns were only marginally significant (Fig. 2e,f, Table 2).

Foliar N and P concentrations in living grass biomass increased significantly along the *D. cinerea* gradient (Fig. 3a,e Table 2), but showed a quadratic relationship along the *M. pigra* gradient, with lowest values at intermediate shrub cover (Fig. 3b,f Table 2). Foliar N:P ratios remained constant along both gradients (Table 2). Total pools of N and P in the aboveground living grass biomass (kg N or P per ha) decreased significantly along both shrub cover gradients (Fig. 3c,d,g,h Table 2).

Vegetation composition along shrub cover gradients

Along the *D. cinerea* gradient we recorded a total of 108 plant species, 35 grasses and 73 forbs (Table S3). Species richness ranged from 9 to 29 species per $100m^2$, and showed a significant quadratic relationship with shrub cover, peaking at 40% cover (Fig. 4c, Table 2). The number and cover of grass species decreased strongly where the cover of *D. cinerea* was > 60% (Fig. 4a,e, Table 2).

In the *M. pigra* sites, we recorded a total of 48 plant species, with 21 grasses and 27 forbs (Table S4). Species richness was much lower than in *D. cinerea* plots and ranged from 1 to 19 species per $100m^2$ plot. Total species number, as well as numbers of grasses and forbs separately, decreased linearly with increasing shrub cover (Fig. 4d,f Table 2). Increasing shrub cover was also associated with a significant decrease in grass cover (Fig. 4b), but had no impact on the cover of forbs (Table 2).

Light

Light intensity (PAR) at ground level decreased significantly along the *D. cinerea* gradient, from 100% in open sites to about 10% in dense sites (Fig. 5, Table 2). *M. pigra* stands reduced the light intensity even more, to 5±3.5 % in mature stands and to only 4±0.6 % in younger stands (means of N=3).

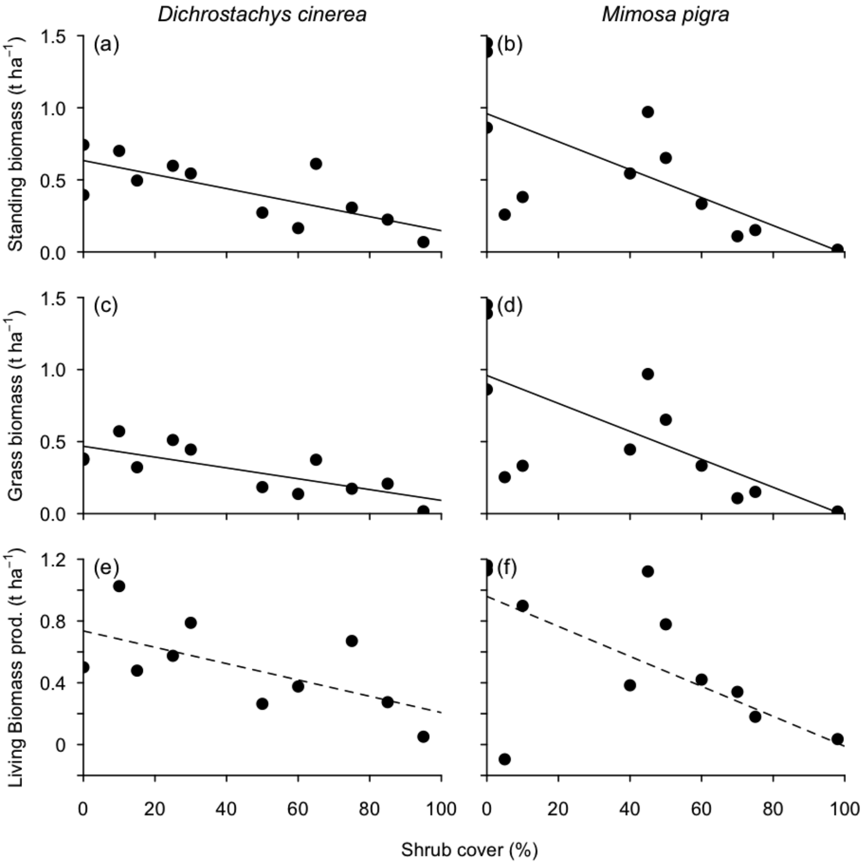


Figure 2 – Standing aboveground total (a,b) and grass biomass (c, d) and production during 50 (e) and 54-56 days (f) along cover gradients of *D. cinerea* and *M. pigra*. Measurements were done at the beginning of the wet season (November to December 2010). Production was assessed by means of moveable cages. Solid lines represent significant linear regressions (p<0.05), dotted lines a marginal significant trend (0.05<p<0.1).

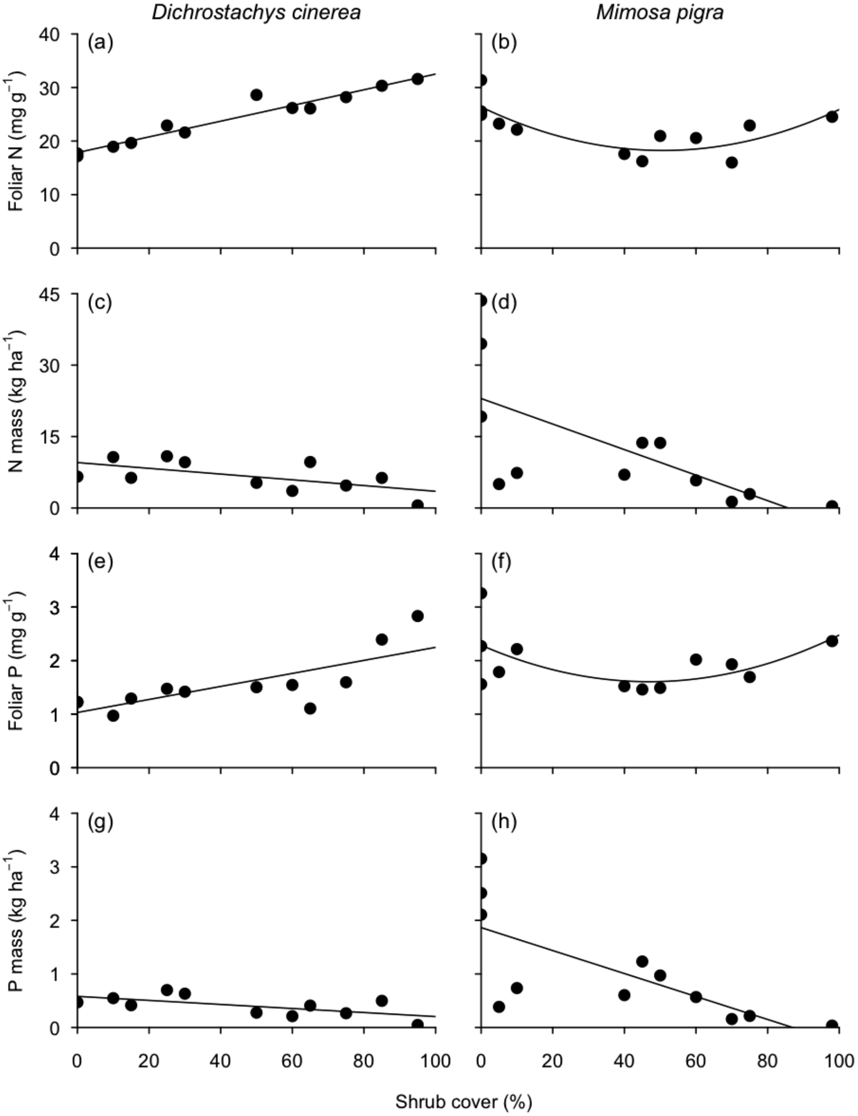


Figure 3 – Grass foliar N (a, b) and P (c, d) concentrations along cover gradients of *D. cinerea* and *M. pigra*. Measurements were done at the beginning of the wet season (December 2010). Linear and quadratic regression lines were drawn where significant (p<0.05).

Table 2 – Characteristics of the herbaceous vegetation in relation to density (cover) of the shrubs *D. cinerea* and *M. pigra.* R^2 values of linear and quadratic (a) regressions are shown, as well significance levels: † p<0.1, * p<0.05, ** p<0.01 *** p<0.001. n.s. not significant. n is number of sites.

	D. cinerea		***M. pigra***	
Variables	**n**	**R^2**	**n**	**R^2**
Total aboveground biomass (Mg ha^{-1})	12	0.47*	12	0.47*
Total aboveground living biomass (Mg ha^{-1})	12	0.47*	12	0.47*
Total grass biomass (Mg ha^{-1})	12	0.54*	12	0.45*
Total living grass biomass (Mg ha^{-1})	12	0.63**	12	0.46*
Total biomass production (Mg ha^{-1})	10	n.s	8	n.s.
Total living biomass production (Mg ha^{-1})	10	0.39†	8	0.28†
Total grass production (Mg ha^{-1})	10	0.37†	8	n.s.
Living grass production (Mg ha^{-1})	10	0.44*	8	0.28†
Total biomass consumption (Mg ha^{-1})	10	n.s.	8	n.s.
Total living biomass consumption (Mg ha^{-1})	10	n.s.	8	n.s.
Total grass consumption (Mg ha^{-1})	10	n.s.	8	n.s.
Living grass consumption (Mg ha^{-1})	10	n.s.	8	n.s.
Grass foliar N (mg g^{-1})	11	0.93***	11	0.47*[a]
N mass (kg ha^{-1})	11	0.36*	11	0.46*
Grass foliar P (mg g^{-1})	11	0.57**	11	0.46*[a]
P mass (kg ha^{-1})	11	0.40*	11	0.53**
Grass foliar N:P	11	n.s.	11	n.s.
Understory vegetation cover (%)	36	0.08†	23	0.28**
Grass cover (%)	36	0.48***[a]	23	0.60***
Forb cover (%)	36	n.s.	23	n.s.
Number of species	36	0.25**[a]	23	0.33**
Number of grass species	36	0.43***[a]	23	0.36**
Number of forb species	36	0.09†	23	0.31**
Light at 0.0 m (%)	20	0.76***	–	–
Light at 0.2 m (%)	20	0.70***	–	–
Light at 0.4 m (%)	20	0.70***	–	–
Light at 1.0 m (%)	20	0.67***	–	–

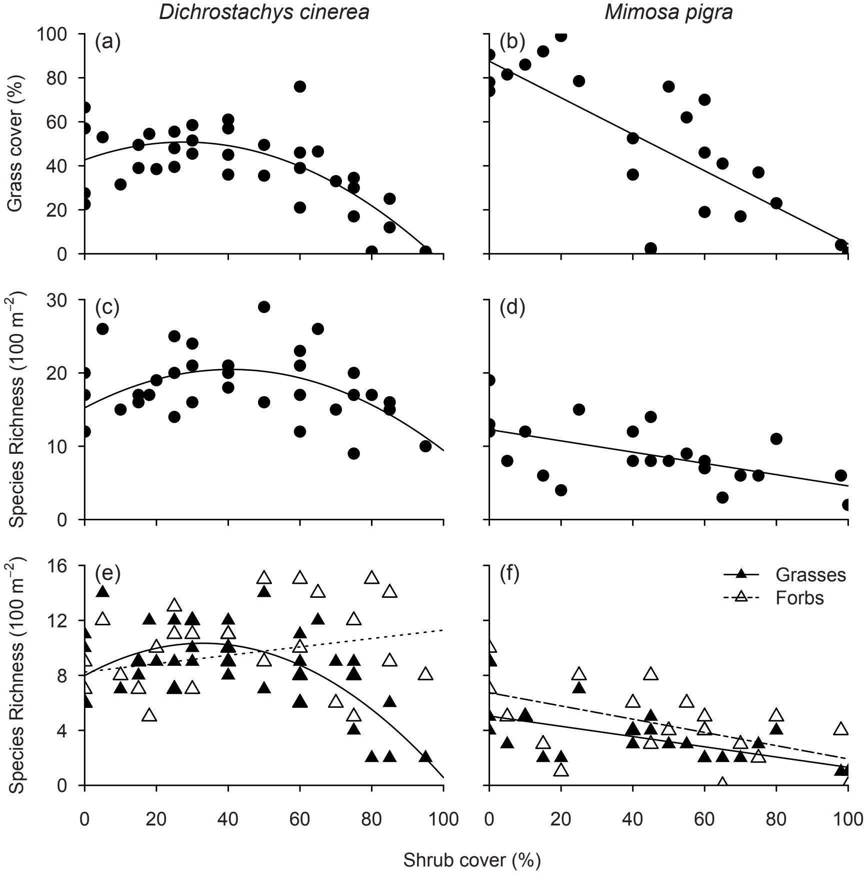


Figure 4 – Percentage grass cover (a, b), total plant species richness per 100m^2 (c, d) and grass and forb richness per 100 m^2 (e, f) along cover gradients of *D. cinerea* and *M. pigra*. Measurements were recorded at the end of the wet season in April to May 2010. Solid lines represent significant linear or quadratic regressions ($p<0.05$), dotted lines marginal significant linear regressions ($0.05<p<0.1$).

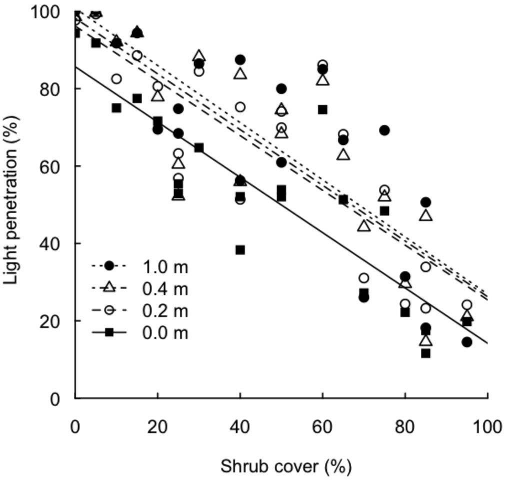


Figure 5 – Light penetration expressed as percentage of full light intensity in an open site measured at four height levels (0, 0.2, 0.4 and 1 m) along a *D. cinerea* cover gradient. Lines represent significant linear regressions ($p<0.05$).

Discussion

Woody encroachment on a spatial scale

Lochinvar National Park has experienced severe woody encroachment by *D. cinerea*, *M. pigra* and several *Acacia* species, changing the character of the area from open grassland (26% of park area with woody vegetation, 50% open grasslands in 1986) to a shrub-dominated landscape (45% woody vegetation, 33% open grasslands) between in 2010 (Fig. 1, Table 1). Observed rates of spread of these species are consistent with those reported for other woody species from grasslands around the world (e.g. Roques et al. 2001, Briggs et al. 2002, Heisler et al. 2003, Laliberte et al. 2004, Robinson et al. 2008, Munyati et al. 2011). Whereas encroachment has been attributed to a variety of factors, including global or regional environmental changes (climate warming, CO_2 enrichment, N deposition) as well as local changes in fire and grazing regimes (Van Auken 2000, Bond et al. 2003, Van Auken 2009, Eldridge et al. 2011), the main cause in our study area was probably a change in flooding regime following the construction of two dams on the Kafue River. Reducing maximum flood levels led to drier conditions at the margins of the floodplain, allowing woody growth of *D. cinerea* and *Acacia* species in the former waterlogged areas (Chapter 1). Similar effects of dams on downstream vegetation have been demonstrated in the Kolope–Setonki sub catchment of the Limpopo River in South Africa and in the Vojm River in northern Sweden (O'Connor 2001, Dolores Bejarano et al. 2011). The effect of hydrology on the encroachment by *M. pigra* is less obvious, partly because this species may still be spreading (Table 1and historic pre dam references of the occurrence of the species are lacking.

Quantity and quality of understory herbage

Understory herbage biomass and production were reduced by c. 70% under dense *D. cinerea* and in some cases completely under dense *M. pigra* (Fig. 2). These negative effects of shrub encroachment on herbage biomass are consistent with results from other grassland ecosystems (e.g. Scholes and Archer 1997, Richter et al. 2001, Kesting et al. 2009), where they have usually been ascribed to competition for light, water and soil nutrients (Belsky 1994, Ludwig et al. 2004). In our study area, we suppose that light was the most limiting factor, as light levels were reduced by c. 80% in dense *D. cinerea* sites (Fig. 5) and by up to c. 95% under *M. pigra* stands. Further, foliar nitrogen and phosphorus concentrations of grasses (an index of herbage quality) were higher under dense cover of *D. cinerea* than in open sites (Fig. 3a,e), implying that the production decrease was likely not due to increased limitation by these nutrients. Also, water is readily available during the rainy season and hence is unlikely to limit growth.

The increased quality of herbage under *D. cinerea* probably reflects higher availabilities of soil N and P resulting from the shrub's high litter production and its ability to fix atmospheric N (Chapter 3, Schulze et al. 1991). Furthermore, lower biomass production under dense cover could contribute to increased herbage quality as nutrients taken up by grasses are less diluted (Ludwig et al. 2008). Unlike *D. cinerea*, *M. pigra* had no beneficial effect on herbaceous quality and at intermediate cover was even associated with lower N and P concentrations in grass biomass (Fig. 3b,f). Foliar δ^{15}N values (3.4± 0.7, N=7) of *M. pigra* did not differ from those of the non-fixing reference species *Combretum imberbe* (5.9±0.4, N=6) and *Diospyros senensis* (3.6±0.4, N=5) (Blaser et al., unpublished data), and it is unclear whether the species fixes atmospheric N under the very wet conditions in our study area.

Table 3 – Results of back of the envelope calculations of encroachment induced biomass and N losses from the ecosystem between 1986 and 2010. To perform the calculations the Park was divided into three zones consisting of the following vegetation types mapped in (Fig 1): 1) Floodplain (Mimosa pigra and Flooplain grassland), 2.) Termitaria (Open termitaria, Mixed shrub termitaria, *Acacias*, Woodland) and 3.) *Vetiveria* belt. Total encroached and open areas for each zone were extracted from (Table 1). Biomass as well as N mass provided under open (0-30% cover) and encroached (31-100% cover) was extracted from Fig 2 and Fig 3, respectively by dividing the gradients into two sections. Results from the *D. cinerea* gradient (Fig 2a and Fig 3c) were used for all calculations in the termitaria zone assuming similar effects as observed under *D. cinerea* for encroaching *Acacias*, mixed shrubs in the tree termitaria and woodland species. Results from the M. pigra gradient (Fig 2b and Fig 3d) were used to estimate losses in the floodplain zone. *Vetiveria* covered areas are listed separately due to their intermediate nature and small extent and were calculated based on *D. cinerea* estimates. Due to their small extent changes in this zone are only of minor importance. Under the assumption of homogenous effects of shrubs over the whole encroached area, the biomass and N mass provided under encroached and open conditions and resulting total amounts per vegetation zone and consequential reduction between the two years could be calculated.

Vegetation zone	Encroaching shrubs species	Grass – 1986		Grass – 2010		Grass reduction	
		Biomass (t)	N (t)	Biomass (t)	N (t)	Biomass (%)	N (%)
1.) Floodplain	*M. pigra*	9665	244	8349	205	-14	-16
2.) Termitaria	*D. cinerea* *Acacia* sp *Albizia* sp. *C. mopane*	13718	159	11322	148	-17	-7
3.) Vetiveria belt	*M. pigra* *D. cinerea*	744	7	992	10	-33	-33

The pools of N and P in the aboveground grass biomass decreased significantly along both shrub gradients (Fig. 3 c,d,g,h), indicating that increases in herbage quality under *D. cinerea* shrubs did not compensate for lower biomass.

From a “back of the envelope” calculation, we estimate that encroachment of the termitaria zone by *D. cinerea*, *Acacia* sp. and other mixed shrubs reduced grass biomass by 17% and total N by 7% between 1986 and 2010. Encroachment by *M. pigra* reduced the grass biomass on the floodplain by 14% and N total available in that biomass by 16% (Table 3). However, this calculation probably underestimates the effect of *M. pigra*, because the spiny shrubs form a barrier that may prevent animals from utilizing understory biomass. In this respect, areas encroached by *D. cinerea* are different, because herbivores graze freely underneath shrubs, where they obtain grass of relatively high quality.

Although the reduction of biomass and N-mass through shrub encroachment, is large enough to have a substantial impact on populations of grazing herbivores, it cannot explain the 50% decline in the population of the lechwe antelope since the early 1970s (Chansa and Kampamba 2009). Much of the observed decline in the lechwe population occurred before 1986 (the earliest stage in our satellite image analysis), though encroachment might be partially responsible for the 25% decrease that occurred between late the 1980s (54293 lechwe, mean of years 1987, 1988, 1989) and early the 2000s (40855 lechwe, mean of years 2001, 2002, 2005; data from Chansa and Kampamba 2009).

The spread of *D. cinerea* may benefit selectively feeding small antelopes such as oribi and common duiker that rely on high quality herbage (Olff et al. 2002), as well as browsers and mixed feeders such as kudu and impala that can utilize the additional browse (Gordon and Prins 2008). Indeed, local wildlife officers reported an increase in impala and kudu, and we frequently spotted these species in areas encroached by *D. cinerea,* where they were rarely seen in the early 1980s (pers. comment G.A. Ellenbroek and G.W. Howard). Hence, woody encroachment not only changes the structure of the vegetation but, by altering the quality and quantity of forage, also influences the abundance of different herbivore guilds.

Effects on vegetation composition

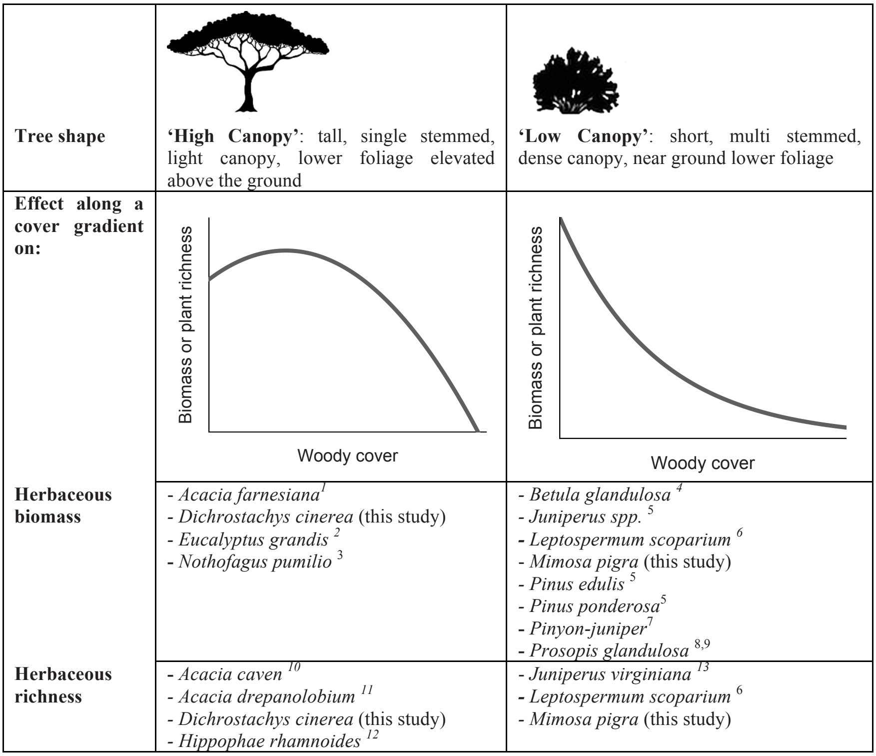
As in other studies of woody plant encroachment (e.g. Briggs et al. 2002, Lett and Knapp 2005, Baez and Collins 2008, Knapp et al. 2008, Price and Morgan 2008, Ratajczak et al. 2012), the increases in cover of both *D. cinerea* and *M. pigra* had a generally negative effect on the species richness and cover of grasses (Fig. 4a,b,c,d). However, the patterns with increasing cover were different for the two species. For *M. pigra* we found a linear decrease, while for *D. cinerea* species richness and abundance followed a unimodal relationship and only decreased at shrub cover above 40%. Unimodal relationships of species richness with increasing shrub cover have also been reported along cover gradients of other woody species (e.g. Rejmanek and Rosen 1992, Anthelme et al. 2001, Pykala et al. 2005, Ovalle et al. 2006, Isermann et al. 2007) and attributed to higher structural and environmental heterogeneity at moderate shrub densities. This may allow shade tolerant and intolerant species to coexist in a small area, leading to a general increase in species richness. As shrub encroachment progresses, however, open patches become smaller and disappear (cf. Martens et al.

2000, Breshears 2006, Breshears and Ludwig 2010) so that species dependent upon open conditions are lost.

The differences in the patterns of species richness and cover along the two gradients were probably due mainly to the differing growth forms of the two shrubs. A recent meta-analysis on effects of shrub encroachment on understory vegetation productivity by Blaser et al (Chapter 3) showed that the growth form of woody plants (i.e. the height of the lower canopy) and/ or their ability to fix nitrogen determines whether beneficial effects on biomass can occur. They argue that whereas shrubs with a lower canopy suppress the herb layer, species with elevated canopies may provide a beneficial microhabitat for the understory. Because plants differ in their light requirements (e.g. for light variables cf. Martens et al. 2000, Breshears 2006, Breshears and Ludwig 2010), however, shading is likely to alter the species composition.

The analysis of Blaser et al (Chapter 3) did not consider the effects of increasing encroachment upon the understory. However, a review of literature reveals that tall, single-stemmed species with open canopies and elevated foliage (‘High Canopy’ species e.g. *D. cinerea*) tend to contribute positively to herbage productivity and richness until a moderately high cover is reached (i.e. a unimodal relationship, Fig. 6). In contrast, short, multi-stemmed trees or shrubs with dense canopies and foliage close to the ground (‘Low Canopy’ species, e.g. *M. pigra*) generally show negative linear or inverse effects along the entire cover continuum, negatively affecting herbage production and richness even at low densities. For both types the probability that encroaching woody species reduce rather than enhance understory productivity and richness increases with increasing woody cover and will ultimately lead to negative effects at high density regardless of the growth form of the encroaching species.

In our study, the species most affected under both shrub species were C_4 grasses (e.g. *Sporobolus ioclados, Digitaria milanjiana*), which have high light requirements and are shade intolerant (Figs 4 g,h; cf. Sage and McKown 2006, Ratnam et al. 2011). Their almost complete disappearance under dense cover of both shrubs underlines that encroachment has major consequences for community composition, transforming open savanna to woodland with *D. cinerea* and open floodplain to dense thickets of *M. pigra* (cf. Parr et al. 2012).



Tree shape	**'High Canopy'**: tall, single stemmed, light canopy, lower foliage elevated above the ground	**'Low Canopy'**: short, multi stemmed, dense canopy, near ground lower foliage
Effect along a cover gradient on:		
Herbaceous biomass	- *Acacia farnesiana*[1] - *Dichrostachys cinerea* (this study) - *Eucalyptus grandis* [2] - *Nothofagus pumilio* [3]	- *Betula glandulosa* [4] - *Juniperus spp.* [5] - *Leptospermum scoparium* [6] - *Mimosa pigra* (this study) - *Pinus edulis* [5] - *Pinus ponderosa*[5] - *Pinyon-juniper*[7] - *Prosopis glandulosa* [8,9]
Herbaceous richness	- *Acacia caven* [10] - *Acacia drepanolobium* [11] - *Dichrostachys cinerea* (this study) - *Hippophae rhamnoides* [12]	- *Juniperus virginiana* [13] - *Leptospermum scoparium* [6] - *Mimosa pigra* (this study)

[1] Scifres et al. (1982), [2] Cameron et al. (1989), [3] Sanchez-Jardon et al. (2010), [4] Bork and Burkinshaw (2009), [5] Jameson (1967), [6] Price & Morgan (2008), [7] Pieper (1990), [8] Teague et al. (2008) [9] Mohamed et al. (2011), [10] Ovalle et al. (2006),[11] Riginos & Grace (2008), [12] Isermann (2007), [13] Briggs et al. (2002).

Figure 6 – Predicted effects of woody species (trees and shrubs) with contrasting canopy architecture (i.e. the height of the lower canopy) on understory herbaceous biomass or plant richness in grassland ecosystems as a function of canopy coverage. Unimodal relationships for herbaceous biomass and richness under tall single stemmed trees, negative linear or inverse relationships under short multi-stemmed trees. For each "encroachment type" we present examples from the literature where the predicted patterns have been observed.

General implications

Our study clearly shows that shrub encroachment has large effects on herbaceous productivity and richness of the floodplain ecosystem by altering the grass to tree dominance. Changes in woody cover induced by hydrology, or in combination with other factors, not only affect vegetation but - by reducing the herbaceous biomass produced and changing its species composition - also reduce the food supply for herbivores. However, the two woody species we studied differ in their effects on richness and productivity along gradients of increasing density. The canopy architecture of the encroaching shrubs seems to be a main determinant of the possibility of beneficial effects at low shrub cover, but all shrubs lead to negative effects on productivity and richness at high density.

Acknowledgements

We thank Benjamin Wishikoti, Osten Mwiimbwe, Michael Sinjote, Chris Nchimunya, Rodger and Event Ngandu, Kenrod Chipeka, George Mbulo, Cliff Mwiinga, Eddy Zeko and Aud Halbritter for invaluable assistance during fieldwork. We acknowledge Mike Bingham, who assisted with plant identification and Britta Jahn-Humphrey and Marilyn Gaschen, who supported laboratory analyses. We further extend our gratitude to the Zambia Wildlife Authority (ZAWA) for enabling us to undertake this project in Lochinvar National Park and supporting us with field-guides, housing and office space. Funding for this study was provided the Competence Center for Environment and Sustainability (CCES) at the ETH domain.

References

Anthelme, F., J. L. Grossi, J. J. Brun, and L. Didier. 2001. Consequences of green alder expansion on vegetation changes and arthropod communities removal in the northern French Alps. Forest Ecology and Management **145**:57-65.

Archer, D. R. 1971. Relief, drainage and geology.*in* D. H. Davies, editor. Zambia in Maps. University Press, London.

Archer, S., T. W. Boutton, and K. A. Hibbard. 2001. Trees in Grasslands: Biogeochemical Consequences of Woody Plant Expansion. Pages 115-137 *in* E. D. Schulze, M. Heimann, S. Harrison, E. Holland, J. Lloyd, I. Prentice, and D. Schimel, editors. Global Biogeochemical Cycles in the Climate System. Academic Press, San Diego.

Archer, S., D. S. Schimel, and E. A. Holland. 1995. Mechanism of shrubland expansion: land use, climate or CO_2? Climatic Change **29**:91-99.

Baez, S. and S. L. Collins. 2008. Shrub Invasion Decreases Diversity and Alters Community Stability in Northern Chihuahuan Desert Plant Communities. Plos One **3**.

Belsky, A. J. 1992. Effects of trees on nutritional quality of understorey gramineous forage in tropical savannas. Tropical Grasslands **26**:12-20.

Belsky, A. J. 1994. Influences of Trees on Savanna Productivity: Tests of Shade, Nutrients, and Tree-Grass Competition. Ecology **75**:922-932.

Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. Journal of Applied Ecology **30**:143-155.

Blank, L. and Y. Carmel. 2012. Woody vegetation patch types affect herbaceous species richness and composition in a Mediterranean ecosystem. Community Ecology **13**:72-81.

Bond, W. J., G. F. Midgley, and F. I. Woodward. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. Global Change Biology **9**:973-982.

Bork, E. W. and A. M. Burkinshaw. 2009. Cool-Season Floodplain Meadow Responses to Shrub Encroachment in Alberta. Rangeland Ecology & Management **62**:44-52.

Breshears, D. D. 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? Frontiers in Ecology and the Environment **4**:96-104.

Breshears, D. D. and J. A. Ludwig. 2010. Near-ground solar radiation along the grassland–forest continuum: Tall-tree canopy architecture imposes only muted trends and heterogeneity. Austral Ecology **35**:31-40.

Briggs, J. M., G. A. Hoch, and L. C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to Juniperus virginiana forest. Ecosystems **5**:578-586.

Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: > 50 years of data suggests CO_2 as a driver. Global Change Biology **18**:675-684.

Cameron, D. M., S. J. Rance, R. M. Jones, D. A. Charlesedwards, and A. Barnes. 1989. Project STAG - an experimental-study in agroforestry. Australian Journal of Agricultural Research **40**:699-714.

Chabwela, H. N. W. and W. Mumba. 1998. Case Study: Zambia.Integrating Water Conservation and Population. Strategies on the Kafue Flats

Chansa, W. and G. Kampamba. 2009. The population status of the Kafue Lechwe in the Kafue Flats, Zambia. African Journal of Ecology:no-no.

Dolores Bejarano, M., C. Nilsson, M. GonzÁLez Del TÁNago, and M. Marchamalo. 2011. Responses of riparian trees and shrubs to flow regulation along a boreal stream in northern Sweden. Freshwater Biology **56**:853-866.

Douthwaite, R. J. and L. P. Van Lavieren. 1977. A Description of the vegetation of Lochinvar National Park, Zambia. Technical Report 34, . National Council for Scientific Research, Lusaka, Zambia.

Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters **14**:709-722.

Ellenbroek, G. A. 1987. Ecology and productivity of an African wetland system: The Kafue Flats, Zambia. PhD Thesis. Junk Publisher.

Engle, D. M., J. F. Stritzke, and P. L. Claypool. 1987. Herbage standing crop around eastern redcedar trees. Journal of Range Management **40**:237-239.

Genet, B. S. 2007. Shrub encroachment into grassland and its impact on Kafue Lechwe in Lochinvar National Park, Zambia. International Institute for Geo-information Science and Earth Observation, Enschede, The Netherlands.

Hagenah, N., H. Munkert, K. Gerhardt, and H. Olff. 2009. Interacting effects of grass height and herbivores on the establishment of an encroaching savanna shrub. Plant Ecology **201**:553-566.

Handlos, D. M., W. L. Handlos, and G. W. Howard. 1976. A Study of the Diet of the Kafue Lechwe (Kobus Lechwe) by Analysis of Rumen Contents. Pages 197-211 Proceedings of the Fourth Regional Wildlife Conference for Eastern and Central Africa. National Parks & Wildlife Service, Chichele Lodge, Zambia.

Heisler, J. L., J. M. Briggs, and A. K. Knapp. 2003. Long-term patterns of shrub expansion in a C-4-dominated grassland: Fire frequency and the dynamics of shrub cover and abundance. American Journal of Botany **90**:423-428.

Howard, K. S. C., D. J. Eldridge, and S. Soliveres. 2012. Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. Basic and Applied Ecology **13**:159-168.

Isermann, M., M. Diekmann, and S. Heemann. 2007. Effects of the expansion by Hippophae rhamnoides on plant species richness in coastal dunes. Applied Vegetation Science **10**:33-42.

Jameson, D. A. 1967. Relationship of tree overstory and herbaceous understory vegetation. Journal of Range Management **20**:247-&.

Kesting, S., N. Wrage, and J. Isselstein. 2009. Herbage mass and nutritive value of herbage of extensively managed temperate grasslands along a gradient of shrub encroachment. Grass and Forage Science **64**:246-254.

Knapp, A. K., J. M. Briggs, S. L. Collins, S. R. Archer, M. S. Bret-Harte, B. E. Ewers, D. P. Peters, D. R. Young, G. R. Shaver, E. Pendall, and M. B. Cleary. 2008. Shrub encroachment in North American grasslands: shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. Global Change Biology **14**:615-623.

Laliberte, A. S., A. Rango, K. M. Havstad, J. F. Paris, R. F. Beck, R. McNeely, and A. L. Gonzalez. 2004. Object-oriented image analysis for mapping shrub encroachment from 1937 to 2003 in southern New Mexico. Remote Sensing of Environment **93**:198-210.

Lett, M. S. and A. K. Knapp. 2005. Woody plant encroachment and removal in mesic grassland: Production and composition responses of herbaceous vegetation. American Midland Naturalist **153**:217-231.

Ludwig, F., H. de Kroon, F. Berendse, and H. H. T. Prins. 2004. The influence of savanna trees on nutrient, water and light availability and the understorey vegetation. Plant Ecology **170**:93-105.

Ludwig, F., H. De Kroon, and H. H. T. Prins. 2008. Impacts of savanna trees on forage quality for a large African herbivore. Oecologia **155**:487-496.

Martens, S. N., D. D. Breshears, and C. W. Meyer. 2000. Spatial distributions of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecological Modelling **126**:79-93.

McNaughton, S. J. 1979. Grazing as an optimization process - grass ungulate relationships in the Serengeti. American Naturalist **113**:691-703.

McNaughton, S. J., D. G. Milchunas, and D. A. Frank. 1996. How can net primary productivity be measured in grazing ecosystems? Ecology **77**:974-977.

Mohamed, A. H., J. L. Holechek, D. W. Bailey, C. L. Campbell, and M. N. DeMers. 2011. Mesquite encroachment impact on southern New Mexico rangelands: remote sensing and geographic information systems approach. Journal of Applied Remote Sensing **5**.

Mumba, M. and J. R. Thompson. 2005. Hydrological and Ecological Impacts of Dams on the Kafue Flats Floodplain System, Southern Zambia. Physics and Chemistry of the Earth **30**:442-447.

Munyati, C., P. Shaker, and M. G. Phasha. 2011. Using remotely sensed imagery to monitor savanna rangeland deterioration through woody plant proliferation: a case study from communal and biodiversity conservation rangeland sites in Mokopane, South Africa. Environmental Monitoring and Assessment **176**:293-311.

O'Connor, T. G. 2001. Effect of small catchment dams on downstream vegetation of a seasonal river in semi-arid African savanna. Journal of Applied Ecology **38**:1314-1325.

Olff, H., M. E. Ritchie, and H. H. T. Prins. 2002. Global environmental controls of diversity in large herbivores. Nature **415**:901-904.

Ovalle, C., A. Del Pozo, M. A. Casado, B. Acosta, and J. M. de Miguel. 2006. Consequences of landscape heterogeneity on grassland diversity and productivity in the espinal agroforestry system of central Chile. Landscape Ecology **21**:585-594.

Owen-Smith, N. 2008. The comparative population dynamics of browsing and grazing ungulates. Pages 149-177 *in* I. J. Gordon and H. H. T. Prins, editors. The ecology of browsing and grazing. Springer Berlin Heidelberg.

Parr, C. L., E. F. Gray, and W. J. Bond. 2012. Cascading biodiversity and functional consequences of a global change-induced biome switch. Diversity and Distributions **18**:493-503.

Pieper, R. D. 1990. Overstory-understory relations in pinyon-juniper woodlands in New-Mexico. Journal of Range Management **43**:413-415.

Price, J. N. and J. W. Morgan. 2008. Woody plant encroachment reduces species richness of herb-rich woodlands in southern Australia. Austral Ecology **33**:278-289.

Pykala, J., M. Luoto, R. K. Heikkinen, and T. Kontula. 2005. Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. Basic and Applied Ecology **6**:25-33.

Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology **93**:697-703.

Ratnam, J., W. J. Bond, R. J. Fensham, W. A. Hoffmann, S. Archibald, C. E. R. Lehmann, M. T. Anderson, S. I. Higgins, and M. Sankaran. 2011. When is a 'forest' a savanna, and why does it matter? Global Ecology and Biogeography **20**:653-660.

Rejmanek, M. and E. Rosen. 1992. Influence of colonizing shrubs on species-area relationships in alvar plant-communities. Journal of Vegetation Science **3**:625-630.

Richter, C. G. F., H. A. Snyman, and G. N. Smit. 2001. The influence of tree density on the grass layer of three semi-arid savanna types of southern Africa. African Journal of Range and Forage Science **18**:103-109.

Riginos, C. and J. B. Grace. 2008. Savanna tree density, herbivores, and the herbaceous community: Bottom-up vs. top-down effects. Ecology **89**:2228-2238.

Riginos, C., J. B. Grace, D. J. Augustine, and T. P. Young. 2009. Local versus landscape-scale effects of savanna trees on grasses. Journal of Ecology **97**:1337-1345.

Robinson, T. P., R. D. van Klinken, and G. Metternicht. 2008. Spatial and temporal rates and patterns of mesquite (Prosopis species) invasion in Western Australia. Journal of Arid Environments **72**:175-188.

Roques, K. G., T. G. O'Connor, and A. R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology **38**:268-280.

Sage, R. F. and A. D. McKown. 2006. Is C(4) photosynthesis less phenotypically plastic than C(3) photosynthesis? Journal of Experimental Botany **57**:303-317.

Sanchez-Jardon, L., B. Acosta, A. del Pozo, M. A. Casado, C. Ovalle, H. F. Elizalde, C. Hepp, and J. M. de Miguel. 2010. Grassland productivity and diversity on a tree cover gradient in Nothofagus pumilio in NW Patagonia. Agriculture Ecosystems & Environment **137**:213-218.

Scholes, R. J. and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual Review of Ecology and Systematics **28**:517-544.

Schulze, E. D., G. Gebauer, H. Ziegler, and O. L. Lange. 1991. Estimates of nitrogen-fixation by trees on an aridity gradient in Namibia. Oecologia **88**:451-455.

Scifres, C. J., J. L. Mutz, R. E. Whitson, and D. L. Drawe. 1982. Interrelationships of huisache canopy cover with range forage on the coastal prairie. Journal of Range Management **35**:558-561.

Teague, W. R., R. J. Ansley, W. E. Pinchak, S. L. Dowhower, S. A. Gerrard, and J. A. Waggoner. 2008. Interannual herbaceous biomass response to increasing honey mesquite cover on two soils. Rangeland Ecology & Management **61**:496-508.

Treydte, A. C., I. M. A. Heitkonig, H. H. T. Prins, and F. Ludwig. 2007. Trees improve grass quality for herbivores in African savannas. Perspectives in Plant Ecology Evolution and Systematics **8**:197-205.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics **31**:197-215.

Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management **90**:2931-2942.

Vetaas, O. R. 1992. Micro-site effects of trees and shrubs in dry savannas. Journal of Vegetation Science **3**:337-344.

Supporting information

Table S1 Likelihood of change according to ecological assumptions

Table S2 Accuracy assessment of the remote sensed maps.

Table S3 Vegetation composition along a shrub cover gradient of *Dichrostachys cinerea.*

Table S4 Vegetation composition along a shrub cover gradient of *Mimosa pigra*.

Table S1 – List of classes above 10ha that were reclassified in the 1994.95 image based on ecological assumptions of likelihood of changes. The Corrected class 1994-95 column indicated the finall classification for observed unlikely changes.

Area (ha)	**Classified class 1994-95**	**Classified class 2008-10**	**Likeliness of class change**	**Corrected class 1994-95**
19	Mimosa	Tree Termitaria	unlikely	Tree Termitaria
15	Mimosa	Woodland	unlikely	Woodland
451	Mimosa	FP grass	very unlikely	FP Grass
38	Mimosa	Open Termitaria	very unlikely	Open Termitaria
45	Dichrostachys	Open Termitaria	very unlikely	Open Termitaria
11	Acacia	Mimosa	unlikely	Mimosa
35	Acacia	FP grass	very unlikely	FP Grass
504	Acacia	Open Termitaria	very unlikely	Open Termitaria
33	Acacia	Vetiveria Belt	unlikely	Vetiveria Belt
45	Tree Termitaria	Mimosa	unlikely	Mimosa
160	Tree Termitaria	FP grass	very unlikely	FP Grass
1093	Tree Termitaria	Open Termitaria	very unlikely	Open Termitaria
235	Tree Termitaria	Vetiveria Belt	unlikely	Vetiveria Belt
31	Woodland	Mimosa	unlikely	Mimosa
30	Woodland	Dichrostachys	very unlikely	Dichrostachys
185	Woodland	Acacia	very unlikely	Acacia
656	Woodland	Tree Termitaria	unlikely	Tree Termitaria
181	Woodland	FP grass	very unlikely	FP Grass
567	Woodland	Open Termitaria	very unlikely	Open Termitaria
30	Woodland	Vetiveria Belt	unlikely	Vetiveria Belt
393	Open Termitaria	FP grass	very unlikely	FP Grass
55	Vetiveria Belt	FP grass	very unlikely	FP Grass

Table S2 – Overview of accuracy statistics for the 3 classified images from the periods 1986, 1994-1995 and 2008-2010. Statistics were calculated using confusion matrices of classified data and reference data.

	Cover (%)			**Users accuracy (%)**		
	1986	***1994-1995***	***2008-2010***	***1986***	***1994-1995***	***2008-2010***
Mimosa	-	0.9	3.8	-	39.3	76.7
Dichrostachys	-	2.9	4.2	-	54.0	69.9
FP Grass	24.7	25.4	19.6	92.6	83.7	82.1
Vetiveria belt	1.9	3.7	2.6	31.0	24.0	46.2
Open Termitaria	23.8	17.4	10.8	71.9	78.1	74.7
Tree Termitaria	7.8	11.1	13.0	27.8	25.0	45.3
Acacia	7.4	4.2	5.2	16.7	38.9	36.4
Woodland	11.1	10.8	19.1	63.6	66.7	52.2
Bare/ Swamp	8.3	4.8	3.0	15.8	60.0	55.2
Water	15.1	18.8	18.8	100.0	100.0	98.2

	Producers accuracy (%)			**Area weighted producers acc. (%)**		
	1986	***1994-1995***	***2008-2010***	***1986***	***1994-1995***	***2008-2010***
Mimosa	-	100.0	65.9	-	100.0	31.88
Dichrostachys	-	95.9	93.8	-	82.7	91.18
FP Grass	75.4	83.7	75.2	75.4	94.7	93.70
Vetiveria belt	26.7	66.7	66.7	26.7	31.9	29.85
Open Termitaria	78.9	41.4	48.7	78.9	52.7	54.98
Tree Termitaria	71.3	53.1	44.4	71.3	51.7	46.44
Acacia	56.0	46.7	31.3	56.0	20.3	16.45
Woodland	80.6	60.9	77.8	80.6	60.4	91.38
Bare/ Swamp	66.8	42.9	66.7	66.8	13.7	38.15
Water	67.1	89.9	91.5	67.1	92.6	98.02

	Kappa		
	1986	***1994-1995***	***2008-2010***
Mimosa	-	0.38	0.74
Dichrostachys	-	0.51	0.64
FP Grass	0.87	0.75	0.78
Vetiveria belt	0.29	0.23	0.45
Open Termitaria	0.57	0.70	0.71
Tree Termitaria	0.25	0.22	0.41
Acacia	0.15	0.38	0.31
Woodland	0.63	0.66	0.49
Bare/ Swamp	0.14	0.59	0.54
Water	1.00	1.00	0.98

	Overall map statistics		
	1986	***1994-1995***	***2008-2010***
Accuracy (%)	62.2	70.5	70.0
Area weighted acc. (%)	75.2	80.0	75.1
Kappa	0.50	0.63	0.66

Table S3 – Vegetation composition along a shrub cover gradient of *Dichrostachys cinerea.* Numbers in table represent the percentage cover of each species in a 100m^2 plot.

		Open to moderately dense														Moederately dense									Moderate to very dense									Very dense			
	Canopy cover (%	0	0	0	0	0	5	10	15	15	18	20	25	25	25	30	30	30	40	40	40	40	50	50	60	60	60	65	70	70	75	75	75	80	85	85	95
Species name	**Functional group**																																				
Blepharis caloneura	Forb	2				1	5	6		4		1		3	20			5				1		2				1	2		2			<1	<1	<1	<1
Panicum novemnerve	Grass	4	60	10	<1		2	2	5	1	15	2	15	1	4	30	25	3	25	4	15	4	5	2	1	15		2	5	1	<1		15		4	4	<1
Tephrosia villosa	Forb				<1		<1	<1		<1		<1		<1	<1			3	<1		<1	<1		3				1		<1	<1				<1		<1
Sida alba	Forb				<1											<1	<1				<1				<1			<1		1	1	<1		<1		<1	<1
Commelina subulata	Forb								<1		<1				<1	2	2	<1	<1	<1		<1		<1			<1										<1
Vernonia cinerea	Forb	4													5													<1		2	1			2		<1	<1
Sporobolus ioclados	Grass	30				20	20	1	8	15		20		30				25	3	45		5	20	4	3	<1	60	8	8	25	4			<1	10	8	
Brachiaria xantholeuca	Grass						3				<1	<1				<1		<1	1	<1		<1		1	1		1	<1	1	<1		1			2		
Echinocloa colona	Grass		<1	1	4	1	4		<1		3		1			5	4			2					15		1	1			1	10		<1	1		
Chloris virgata	Grass	2												1			<1	<1			2		2			<1				3	2		<1		4		
Eragrostis viscosa	Grass	2					2	2		<1		<1		3	1			2				2	4					2		8					4		
Hibiscus canabinus	Forb												1		2			2				<1													2		
Cassia mimosoides	Forb									<1		<1			<1							<1		<1				<1	<1						<1		
Hygrophila auriculata	Forb	3		5	3		3			8		3		5	10	20	25	20	3	3	10		5	3	5		3	5	8	3	3	5		<1			
Vernonia petersii	Forb						1	20		<1		2						<1			<1	5	20		<1			2		1		<1		1			
Justicia betonica	Forb			<1																		1		<1						<1	2			1			
Hibiscus sp.	Forb				<1												<1						<1		<1							<1		1			
Indigofera fanshaweii	Forb	<1				<1				<1				<1						1														<1			
Epaltes alata	Forb		1	1	1	<1	15	4	1	2	2	4	3	4		4	2		1	2	45	15	2	10	1	2	<1	20	15			1	3				
Dactyloctenium aegyptium	Grass					1															<1						<1			<1	<1		<1				
Heliotropium ovalifolium	Forb			<1	<1											<1	<1				<1			<1									<1				
Tephrosia pumila	Forb		<1																														<1				
Eragrostis gangetica	Grass															<1	4																1				
Dichanthium insculptum	Grass	15		5	3	3	5		15	25	10	5		15	1			8	20	3	2	<1		20	2		4	20	8	1	20	2					
Sporobolus pyramidalis	Grass				10					1							2				1				15			1				5					
Eragrostis heteromera	Grass	1		5	8		1	1	4	5	3	8	5		15	<1	5				2	20		4	2				1			8					
Digitaria eriantha	Grass			1	4		1				3		25	1	4				5			3						2			1	2					
Vetiveria nigritana	Grass				20																				4							1					
Crotalaria kapirensis	Forb					1	<1					<1			2					<1		<1		<1	<1			<1		<1	<1	<1					
Setaria pumila	Grass				2						15		<1		2	3	5							1	1		2					4					
Vigna longifolia	Forb										<1		<1		<1										<1	10						<1					
Digitaria milanjiana	Grass				5			20	5									5	3	1					3		2		1			2					
Desmodium sp.	Forb						<1		<1																							<1					
Gomphrena celosioides	Forb	<1													<1																1						
Chloris pycnothrix	Grass	1					1			<1	<1			<1	4			1			10		1	5					2		1						
Eragrostis inamoena	Grass	<1					4	<1		1					<1	8	2						3	<1				5	5	<1							
Porphyrostemma clevalieri	Forb													1										<1						<1							
Eriospermum abyssinicum	Forb						<1	<1	<1		1	<1	<1	<1	<1				<1	<1			<1	<1				<1		<1							
Oldenlandia herbacea	Forb						<1	<1				<1		<1									<1				<1	<1	<1								
Chloris gayana	Grass													4						4			1						2								
Cyperaceae sp. A	Forb		3				<1		<1	<1				<1		<1	<1		<1	<1								<1									
Stylosanthes fruticosa	Forb	<1					<1	2	<1			<1		<1	<1				<1	<1			<1	<1			<1	1									
Alloteropsis cimicina	Grass										<1	<1	<1		1	<1	<1				<1	<1		<1		4		4									
Panicum coloratum	Grass					3																					5	<1									
Sesbania microphyla	Forb		<1	<1	<1				<1				<1				<1		<1	<1					<1		<1										
Kylinga sp.	Grass																			1							<1										
Digitaria ternata	Grass		1																							<1											
Corchorus schimperi	Forb						<1		<1											<1					<1	<1											
Aspilia kotschyi	Forb		15	10		3			8		15		30		<1	<1	<1		5					<1		5											
Brachiaria rugulosa	Grass				1											10	3									<1											
Digitaria scalarum	Grass		2																						<1												
Cyperaceae sp. B	Forb	<1													2						1			<1													
Cynodon dactylon	Grass						2	5							1		1					1		5													
Dichandria sp.	Grass						4					1									2			2													
Spermacoce sp.	Forb	<1																			2			2													
Eragrostis sp. C	Grass														4									2													
Zornia glochidiata	Forb							<1	<1										<1	<1																	
Ipomea aquatica	Forb													<1		<1	<1			<1																	
Cyperus rotundus	Forb			<1		<1			1		2		1						<1	<1																	
Emilia protracta	Forb																			<1																	
Eragrostis macilenta	Grass	1	<1				4																														
Fimbristylis sp.	Forb					<1																															
Acanthosp.ermum hispidum	Forb																				<1									<1							
Aristida sp.	Grass																							2									2				
Echinocloa sp. B	Grass																	<1			4																<1
Achyranthes asp.era	Forb																						<1											1	2	1	2
Dicliptera verticillata	Forb															1	3						5					2	25	4	2			15	16	4	75
Leucas martinicensis	Forb																														4					3	
Bidens pilosa	Forb																											1						<1	<1		
Kalanchoe lanceolata	Forb																													<1	<1			<1			
Triumfetta sp.	Forb																									1							1				
Cyathula prostrata	Forb																																			<1	1
Monechma debile	Forb																																	<1	1		
Chlorophytum polystachyun	Forb																																				
Commelina carsonii	Forb		<1																																		
Vernonia glabra	Forb		<1																																		
Oryza longistaminata	Grass																																				
Brachiaria humidicola	Grass																																				
Crotalaria sp.	Forb																																				
Alectra orobanchoides	Forb						<1																														
Eragrostis bicolor	Grass										2																										
Eragrostis sp. E	Grass											1																									
Indigofera spicata	Forb												<1																								
Herb sp. B	Forb													<1																							
Hibiscus trionum	Forb															<1																					
Vernonia paskaena	Forb															<1																					
Plectranthus flaccidus	Forb																<1																				
Phyllanthus maderasp.aten	Forb																	<1																			
Panicum repens	Grass																				5																
Calostestophana divaricata	Forb																				<1																
Evolvulus alsinoide	Forb																					3															
Spermatococe senensis	Forb																					<1															
Herb sp. E	Forb																							1													
Crotalaria natalitia	Forb																								<1												
Indigofera suffruticosa	Forb																													<1							
Herb sp. I	Forb																													<1							
Herb sp. J	Forb																													<1							
Indigofera schimperi	Forb																														1						
Disperma quadrangulare	Forb																																	<1			
Herb sp. C	Forb																																	<1			
Herb sp. D	Forb																																		1		
Commelina africana	Forb																																			<1	
Herb sp. A	Forb																																			1	
Herb sp. F	Forb																																			<1	
Herb sp. G	Forb																																			1	
Plectranthus tetragonus	Forb																																			<1	
Sphaeranthus angolensis	Forb																																			<1	
Sphaeranthus humilis	Forb																																			1	

Table S4 – Vegetation composition along a shrub cover gradient of *Mimosa pigra*. Numbers in table represent the percentage cover of each species in a $100m^2$ plot.

		Open to moderate								**Moderately dense**						**Moderately to very**						**Very dense**		
	Canopy Cover (%)	**0**	**0**	**0**	**5**	**10**	**15**	**20**	**25**	**40**	**40**	**45**	**45**	**50**	**55**	**60**	**60**	**60**	**65**	**70**	**75**	**80**	**98**	**100**
Species Name	**Functional Group**																							
Utricularia stellaris	Forb		<1		<1	<1				2	<1	<1		<1		<1							<1	<1
Paspalidium obtusifolium	Grass		70		<1	80				20	10	<1	<1	2		15	60				2	1	4	
Nymphaea caerulea	Forb				<1	5	1	1		5	15	3	6	3		6	4	1		1	4	<1	2	
Ipomea aquatica	Forb			<1	<1	1	<1			1	<1	2		<1		1	<1	<1		2	<1	<1	1	
Oryza longistaminata	Grass					1		98		5						4		45	4O	15	10	16		
Leersia hexandra	Grass	85	<1						60													2		
Ludwigia sp	Forb		<1		4								<1					4		8		<1		
Aeschynomene nilotica	Forb		<1			<1				<1			<1									<1		
Hibiscus sp	Forb		<1			<1																<1		
Leersia denudata	Grass				80	1	90	1		25	25		1	70	60		10			2	25			
Nymphaea lotus	Forb		<1		5							15				4	1							
Sesbania microphylla	Forb	<1		<1					<1						<1									
Ambrosia maritima	Forb	3	<1	2					1						<1									
Aspilia kotschyi	Forb								<1						<1									
Echinochloa colona	Grass	2		1					<1						1									
Melochia corchorifolia	Forb	<1		<1											<1									
Eleocharis dulcis	Grass				1	2	2			3	1	<1	<1											
Sporobolus pyramidalis	Grass								<1				<1											
Echinochloa scabra	Grass		<1			2						1												
Vernonia sp	Forb	<1										<1												
Cyperus longus	Grass	<1	3	<1					1			<1												
Paspalum scrobiculatum	Grass	<1							1			<1												
Nymphoides indica	Forb					2				30														
Herb 2 (floating hydrophyte)	Forb									<1	1					1								
Alternanthera sessilis	Forb											<1											<1	
Vossia Cuspidata	Grass																		1			4		
Cassia mimosoides	Forb	2		<1					<1															
Emilia protracta	Forb	<1							<1															
Fimbristylis sp	Grass	<1							<1															
Heliotropium ovalifolium	Forb	<1		<1																				
Setaria pumila	Grass	<1		<1																				
Sida alba	Forb	1							<1															
Vigna longifolia	Forb	<1																						
Panicum novermnerve	Grass	<1																						
Digitaria scalarum	Grass	<1																						
Eragrostis sp	Grass	<1																						
Hibiscus trionum	Forb	<1																						
Centrostachys aquatica	Forb		<1																					
Crotalaria sp	Forb			<1																				
Marsilea sp	Forb						<1																	
Cynodon dactylon	Grass								15															
Acroceras macrum	Grass											<1												
Cyperus rotundus	Grass														1									
Euphorbiaceae	Forb														<1									
Ethulia sp	Forb														<1									
Herb 1	Forb																	1						
Sacciolepis africana	Grass																	1						
Echinochloa pyramidalis	Grass																						<1	

Chapter 5

The semi-aquatic antelope Kafue lechwe shows a remarkable, but effective, food adaptation upon changed flooding conditions and shrub encroachment

Wilma J. Blaser, Griffin K. Shanungu, Franziska Peter, Peter J. Edwards and Harry Olde Venterink

Abstract

Declining populations of many African herbivores have been linked to the destruction and fragmentation of habitats, increasing competition for food through cattle, and illegal hunting. However, the exact causes usually remain unclear, partly because of insufficient knowledge about the feeding ecology of herbivores and how their populations may be affected by periods of food scarcity. We studied annual spatial movement and changes in the nutritional status of the vulnerable semi-aquatic antelope, the Kafue lechwe (*Kobus leche kafuensis*), in relation to hydrology (accessibility of the floodplain area) and food supply in the Kafue Flats floodplain ecosystem. The annual migration pattern of lechwe was strongly linked to flood height and food resources in the wet season habitat (not flooded and accessible throughout the year). Faecal nitrogen levels indicated that lechwe suffer from nutritional stress at the beginning of the dry season when they are forced to remain in termitaria grasslands until the floods recede. During this period of food scarcity, lechwe – although considered a strict grazer - were found to consume seedpods of the encroaching shrub *Dichrostachys cinerea,* with positive effects on their nutritional status. We conclude that the migrating lechwe antelope is strongly dependent on both wet and dry season feeding habitats. A critical factor affecting its carrying capacity is the timing of the flood, which is strongly dependent on dam management. This affects both grass production as the waters rise and animals' access to the floodplain as the waters fall. The ability of large herbivores to adapt their diet is one reason why effects of interactions among environmental alterations on herbivore populations are so difficult to predict.

Introduction

Populations of most African herbivores are declining, with many species now classified as vulnerable or endangered (IUCN red list). For example, severe declines have been reported in numbers of tsessebe *Damaliscus lunatus lunatus*, roan *Hippotragus equinus,* wildebeest *Connochaetes taurinus*, topi *Damaliscus lunatus jimela* and Thompson's gazelle *Eudorcas thomsonii* (Dunham et al 2004, Hamington 1999, Sinclair 1979, Rodgers 1982). There are various causes for these losses, including destruction and fragmentation of habitats, increasing competition for food through cattle, and illegal hunting (Prins 1992, Ottichilo et al. 2000, Gordon 2009, Western et al. 2009). Also, environmental changes at a local, regional or global scale can all lead to an increase in the cover of woody species in African savannas or wetlands (Van Auken 2000, Bond et al. 2003, Van Auken 2009, Eldridge et al. 2011, Buitenwerf et al. 2012), which can have negative effects on grazing ungulates. In particular cases, however, it is often unclear which factor or factors are responsible for a decline in herbivore populations, making it difficult to determine the most appropriate forms of management. Part of the problem is that we know too little about the feeding ecology of many species, including their food requirements in the different seasons, the times of year when food supply becomes critical, and how these factors are affected by environmental changes (Sinclair et al. 1985, Maduma et al. 1999, Halsdorf 2011, Staeli 2012).

The Kafue lechwe*, Kobus leche* ssp. *kafuensis* Haltenorth, 1963 is an endemic subspecies restricted to the Kafue Flats, a vast floodplain ecosystem along the Kafue River in Zambia (Fig. 1). It feeds on grasses in the seasonally flooded plains and the adjoining drier grasslands with scattered termite mounts, commonly referred to as termitaria grasslands (Handlos et al. 1976, Rees 1978c, Ellenbroek 1987). The population of Kafue lechwe has declined strongly since the early 1970s (Fig. 1b). Although the reasons for the decline are not well understood, changes in floodplain hydrology following the construction of two dams on the Kafue River are probably responsible, at least in part (Fig. 1d; (Mumba and Thompson 2005, Chapter 1). When the dams became operational the area of seasonally flooded grasslands was greatly reduced (Fig 1c, d), thereby reducing an important part of the food supply for lechwe (Sayer and Van Lavieren 1975, Schuster 1976, 1977, Rees 1978a, b). For instance, after the dams were constructed about 40% of the floodplain grassland in Lochinvar

National Park remained permanently flooded (Chunga Lagoon in Fig. 1d), with water levels too deep and hydrological conditions too stable for floodplain grasses to develop and grow (Denny 1985, Sheppe 1985) and for lechwe to graze (>0.5m; Vesey-Fitzgerald 1965). Furthermore, the termitaria areas and the upper parts of the floodplain have recently become heavily encroached by leguminous shrubs such as *Mimosa pigra*, *Dichrostachys cinerea* and *Acacia* species (Fig. 1d). Shanungu et al. (unpublished, Chapter 4) estimated that shrub encroachment caused a 14% reduction in grass biomass in the floodplain and 17% in the termitaria. In the case of encroachment by *D. cinerea* the reduction in total grass biomass was partly compensated for by its higher nutritional quality, but this was not the case for *M. pigra*. Another probable reason for the decline in lechwe is poaching (Ward 2010).

Previous studies have concluded that lechwe feed exclusively upon grasses (Handlos et al. 1976, Rees 1978c, Estes 1991), obtaining most of their nutrition from the semi-aquatic grasses of the seasonally flooded areas. However, we noted that dung pellets deposited in the termitaria grassland often contained *D. cinerea* seeds (Fig 1f), suggesting that the seedpods of this encroaching shrub have become a valuable component of the diet during the period when floodplain grasses are not accessible. One way to evaluate whether this is indeed the case would be to monitor the frequency of seed pods in dung as well as seasonal changes in dietary quality by measuring N and P concentrations in lechwe dung (cf. Leslie et al. 2008). It may also be that lechwe have promoted the spread of *D. cinerea,* especially since we observed seedlings of *D. cinerea* growing out of dung. To demonstrate this, however, it would be important to know whether the lechwe disperse seeds and enhance germination of *D. cinerea*, as has been found for some other herbivore species (Vanstaden et al. 1994). Other activities of lechwe might also favor the spread of *D. cinerea*; for example, seedlings might benefit from short, open vegetation due to grazing (cf. Sankaran et al. 2005, Riginos and Young 2007), and from nutrient enrichment through dung. Generally, savanna grasses are more responsive to fertilization than woody plants, but this knowledge is primarily based on response to inorganic mineral nutrients (Hagenah et al. 2009, Ramsar 2013), and plant responses to dung of wild ungulates are less understood and could be different.

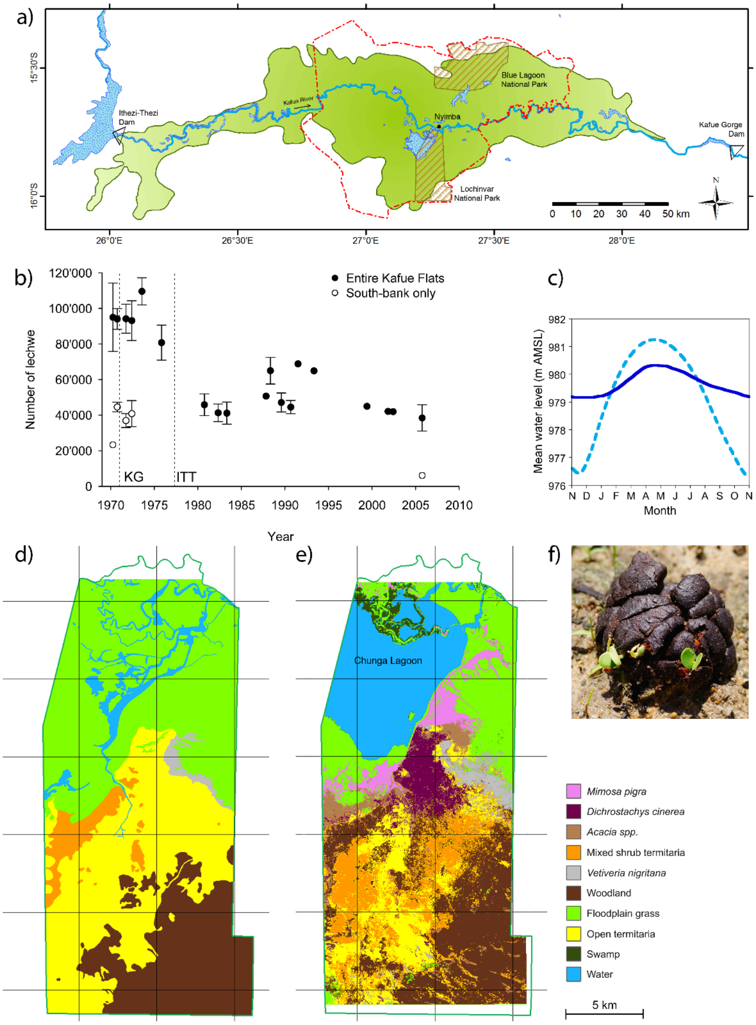


Figure 1 – (a) Map of the Kafue Flats with the location of the two dams, the game management area (red dashed line), Blue Lagoon and Lochinvar National Park (hatched areas) and the hydrological gauging station at Nyimba village (adopted from Zurbruegg 2012). (b) Kafue lechwe population (mean and SE if available) over time (1970-2005) based on a survey of historical estimates from aerial surveys (compiled by Chansa and Kampamba 2009. Closed dots indicate estimates of the whole population, open dots estimates of the south bank population only (if available). Dashed lines indicate the time of dam completion; KG: Kafue Gorge Dam, ITT: Ithezi-Thezi Dam. (c) Hydrograph at Nyimba gauging station for the pre-dam (1962-1971, dashed line) and post-dam (1977-2010, solid line) period (Chapter 1). (d) Dry season distribution of main vegetation types under pre-dam conditions (1970) drawn after a vegetation map of Douthwaite and Van Lavieren (1977). (e) Dry season distribution of main vegetation types 30 years after dam construction (2010), determined from satellite image analysis (Chapter 4). (f) *Dichrostachys cinerea* seedling growing from a lechwe dung pellet.

The overall aim of this study was to investigate whether shrub encroachment and recent changes in floodplain hydrology have been responsible for the decline in numbers of Kafue lechwe. We used four approaches. First, we described the annual spatial movement of lechwe in relation to the hydrology and food supply in Lochinvar National Park. Previous studies have shown a strong dependence of this endemic antelope on the seasonal flooding, but all of these investigations were conducted either before or soon after the construction of the dams (Vesey-Fitzgerald 1965, Sheppe and Osborne 1971, Rees 1978b, Chabwela and Ellenbroek 1990). Second, we evaluated seasonal changes in dietary quality by monitoring N and P concentrations in lechwe dung and comparing them with threshold levels for dietary deficiencies in grazing herbivores (Wrench et al. 1997). Third, we quantified the consumption of *D. cinerea* seeds, and investigated whether they enhanced the nutritional quality of the diet at certain times of year. Fourth, we made various studies to establish whether lechwe have promoted encroachment by dispersing seeds or facilitating their establishment.

Methods

Kafue Lechwe and Lochinvar National Park

Kafue Lechwe (*Kobus leche* ssp. *kafuensis* Haltenorth, 1963),is a semi-aquatic antelope subspecies, endemic to the Kafue Flats. It is a ruminant grazer, and has previously been described as feeding only on grasses (Handlos et al. 1976, Rees 1978c, IUCN 2008). It is now restricted to the Kafue Flats game management area on the North and South bank of the Kafue River, centered around Blue Lagoon National Park and Lochinvar National Park, respectively (Fig. 1a). Lechwe are able to swim across river channels and hence might migrate between the two river banks and two National Parks. However, reports by Gallagher et al. (1972) indicates that migration might be restricted, by reporting tuberculosis infection of the South bank but not the North bank population. Estimates of the total Lechwe population and that of the South bank population over time are shown in Fig. 1b.

The study presented here was conducted between March 2010 and April 2011 in Lochinvar National Park, and the adjacent game management area on the South bank of the Kafue (Fig. 1a). Lochinvar National Park is a former cattle ranch in which larger carnivores were systematically exterminated but wild herbivores were protected and are still found in large herds. The Kafue lechwe is by far the most abundant herbivore in the park. The last aerial lechwe survey estimated the 'South Bank' population at 6137 individuals (Chansa and Kampamba 2009). Other large herbivores in the park are: plain zebra (*Equus burchelli* – estimated population: 800 individuals), buffalo (*Syncerus caffer,* 200-300 ind.), wildebeest (*Connochaetus taurinus,* 31 ind.), oribi (*Ourebia ourebia,* 150 ind.). The park also contains small populations of browsers and mixed feeders, such as kudu (*Tragelaphus strepsiceros,* 50 ind), impala (*Aepyceros melampus* 100 ind), common duiker (*Sylvicapra grimmia*, no estimate) and bushbuck (*Tragelaphus scriptus*, no estimate).

The lechwe uses three main types of habitat, all closely associated with the river (Sheppe and Osborne 1971, Rees 1978b). (1) Seasonally flooded floodplain grassland is dominated by tall floodplain grasses such as *Oryza longistaminata, Vossia cuspidata, Echinochloa stagnina* and *Leersia hexandra.* This habitat can only be accessed by lechwe during the dry season. (2) Inundated watermeadow contain grasses such as *Leersia denudata, Panicum repens*, *Eleocharis dulcis*, *Acroceras macrum and Paspalidium obtusifolium*. These areas can partially be accessed at the fringes throughout the year but become fully accessible as soon as the floods start to recede. (3) Termitaria grassland, characterized by abundant termite mounds, occurs immediately above the flood line and is accessible throughout the year. The main forage species in this habitat are *Sporobolus ioclados, Digitaria milanjiana, Cynodon dactylon,* and *Sporobolus pyramidalis* but lower lying areas within this zone in Lochinvar are flooded and contain typical watermeadow grasses that provide good forage (Ellenbroek 1987).

The mean annual temperature in the Kafue Flats is 20.6°C and mean (2000-2011) annual precipitation is 753 mm which almost all falls in the wet season (November to April; Ellenbroek 1987, Mumba and Thompson 2005). Floods in the floodplains rise slowly during the rains, peak in late April to May, and fall during the later part of the dry season (Sheppe and Osborne 1971, Ellenbroek 1987). The construction of two dams on the Kafue River caused major changes in the floodplain hydrology with raised low flows and lowered high flows. In all but the driest years, an annual peak discharge is still released to the Flats but is delayed by ca. one month compared to pre-dam conditions.

Monitoring lechwe population and migration

We monitored the distribution of Kafue lechwe in Lochinvar National Park and the adjacent game management area on the South bank of the Kafue Flats, conducting monthly surveys by car or boat depending on the flood levels, between March 2010 and April 2011. We selected the main routes and areas to be inspected based on lechwe occurrence reports of the Park rangers from the period 2007 to 2009. The same experienced senior wildlife guard did all counting using binoculars. In April 2011, when high water restricted access to many areas, we performed an additional aerial survey to count animals in the western part of the park.

Daily measured water levels of the Kafue River during the study period were obtained from ZESCO hydrological gauge station at Nyimba (see Fig. 1a for location).

Estimating lechwe food: standing herbaceous biomass and quality

We measured the standing biomass of the herbaceous vegetation on six occasions between May 2010 and February 2011. For this purpose, we randomly selected 10 sites in floodplain grassland, 10 in water-meadows, and 13 in termitaria grassland. On each occasion, we clipped all aboveground biomass within a 0.25 m^2 quadrat in each site. To avoid clipping the same patch twice, a new sampling point was then selected to be clipped on the next occasion. We were unable to cut vegetation in areas that were flooded to a depth greater than 85 cm. This did not cause missing information in terms of lechwe food, since lechwe can only graze in areas flooded less than 50 cm (Vesey-Fitzgerald 1965). Clipped biomass was separated into grasses and forbs, and further into living and dead biomass. Each subset was dried and weighed. Subsamples of the living grass material were ground, and after Kjeldahl digestion, total N and P concentrations were determined by means of an auto-analyzer (Seal, Analytical).

Lechwe dung sampling and analysis

At regular intervals between March 2010 and March 2011, we collected fresh lechwe dung pellets throughout Lochinvar National Park and the adjacent game management area, using GPS to record the locations. A total of 270 pellet groups were sampled. After drying, samples were crushed with a hammer and the presence or absence of *D.*

cinerea seeds in each sample was recorded. A subset of 127 samples (covering the entire year and both dung pellets with and without seeds) were ground and total nitrogen and phosphorus concentrations determined as for plant material. Total C concentrations were determined using a dry combustion analyzer (CN-2000, LECO Corp., St Joseph, Minesota USA). Dung N and P concentrations were compared with the thresholds of Wrench et al. (1997) to assess whether food N and P supply were sufficient or not ($N > 14$ mg/g, $P > 2$ mg/g).

The spatial distribution of dung samples containing *D. cinerea* seeds were plotted on a current vegetation map (Chapter 4) to determine whether lechwe distribute seeds outside the *D. cinerea* encroached areas.

Influence of lechwes on germination of Dichrostachys cinerea seeds

We carried out three experiments to investigate how lechwe affected the regeneration niche of *D. cinerea*. In the first experiment, designed to investigate how ingestion affected germination, we used seeds either from lechwe dung pellets or directly under *D. cinerea* shrubs (control), collected in July 2010 in Lochinvar National Park. In February 2011, we placed batches of ten seeds on two moist filter papers (Himeda) in Petri-dishes (9 cm) and covered them with a further two filter papers. There were three treatments - seeds from dung, untreated control seeds, and control seeds scarified by scratching them with sandpaper – and 10 replicates of each. The Petri-dishes were kept indoors at room temperature (24-26°C) and the filter papers moistened as necessary. Germination (radicle >2mm) was recorded daily for three weeks and seeds removed when they germinated.

In two further field experiments, conducted in Lochinvar National Park, we tested whether germination of *D. cinerea* was influenced by clipping of the vegetation or correlated to vegetation cover (simulating grazing effect of lechwe). Both experiments were carried out under non-flooded conditions in an area of termitaria grassland partially invaded by *D. cinerea*. In one experiment we compared germination of *D. cinerea* seeds in nine pairs of clipped and unclipped 0.25 m^2 plots. The pairs were located spread over a 4 km stretch along the main park road in sites with similar vegetation and (unshaded) site conditions. The vegetation in the clipped plots was cut to 3-4 cm every 6th day (corresponding to intensely grazed areas, pers.

observation). Cages (60×60 cm) were placed over all plots to protect them against herbivory and trampling.

The other field experiment was performed along a vegetation cover gradient of ten 0.25 m^2 sites with a vegetation cover ranging from 0 to 87 %, located within an area of 50 m^2. The area was heavily grazed by lechwe and dominated by the grasses *Chloris virgata, Chloris pycnothrix, Sporobolus ioclados, Dactylocterium egyptum* and *Eragrostis viscosa*. Vegetation cover was determined by analysing photographs of each 0.25 m^2 site, taken vertically from above, with ImageJ (Version 1.45e), comparing pixels with plant coverage (living and dead) with those without. For both field experiments we used *D. cinerea* seeds collected in 2009. Single seeds were scarified with sandpaper and glued (Pritt KidsArt Project Glue, water-soluble, solvent and acid free, non-toxic glue) on a wooden toothpick, which was tagged for easier recognition in the field. In February 2011 (mid rainy season), we planted 25 seeds in each plot at a depth of 1cm, and in a grid with seeds spaced 10 cm apart. Seed germination was monitored every third day over a 23-day period. Seeds were considered germinated as soon as the two cotyledon leaves were visible. Germination rate of these scarified seeds was 96 ± 2 % when germinated in Petri-dishes kept at room temperature (24-26°C).

Influence of lechwe dung on growth of D. cinerea and a competing grass

We studied the influence of lechwe dung on the growth of *D. cinerea* seedlings and of the C4 grass *Cynodon dactylon* (common in the termitaria area), either when grown in monocultures or in species mixtures. The experiment was carried out in a heated (c. 25°C) greenhouse at ETH Zurich, using lechwe dung and soil collected in Lochinvar National Park (under *D. cinerea* shrubs) in March-April 2011. *D. cinerea* seedlings were grown from scarified seeds that had been collected in Lochinvar in 2009. *Cynodon dactylon* seedlings were grown from seeds obtained from B and T World Seeds, Paguignan, France. Plants grew under natural (Zürich) light conditions. At the start of the experiment (end of April 2011), four seedlings were transferred to 360ml pots filled with a 1:1 mixture of perlite and dried and sieved soil (1mm). The monocultures had four seedlings of one species, the mixtures two seedlings of both species. Half of the pots were fertilized with 15g of lechwe dung, which had been dried and ground, and then mixed with the soil. Each treatment was replicated 8 times. Each pot was placed on an absorbant disc, which ensured that the soil remained moist. After 66 days, plants were harvested, dried (48h, 70°C) and weighed.

Statistical analysis

We calculated Pearson correlations of monthly percentages of the lechwe population per habitat (termitaria, water-meadows and floodplain) to mean living biomass per habitat type (for the months available), and to mean monthly water levels of the Kafue River.

A sine curve was regressed through the distribution of dung N and P concentrations versus time, and we calculated correlations between these concentrations to river water level. For the period that dung N concentrations indicated a diet below the nutritional threshold of 14 mg g^{-1} (Wrench et al. 1997; period from March 11th 2010 to June 16th 2010), we used Students t-tests to calculated whether nutrient concentrations and ratios differed significantly between dung pellets with and without *D. cinerea* seeds, and to test if measured levels significantly differed from nutritional thresholds.

The germination experiments were analyzed with a t-test (Petri-dish germination), paired t-test (Clipping experiment) and a regression analysis (Cover experiment). Results of the competition experiment were tested with a type II ANOVA, to account for unbalanced experimental data, and Tukey posthoc tests were carried out. Dry weight of the aboveground biomass was square root transformed to fulfill assumptions of normality.

All statistical analyses were conducted using R version 2.10.1 (R Foundation for Statistical Computing 2009).

Results

Lechwe migration patterns related to flooding and grass biomass

During the dry season lechwe are confined to the open floodplain and can be seen relatively easily. The estimated population in Lochinvar National Park and the adjacent game management area on the Kafue Flats South Bank during the period September to December 2010 was 17,561 (mean of four counts ranging between 16,862 and 18,718). The group sizes ranged from a single individual to compact herds of several thousands.

The lechwe showed an annual migration pattern that was closely related to the height of the water (Fig. 2, 3a, 3b). At the peak of the flood (April-May), animals were concentrated above the high water line in the termitaria zone. As the water receded (July-August), they moved onto the shallowly inundated water-meadows, and later onto the floodplain, remaining during the dry season in areas close to permanent water bodies. As the floodwaters rose again (December-January), animals moved back to the termitaria zone. Hence, the percentage of the lechwe population occupying the termitaria was positively correlated to flooding height (R= 0.89, $p < 0.001$), while the percentage of lechwe population occupying the deep flooded floodplain was negatively correlated (R = -0.91, $p < 0.001$). The percentage of the population occupying the water-meadows was unrelated to flood height (R= 0.17, p= 0.55).

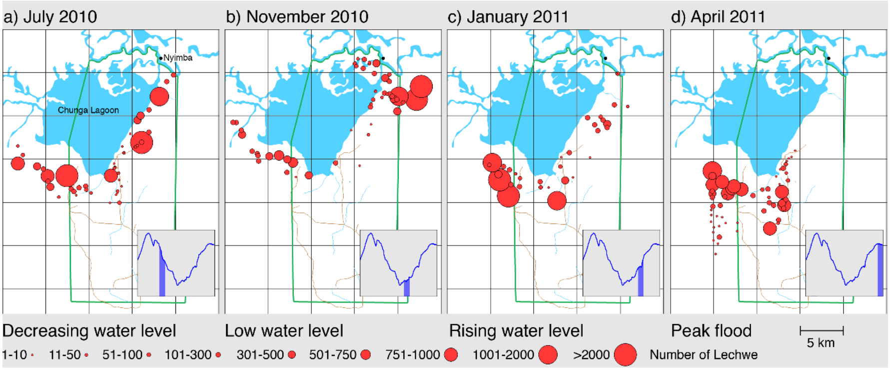


Figure 2 – Number of Kafue lechwe on the South Bank of the Kafue River in July 2010 (a), November 2010 (b), January 2011 (c) and April 2011 (d). The lechwe population was monitored by ground (in a, b, c, d) and aerial surveys (in d). The grey insets show the prevailing water levels of the Kafue River (cf. Fig 3a), green line: boundary of Lochinvar National Park, dashed black line: boundary between the termitaria and seasonally flooded areas.

For the six measurement periods, the percentage of the population in the termitaria area was positively correlated to living aboveground grass biomass (R=0.99, p<0.001, (Fig 4a, d). However, we found no significant correlations between biomass and the percentages of animals in the water-meadow and floodplain area (Fig 4.), nor between percentage of the lechwe population in an area and the N and P concentrations in the vegetation (Fig. S2). Correlations were significant, however, for lechwe numbers and N stock (R=0.99, p<0.001) and P (R=0.99, p<0.001) stock in the termitaria habitat.

Annual patterns of N and P concentrations in lechwe dung

Concentrations of N and P, as well as C:N and C:P ratios in lechwe dung varied seasonally (Fig. 3d,e, Fig. S1b,c), and were significantly ($P<0.002$) correlated to the floodwater level. When the water level was high, from mid-March until mid-June, the average dung N concentration was below the threshold value of 14 mg g^{-1}, indicating an inadequate N-content in the diet (Fig. 3d). The average P concentration in dung was above the threshold of 2 mg g^{-1} throughout the year, but some individual measurements indicated inadequate P-contents in the diet (Fig. 3e).

Dichrostachys seed consumption by lechwe; annual pattern and importance for food quality

Consumption of *D. cinerea* seed pods by lechwe showed a clear seasonal pattern, being highest from April to August when 20-50% of the dung pellets contained seeds (Fig. 3c; 2-49 dung pellets studied in these months). Dung pellets with seeds had significantly higher N and C concentrations and N:P ratio, and a lower C:N ratio, than dung pellets without seeds (Fig. 5). Thus, whereas the mean dung N concentration of the lechwe population dropped below the threshold value of 14 mg g^{-1} for much of this period, the N concentration of dung pellets with seeds was not significantly lower than the threshold (Fig. 5a). Dung P concentrations were not influenced by *D. cinerea* seeds.

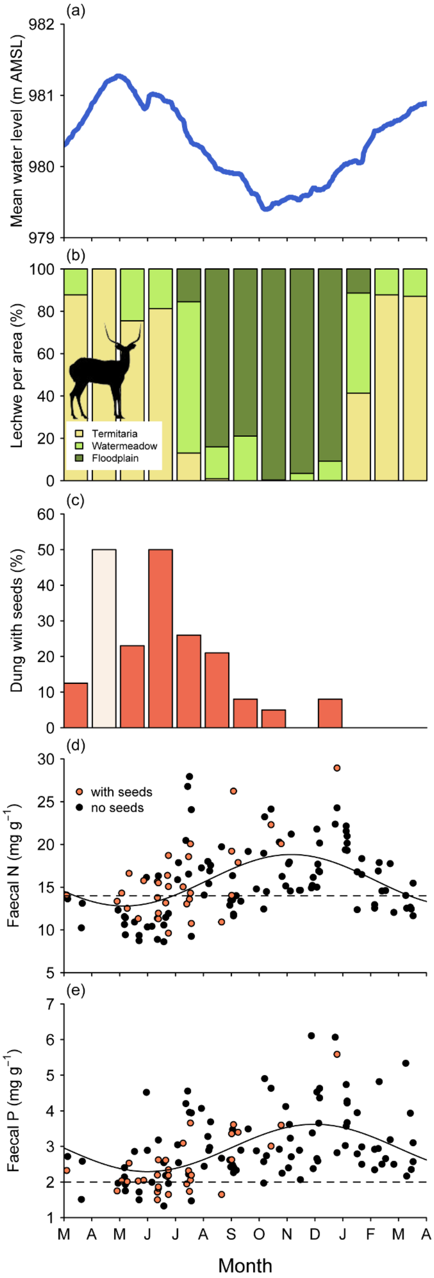


Figure 3 – Seasonal variation in mean daily water levels of the Kafue River (a) the distribution of the lechwe population over the lechwe habitats: termitaria, water-meadows and floodplain (b), proportion of lechwe dung pellets containing *D. cinerea* seeds (c), lechwe dung nitrogen concentrations (d) and lechwe dung phosphorus concentrations (e) between March 2010 and April 2011. Mean daily water levels of the Kafue River in a) were obtained from the ZESCO hydrological gauging station at Nyimba (for detailed location see Fig. 1a). The distribution of lechwe in b) is based on data of Fig. 2 and direct observations of the presence of lechwe in the tree habitats in additional months. In c) the bar for April 2010 has a lighter color because the percentage is based on only two observations. Sample numbers in the other months varied between 8-37; total 270 samples. Filled black dots in d and e) represent samples without *D. cinerea* seeds; red dots represent samples with seeds. In d) and e) dashed horizontal lines indicate critical values for nutritional requirements of herbivores of 14 mg g^{-1} N (Wrench et al. 1997) and 2 mg g^{-1} P (Grant et al. 1995).

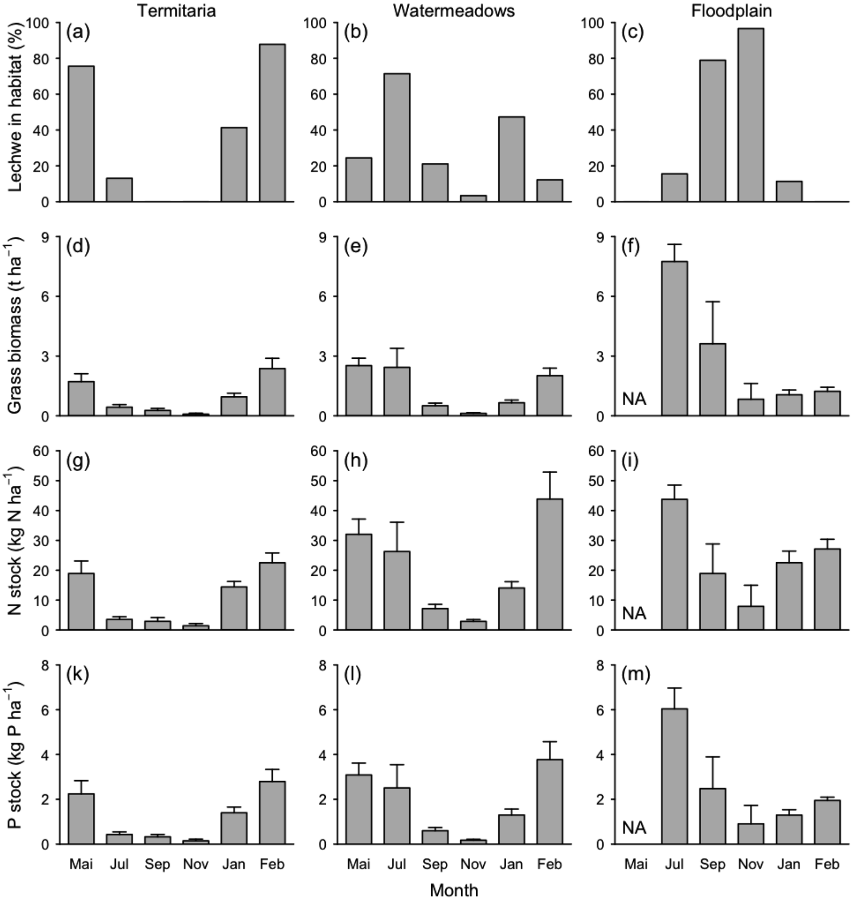


Figure 4 – The proportion of the South bank lechwe population in the main habitats termitaria (a), water-meadows (b) and floodplain grasslands (c) as well as aboveground living grass biomass and amount of N and P in it (d-m) in these habitats. Biomass samples were taken at six moments in time between May 2010 and February 2011 in 10-13 sites in termitaria, 7-10 sites in water-meadows and 8-10 sites in floodplain grasslands in Lochinvar National Park (cf. Fig 3, Chapter 1). Missing data is indicated by NA, while missing bars stand for a value of zero. Mean values and standard errors are provided.

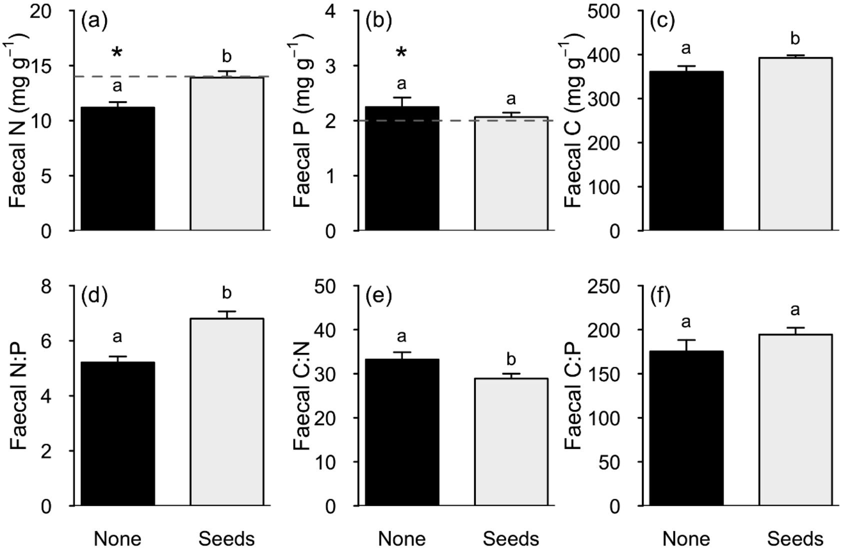


Figure 5 – Nitrogen (a), phosphorus (b) and carbon (c) concentrations and their respective ratios N:P (d), C:N (e), C:P (f) in lechwe dung, separated in pellets that did (Seeds) or did not (None) contain seeds of *Dichrostachys cinerea.* Dashed lines show nutritional requirements for grazing herbivores (cf. Grant et al. 1995, Wrench et al. 1997). Bars are mean ± SE. Different letters indicate significant differences between dung with and without seeds (t-test P<0.05). An asterisk indicates whether the N or P concentrations differ significantly from the nutritional requirement. Only dung pellets collected between March 11th and June 16th 2010 were included in this figure. In this period the mean N dung N concentration of the lechwe population is below the nutritional N requirements (cf. Fig 4c).

Spatial distribution of D. cinerea seeds through lechwe dung

Out of 39 dung samples containing seeds, 46 % were collected within the *D. cinerea* dominated area and 18 % were collected in nearby vegetation dominated by *Acacia* spp.. 36% of the dung pellets with seeds had been transported outside the shrub encroached area and were deposited into open termitaria (10%) or open floodplain grasslands (26%, Fig. 6).

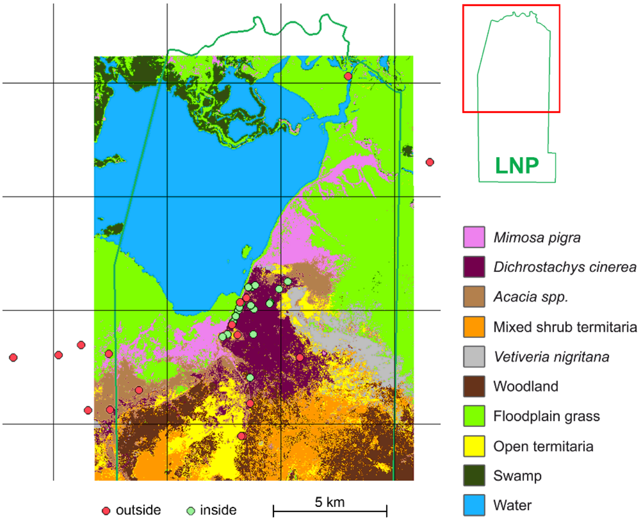


Figure 6 – Distribution of fresh dung pellets with *D. cinerea* seeds in Lochinvar National Park (LNP) plotted on vegetation map of 2010, generated through supervised classification of multitemporal, hyperspectral Landsat TMimages (Chapter 4). Different map colors refer to the main vegetation type prevalent in the respective area (see legend). Red dots mark dung pellets collected outside the *D. cinerea* area and contribute to the spatial spread of *D. cinerea* seeds. Green dots mark dung pellets found within the *D. cinerea* covered area. Dung samples were collected between March 2010 and March 2011.

Influence of lechwes on germination of Dichrostachys cinerea seeds

The germination rate of *D. cinerea* seeds collected from lechwe dung did not differ from that of control seeds (both about 15%; Fig. 7a), but scarifying raised the germination of control seeds to 73±6% (data not shown). Germination of *D. cinerea* seeds in the field increased with increasing vegetation cover (r^2 = 0.44, P=0.04, but was not different between clipped and control plots (Fig. 7c).

Influence of lechwe dung on growth of D. cinerea and a competing grass

The aboveground biomass production of *D. cinerea* seedlings was not affected by fertilization with lechwe dung, nor by competition with the grass *C. dactylon* (Fig. 8a). In contrast, shoot production of *C. dactylon* increased with dung fertilization and was higher in mixtures with *D. cinerea* seedlings than in monocultures (Fig. 8b).

Moreover, fertilization with lechwe dung increased the mortality of *D. cinerea* seedlings (*P*=0.002), but not of *C. dactylon* (data not shown).

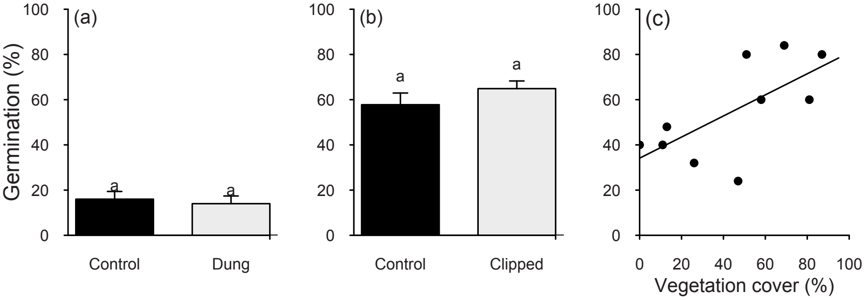


Figure 7 – Germination of *Dichrostachys cinerea* seedlings collected from dung pellets (dung) or just under shrubs (control) (a), and under field conditions in clipped and unclipped grassland plots (b), or along a cover gradient of the vegetation (c). Panel (a) contained ten replicates with ten *D. cinerea* seeds each, panel b) nine replicates with 25 seeds each. Different letters indicate significant differences between treatments (a) t-test, b) paired t-test, p<0.05), regression lines significant linear relationships (p<0.05).

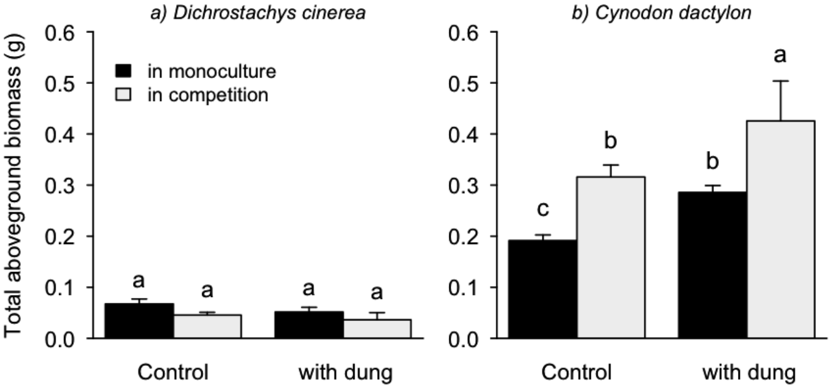


Figure 8 – Response of seedlings of *Dichrostachys cinerea* (a) and *Cynodon dactylon* (b) to fertilization with lechwe dung, when grown in monocultures (4 plants per pot) or in species mixtures (2 plants per species per pot) Pots with dung received 15g dried ground lechwe dung. Plants were grown for 66 days in 0.36 L pots with soil from Lochinvar National Park (mixed with perlite) in a greenhouse in Zurich. Bars show mean ± SE (n= 3-8) Different letters designate significant differences between treatments (Tukey posthoc tests p< 0.05).

Discussion

Lechwes migrate for food, and due to flooding

Our year-round monitoring study of the Kafue lechwe South Bank population showed that this semi-aquatic antelope species follows an annual migration closely linked to the flooding regime. Thus, animal presence was significantly correlated to the water height of the Kafue River (and therefore with water level in the floodplain, Chapter 1), and to the availability of living aboveground grass biomass in the termitaria zone. These results confirm previous descriptive reports (Vesey-Fitzgerald 1965, Sheppe and Osborne 1971, Chabwela and Ellenbroek 1990).

The populations of migratory species are often determined by food availability during periods of food scarcity (Fryxell et al. 1988, Mduma et al. 1999). However, unlike most savanna herbivores, which experience food scarcity at the end of the dry season (e.g. Serneels and Lambin 2001, van der Waal et al. 2003), lechwe encounter these conditions in the wet season. This difference is due to the seasonal accessibility of the large amounts of good quality grass biomass in the floodplain grasslands (Fig. 4). Contrary to most migratory ungulates it therefore seems that the dry season habitat is the habitat that allows the large Kafue lechwe population to regain strength and build up reserves.

The dung analyses (N, P, C:N and C:P; Fig 3d, e; Fig. S1) demonstrate that for lechwe the period of food scarcity falls between mid-March and mid-June, when the N concentration drops below the critical value indicating N deficiency in their diet (Wrench et al., (1997). This evidence of nutritional stress is consistent with high mortality during the period of peak flooding, which is not merely a recent phenomenon (Shanungu et al. unpublished) but also occurred before the dams were constructed (Gallagher et al. 1972, Bell et al. 1973). These data highlight the fragile balance that exists between the timing of flooding and the survival of the lechwe. By the end of this period, all food in the termitaria zone has been exhausted, (Fig. 4d), and the abundant grass biomass in the floodplain grasslands (Fig. 4f) cannot be grazed because the water is still above the critical depth of >0.5 m (cf. Vesey-Fitzgerald 1965).

Browsing Kafue lechwe; a remarkable but effective diet adaptation

Previous studies, including work conducted in Lochinvar National Park (cf. Handlos et al. 1976, Rees 1978c, IUCN 2008), have concluded that the Kafue lechwe and other *Kobus* species are strict grazers (Estes 1991). Our study is the first to report lechwe feeding on the fruits of a woody species, *D. cinerea*, which they consumed during the period when they were restricted to the termitaria grassland (see above; and Fig. 3). Mixed feeding, i.e., the consumption of 'browse' during times of food scarcity by otherwise strict grazers, is a common feature among various African herbivores, such as impala and nyala (Codron et al. 2007, Codron and Codron 2009), Thomson's gazelle (Cerling et al. 2003), and Bohor reedbuck (Halsdorf 2011). Furthermore, the seed pods of *D. cinerea* have been reported to be good dry season protein supplement for goats (Yayneshet et al. 2008, Maphosa et al. 2009). As far as we know, however, this is the first study reporting an apparent change in feeding behaviour by a wild antelope previously thought to be a strict grazer.

The question therefore arises - why do lechwe consume *D. cinerea* seed pods now, but apparently did not do so in the 1970s? The explanation cannot be increased food scarcity in the dry season, since animals also died of starvation at the time of peak flooding before the dams were constructed (Bell et al. 1973). The answer is therefore more likely to be the greatly increased availability of *D. cinerea* following its encroachment into the termitaria areas since 1980 (Chapter 4: Fig 1d, e). Furthermore, dung analysis suggest that lechwe benefit from browsing *D. cinerea* seed pods during the period of food scarcity. Whereas N concentrations in dung samples without seeds fell below the critical threshold of Wrench et al (1997), those in samples with seeds were usually higher (Fig. 5). Moreover, results from an exclosure experiment with *D. cinerea* shrubs in the termitaria area showed that between May and July 2010 the N pool in *D. cinerea* fruits was ten times higher than that in grass biomass (127 *vs.* 12 kg N ha^{-1}; n=3) (data not shown). A comparison with nearby unfenced plots showed that lechwe consumed 100% of these seed pots, and presumably benefited from the additional N they obtained from this resource.

Do lechwes stimulate encroachment of D. cinerea?

By consuming *D. cinerea* fruits in the shrub-encroached area and dropping their dung elsewhere (Fig. 6), lechwe disperse seeds to unencroached areas. As such, lechwe play a similar role as has been demonstrated for other herbivores and shrubs (Miller 1996, Radford et al. 2001, Rodriguez-Perez et al. 2011). However, we found no evidence that lechwe facilitate germination or seedling establishment. First, seeds collected from dung did not germinate better than control seeds, indicating that passage through the digestive system did not increase germination. This is consistent with results of previous germination studies using *D. cinerea* seeds collected from dung of domestic goats, sheep and cattle (Hashim 1990, Shayo and Uden 1998), but different from those collected from nyala dung, in which germination was enhanced (Vanstaden et al. 1994). Second, the germination rate of *D. cinerea* was not higher in vegetation that had been clipped to simulate the effect of lechwe grazing (Fig. 7), although previous experiments with the same and with other shrubs have shown such an effect (Riginos and Young 2007, Hagenah et al. 2009, Goheen et al. 2010). Thirdly fertilization with lechwe dung did not stimulate the growth of the *D. cinerea* seedlings (indeed it increased mortality), though it did have stimulating effect on the grass *Cynodon dactylon* (Fig 8). The latter is consistent with the effect of mineral nutrients on the competitive balance between grasses and shrubs in savanna (Hagenah et al. 2009, Ramsar 2013).

Hence, even though lechwe contribute to the spatial distribution of *D. cinerea* seeds they apparently do not create favorable conditions for *D. cinerea* seed germination and establishment. Based on our small-scale experiments, however, we cannot rule out that initial encroachment of *D. cinerea* might have been stimulated by overgrazing, as has been shown to be critical for the promotion of *D. cinerea* in other savanna regions (e.g in north-eastern Swaziland, Roques et al. 2001).

Lessons to learn for lechwe conservation and water management

Our estimate of the South Bank Kafue lechwe population was rather consistently around 18,000 individuals. This is much higher than the 6,000 lechwe reported for the South Bank population in 2005 (Chansa and Kampamba 2009), Fig 1b). Besides a possible underestimate in the latter study, the difference may be explained by animals moving between the North Bank and South Bank populations (cf. Bell et al. 1973) or by a huge population fluctuation.

Assuming that the same relationships between floodplain hydrology, food supply and habitat use apply for the North Bank population, we can speculate about the relative impacts of the altered flooding regime and shrub encroachment upon the lechwe population since the early 1970s (Fig 1b). First, we note that there is little evidence that the population has decreased linearly, as suggested in some previous studies (Genet 2007, Chansa and Kampamba 2009). An alternative interpretation is that the animal counts reflect two relatively stable states, one of c. 90,000 lechwe before the construction of the second dam in 1977, and one of c. 40,000 lechwe afterwards (cf. Fig. 1b). In the latter case, dam construction could have caused a 'catastrophic shift' in the ecosystem from one state to the other (cf. Trollope et al. 1989). This emphasizes the importance of continued monitoring, since a linear decline or two stable states imply very different future perspectives for the Kafue lechwe population.

The dung analyses indicate that the food supply becomes most critical when the animals are restricted to the termitaria zone from mid-March to mid-June. Hence, food supply in this zone may be the factor limiting the size of the lechwe population, as suggested by Fryxell et al. (1988) and Mduma et al. (1999). Despite being strongly invaded by *D. cinerea* and *Acacia* shrubs, the food supply from this zone has probably not declined, and may even have increased since the construction of the second dam (Chapter 4, Fig 1d, e). Unless these shrubs achieve a cover of >50 %, they have little effect upon understory biomass, whereas the nutritional quality of grasses beneath shrubs is increased (Chapter 4). Moreover, the seed-pods of *D. cinerea* represent a significant addition to the lechwe food supply during this critical period (Fig. 5), which may offset any losses in grass biomass in dense *D. cinerea* habitats (cf. Chapter 4).

With the available data we conclude that encroachment by *D. cinerea* does not explain why there are now 50,000 fewer lechwe than in 1980. Similarly, the greatly reduced area of floodplain grasslands (at least 40% because of the permanent innundation, cf. Fig. 1d,e) also does explain the decrease; not only is there no shortage of grass biomass in this habitat but dung N and P concentrations increase when lechwe feed there (Fig. 3d,e). Assuming that poaching has not taken 50,000 lechwe, although we lack data to proof this, there has to be another factor for the population decline. In our opinion, this critical factor is the timing of flooding, both its rise and fall, which since 1977 has been fully controlled by dam management.

The timing of the recession in June and July determines when lechwe can leave the termitaria grasslands and feed on the better quality herbage of the floodplain (Fig. 4f,i,m). Since most of the female lechwe give birth between July and September (Handlos 1975, Rees 1978d) and are hence strongly reliant upon the nutritionally higher floodplain resources, a later than usual recession might have a disproportionately large impact on females and young lechwe, and consequently upon the population. In the years 1976, 1978 and 1979, for example, the grazing sites on the floodplain could not be entered before August (1976, 1979) or even September (1978; Table S1). In three out of four subsequent years, lechwe were hence confined to the higher areas at least one month longer than during our study period. This would have caused a severe shortage of food, and probably contributed to the large drop in lechwe numbers at that time. If this explanation is correct, it is unclear why the lechwe population did not subsequently recover. A possible explanation might be the invasion of many former leks (important rutting grounds) by *M. pigra,* which might have interfered with lechwe breeding (cf. Chapter 4, Schuster 1976).

The timing of the rising flood also has important consequences for lechwe, because it influences floodplain productivity (Ellenbroek 1987). If the water rises too rapidly, the new shoots of floodplain grasses such as *Vossia cuspidata* become completely submerged and die, greatly reducing the food supply in that year. An example of how this can affect the lechwe population was observed in January 2008, when water levels rose 60 cm in just four days, instead of the normal rate of 1 cm per day in an average year. As a consequence large parts of the floodplain remained bare and only provided limited food when the lechwe started accessing the areas in June to August 2008. This resulted into thousands of lechwe dying, both in Lochinvar National Park and the South Bank as well as in Blue Lagoon National Park on the North Bank of the Kafue Flats (Shanungu et al. unpublished). Hence, water management is of crucial importance for conservation of the Kafue lechwe.

Lessons to learn for other herbivores

This study clearly illustrates the necessity of protecting both the wet and dry season feeding habitats of the Kafue lechwe, and the migration routes between them. This has been shown for other migrating herbivores, such as wildebeest and zebra in Tarangire or Serengeti in Tanzania (cf. Bolger et al. 2008, Dobson et al. 2010, Voeten et al. 2010), but also applies to smaller scale migrations between wetlands and upland zones along rivers. Wetlands and lagoons are of crucial importance for dry-season food supply for herbivores in many protected areas in Africa (e.g. Omphile and Powell 2002), and connections between wetland and upland zones need to be maintained or re-established. Disturbance to migration routes can cause a population collapse (Bolger et al. 2008, Harris et al. 2009, Dobson et al. 2010). Our study shows that the timing of accessibility to these wetlands can also be of crucial importance.

A second important lesson is that wild herbivores may be able to adapt to altered conditions, as illustrated by the recent use of *D. cinerea* fruits by Kafue lechwe. Indeed, such behavioural changes are one of the reasons that the effects of interactions among environmental alterations in natural ecosystems, such as the hydrological change and the shrub encroachment in the Kafue Flats, are so difficult to predict.

Acknowledgements

We thank Benjamin Wishikoti, Osten Mwiimbwe, Michael Sinjote, Chris Nchimunya, Event Ngandu, Chrispin 'Palaman' Mulimbika, George Mbulo, Cliff Mwiinga, Eddy Zeko, Albert Nsovu, Philippe Blaser and Monique Blaser for their assistance during fieldwork. We acknowledge Britta Jahn-Humphrey and Marilyn Gaschen for support of laboratory analyses and thank Karsten Rohwede, Roland Zurbrügg and Florian Koeck for their invaluable help with graphics. We are extremely grateful to Bob Douthwaite, Gerard Ellenbroek, Geoffrey Howard and Wendy Rees who rendered assistance with expert knowledge on historic conditions both remotely and in the field. Research was conducted with permission and support given by the Zambia Wildlife Authority (ZAWA). Funding for this study was provided the Competence Center for Environment and Sustainability (CCES) at the ETH domain.

References

Bell, R. H., J. J. R. Grimsdell, and J. A. Sayer. 1973. Census of the Kafue Lechwe by aerial stratified sampling. East African Wildlife Journal **11**:55-74.

Bolger, D. T., W. D. Newmark, T. A. Morrison, and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters **11**:63-77.

Bond, W. J., G. F. Midgley, and F. I. Woodward. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. Global Change Biology **9**:973-982.

Buitenwerf, R., W. J. Bond, N. Stevens, and W. S. W. Trollope. 2012. Increased tree densities in South African savannas: > 50 years of data suggests CO_2 as a driver. Global Change Biology **18**:675-684.

Cerling, T. E., J. M. Harris, and B. H. Passey. 2003. Diets of East African bovidae based on stable isotope analysis. Journal of Mammalogy **84**:456-470.

Chabwela, H. N. and G. A. Ellenbroek. 1990. The Impact of Hydro-Electric Developments on the Kafue Lechwe and its Feeding Grounds at Kafue Flats, Zambia. Pages 95-101 *in* D. F. Whigham, editor. Wetland Ecology and Managements: Case Studies. Kluwer Academic Publisher, Netherlands.

Chansa, W. and G. Kampamba. 2009. The population status of the Kafue Lechwe in the Kafue Flats, Zambia. African Journal of Ecology **48**: 837–840.

Codron, D. and J. Codron. 2009. Reliability of delta C-13 and delta N-15 in faeces for reconstructing savanna herbivore diet. Mammalian Biology **74**:36-48.

Codron, D., J. A. Lee-Thorp, M. Sponheimer, and J. Codron. 2007. Stable carbon isotope reconstruction of ungulate diet changes through the seasonal cycle. South African Journal of Wildlife Research **37**:117-125.

Denny, P. 1985. The ecology and management of African wetland vegetation-A botanical account of African swamps and swallow water bodies. Dr. W. W Junk Publishers, Netherlands.

Dobson, A. P., M. Borner, A. R. E. Sinclair, P. J. Hudson, T. M. Anderson, G. Bigurube, T. B. B. Davenport, J. Deutsch, S. M. Durant, R. D. Estes, A. B. Estes, J. Fryxell, C. Foley, M. E. Gadd, D. Haydon, R. Holdo, R. D. Holt, K. Homewood, J. G. C. Hopcraft, R. Hilborn, G. L. K. Jambiya, M. K. Laurenson, L. Melamari, A. O. Morindat, J. O. Ogutu, G. Schaller, and E. Wolanski. 2010. Road will ruin Serengeti. Nature **467**:272-273.

Douthwaite, R. J. and L. P. Van Lavieren. 1977. A Description of the vegetation of Lochinvar National Park, Zambia. Technical Report 34, . National Council for Scientific Research, Lusaka, Zambia.

Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters **14**:709-722.

Ellenbroek, G. A. 1987. Ecology and productivity of an African wetland system: The Kafue Flats, Zambia. PhD Thesis. Junk Publisher.

Estes, R. D. 1991. The behavior guide to African mammals: including hoofed mammals, carnivores, primates. University of California Press, Berkeley.

Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? . American Naturalist **131**:781-798.

Gallagher, J., I. Macadam, J. Sayer, and L. P. Van Lavieren. 1972. Pulmonary tuberculosis in free living lechwe antelope in Zambia. Tropical Animal Health and Production **4**:204-213.

Genet, B. S. 2007. Shrub encroachment into grassland and its impact on Kafue Lechwe in Lochinvar National Park, Zambia. International Institute for Geo-information Science and Earth Observation, Enschede, The Netherlands.

Goheen, J. R., T. M. Palmer, F. Keesing, C. Riginos, and T. P. Young. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. Journal of Animal Ecology **79**:372-382.

Gordon, I. J. 2009. What is the future for wild, large herbivores in human-modified agricultural landscapes? Wildlife Biology **15**:1-9.

Grant, C. C., H. H. Meissner, and W. A. Schultheiss. 1995. The nutritive value of veld as indicated by faecal phosphorus and nitrogen and its relations to the condition and movement of prominent ruminants during the 1992-1993 drought in the Kruger National Park. Koedoe **38**:17-31.

Hagenah, N., H. Munkert, K. Gerhardt, and H. Olff. 2009. Interacting effects of grass height and herbivores on the establishment of an encroaching savanna shrub. Pages 189-202 *in* A. G. Valk, editor. Herbaceous Plant Ecology. Springer Netherlands.

Halsdorf, S. 2011. Patterns of resource use by grazers in a humid costal savanna in Tanzania. Swiss Federal Institute of Technology, ETH Zurich, Switzerland.

Handlos, D. M., W. L. Handlos, and G. W. Howard. 1976. A Study of the Diet of the Kafue Lechwe (Kobus Lechwe) by Analysis of Rumen Contents. Pages 197-211 Proceedings of the Fourth Regional Wildlife Conference for Eastern and Central Africa. National Parks & Wildlife Service, Chichele Lodge, Zambia.

Handlos, W. L. 1975 Aspects of the Kafue Basin Ecology. University papers on the Lower Kafue Basin presented by the Kafue Basin Research Committee of the University of Zambia Senate. unpublished.

Harris, G., S. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt, and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research **7**:55-76.

Hashim, I. M. 1990. Germination of Kadad (*Dichrostachys cinerea*) seed following pod digestion by goats, and various chemical treatments. Forest Ecology and Management **38**:105-110.

IUCN. 2008. Kobus leche.in A. S. Group, editor. IUCN Red list of Threatened Species. IUCN.

Leslie, D. M., Jr., R. T. Bowyer, and J. A. Jenks. 2008. Facts from feces: Nitrogen still measures up as a nutritional index for mammalian herbivores. Journal of Wildlife Management **72**:1420-1433.

Maphosa, V., J. Sikosana, and V. Muchenje. 2009. Effect of doe milking and supplementation using *Dichrostachys cinerea* pods on kid and doe performance in grazing goats during the dry season. Tropical Animal Health and Production **41**:535-541.

Mduma, S. A. R., A. R. E. Sinclair, and R. Hilborn. 1999. Food regulates the Serengeti wildebeest: a 40-year record. Journal of Animal Ecology **68**:1101-1122.

Miller, M. F. 1996. Dispersal of Acacia seeds by ungulates and ostriches in an African savanna. Journal of Tropical Ecology **12**:345-356.

Mumba, M. and J. R. Thompson. 2005. Hydrological and ecological impacts of dams on the Kafue Flats floodplain system, Southern Zambia. Physics and Chemistry of the Earth **30**:442-447.

Omphile, U. J. and J. Powell. 2002. Large ungulate habitat preference in Chobe National Park, Botswana. Journal of Range Management **55**:341-349.

Ottichilo, W. K., J. De Leeuw, A. K. Skidmore, H. H. T. Prins, and M. Y. Said. 2000. Population trends of large non-migratory wild herbivores and livestock in the Masai Mara ecosystem, Kenya, between 1977 and 1997. African Journal of Ecology **38**:202-216.

Prins, H. H. T. 1992. The pastoral road to extinction - competition between wildlife and traditional pastoralism in East-Africa. Environmental Conservation **19**:117-123.

Radford, I. J., D. M. Nicholas, J. R. Brown, and D. J. Kriticos. 2001. Paddock-scale patterns of seed production and dispersal in the invasive shrub Acacia nilotica (Mimosaceae) in northern Australian rangelands. Austral Ecology **26**:338-348.

Ramsar. 2013. Ramsar Sites in order of their addition to the Ramsar List of Wetlands of International Importance, Ramsar Concention, Gland.

Rees, W. A. 1978a. Do the Dams Spell Disaster for the Kafue Lechwe? Oryx **14**:231-235.

Rees, W. A. 1978b. Ecology of Kafue Lechwe - as affected by Kafue Gorge hydroelectric scheme. Journal of Applied Ecology **15**:205-217.

Rees, W. A. 1978c. Ecology of Kafue Lechwe - its nutritional-status and herbage intake. Journal of Applied Ecology **15**:193-203.

Rees, W. A. 1978d. The ecology of the Kafue Lechwe: The good supply. The Journal of Applied Ecology **15**:177-191.

Riginos, C. and T. P. Young. 2007. Positive and negative effects of grass, cattle, and wild herbivores on Acacia saplings in an East African savanna. Oecologia **153**:985-995.

Rodriguez-Perez, J., K. Wiegand, and D. Ward. 2011. Interaction between ungulates and bruchid beetles and its effect on Acacia trees: modeling the costs and benefits of seed dispersal to plant demography. Oecologia **167**:97-105.

Roques, K. G., T. G. O'Connor, and A. R. Watkinson. 2001. Dynamics of shrub encroachment in an African savanna: relative influences of fire, herbivory, rainfall and density dependence. Journal of Applied Ecology **38**:268-280.

Sankaran, M., N. P. Hanan, R. J. Scholes, J. Ratnam, D. J. Augustine, B. S. Cade, J. Gignoux, S. I. Higgins, X. Le Roux, F. Ludwig, J. Ardo, F. Banyikwa, A. Bronn, G. Bucini, K. K. Caylor, M. B. Coughenour, A. Diouf, W. Ekaya, C. J. Feral, E. C. February, P. G. H. Frost, P. Hiernaux, H. Hrabar, K. L. Metzger, H. H. T. Prins, S. Ringrose, W. Sea, J. Tews, J. Worden, and N. Zambatis. 2005. Determinants of woody cover in African savannas. Nature **438**:846-849.

Sayer, J. A. and L. P. Van Lavieren. 1975. The ecology of the Kafue lechwe oopulation of Zambia before the operation of hydro electric dams on the Kafue River. East African Wildlife Journal **13**:9-38.

Schuster, R. H. 1976. Reproductive Social Organization of Kafue Lechwe: Implications for Management and Survival. Pages 163-187 Proceedings of the Fourth Regional Wildlife Conference for Eastern and Central Africa. National Parks & Wildlife Service, Chichele Lodge, Zambia.

Schuster, R. H. 1977. The Social Organization of the Kafue Lechwe in Relation to the Ecology of the Kafue Flats. Pages 57-67 *in* G. J. Williams and G. W. Howard, editors. Development and Ecology in the Lower Kafue Basin in the Nineteen Seventies. Papers from the Kafue Basin Research Committee of the University of Zambia, Lusaka.

Serneels, S. and E. F. Lambin. 2001. Impact of land-use changes on the wildebeest migration in the northern part of the Serengeti-Mara ecosystem. Journal of Biogeography **28**:391-407.

Shayo, C. M. and P. Uden. 1998. Recovery of seed of four African browse shrubs ingested by cattle, sheep and goats and the effect of ingestion, hot water and acid treatment on the viability of the seeds. Tropical Grasslands **32**:195-200.

Sheppe, W. and T. Osborne. 1971. Patterns of use of a flood plain by Zambian mammals. Ecological Monographs **41**:179-205.

Sheppe, W. A. 1985. Effects of humn activities on Zambia Kafue Flats ecosystems. Environmental Conservation **12**:49-57.

Staeli, A. 2012. Ungulate grazers in a tallgrass savanna. Implications of low resource quality for feeding and mating strategies. Swiss Federal Institute of Technology, ETH Zurich, Switzerland.

Trollope, W. S. W., F. O. Hobson, J. E. Danckwerts, and J. P. Van Niekerk. 1989. Encroachment and control of undesirable plants. Pages 73–89 *in* J. E. Danckwerts and W. R. Teague, editors. Veld Management in the Eastern Cape Department of Agriculture and Water Supply, Pretoria, South Africa.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecology and Systematics **31**:197-215.

Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of Environmental Management **90**:2931-2942.

van der Waal, C., G. N. Smit, and C. C. Grant. 2003. Faecal nitrogen as an indicator of the nutritional status of kudu in a semi-arid savanna. South African Journal of Wildlife Research **33**:33-41.

Vanstaden, J., K. M. Kelly, and W. E. Bell. 1994. The role of natural agents in the removal of coat-imposed dormancy in *Dicrostachys cinerea* (L) Wight et arn seeds. Plant Growth Regulation **14**:51-59.

Vesey-Fitzgerald, L. D. E. F. 1965. Lechwe Pasture. The Puku. The Occasional Paper of the Department of Game and Fisheries. **3**:143-147.

Voeten, M. M., C. A. D. M. van de Vijver, H. Olff, and F. van Langevelde. 2010. Possible causes of decreasing migratory ungulate populations in an East African savannah after restrictions in their seasonal movements. African Journal of Ecology **48**:169-179.

Ward, D. 2010. A resource ratio model of the effects of changes in CO2 on woody plant invasion. Plant Ecology **209**:147-152.

Western, D., R. Groom, and J. Worden. 2009. The impact of subdivision and sedentarization of pastoral lands on wildlife in an African savanna ecosystem. Biological Conservation **142**:2538-2546.

Wrench, J. M., H. H. Meissner, and C. C. Grant. 1997. Assessing diet quality of African ungulates from faecal analyses: The effect of forage quality, intake and herbivore species. Koedoe **40**:125-136.

Yayneshet, T., L. O. Eik, and S. R. Moe. 2008. Feeding Acacia etbaica and Dichrostachys cinerea fruits to smallholder goats in northern Ethiopia improves their performance during the dry season. Livestock Science **119**:31-41.

Zurbruegg, R. 2012. Biogeochemistry of a large tropical floodplain system (Kafue Flats, Zambia): River-floodplain exchange and dam impacts. Swiss Federal Institute of Technology, ETH Zurich, Switzerland.

Supporting information

Table S1 First day after the flooding period that the floodplain could be accessed by Kafue lechwe for the period 1963-2010.

Figure S1 Seasonal variation in daily water levels of the Kafue River and the lechwe dung C:N and C:P ratios.

Figure S2 Foliar nitrogen concentrations in living grass biomass in the main lechwe habitats.

Table S1 – First day after the flooding period that the floodplain could be accessed by Kafue lechwe under the assumption that lechwe can access key floodplain areas when the water levels at Nyimba hydrological gauging station are below 980.6 m asl. This value is based on observations of the accessibility of the floodplain in 2010 where we did not observe increased mortalities in Lechwe numbers. Shaded years had access dates later than observed in 2010, and years marked with an asterisk represent years where the accessibility was delayed by 1-2 months. Elevations were measured by means of land surveying with a level instrument (differential leveling) in October 2010

Period	**Year**	**accessibility at 980.7 m asl**	**accessibility at 980.6 m asl**	**accessibility at 980.5 m asl**
Before both dams	1963*	15. Sep	21. Sep	25. Sep
	1964	10. Jul	15. Jul	18. Jul
	1965	16. Jun	20. Jun	23. Jun
	1966	all year	all year	13. May
	1967	all year	all year	all year
	1968	all year	all year	all year
	1969*	1. Aug	7. Aug	14. Aug
	1970	19. May	6. Jun	9. Jul
After first dam	1971	25. Jun	4. Jul	8. Jul
	1972	all year	all year	23. May
	1973	all year	all year	all year
	1974	before 13. Jun	before 13. Jun	13. Jun
	1975	27. Jun	2. Jul	7. Jul
	1976*	30. Jul	3. Aug	8. Aug
After second dam	1977	17. May	23. May	1. Jun
	1978*	31. Aug	6. Sep	10. Sep
	1979*	2. Aug	9. Aug	13. Aug
	1980	19. Jun	26. Jun	2. Jul
	1981	8. Jul	13. Jul	18. Jul
	1982	all year	all year	all year
	1983	all year	all year	all year
	1984	all year	all year	all year
	1985	before 14. Jul	before 14. Jul	14. Jul
	1996	all year	all year	all year
	1997	all year	all year	all year
	1998	all year	all year	all year
	1999	all year	all year	9. Jun
	2000	all year	all year	all year
	2001	18. Jun	25. Jun	2. Jul
	2002	all year	all year	all year
	2003	all year	all year	all year
	2004	all year	all year	all year
	2005	all year	all year	all year
	2006	all year	all year	25. May
	2007	24. Apr	23. May	31. May
	2008	11. May	16. May	22. May
	2009	22. Jun	1. Jul	5. Jul
Reference year	2010	6. Jul	11. Jul	12 .Jul

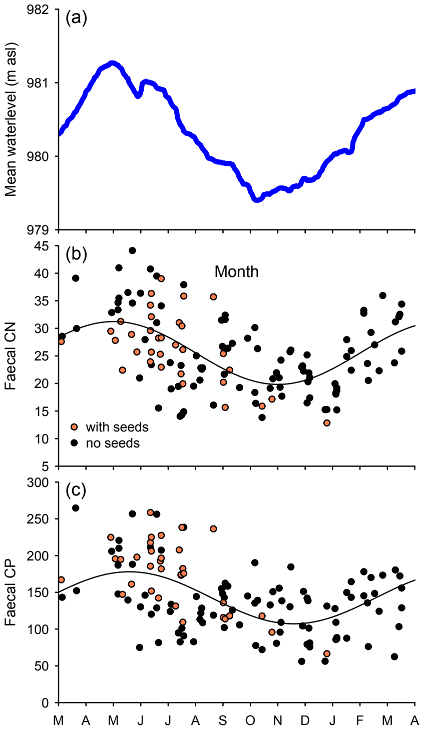
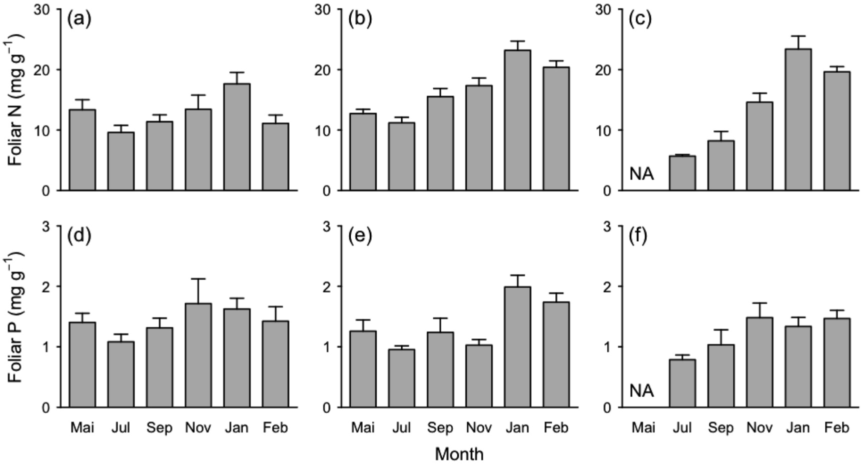


Figure S1 – Seasonal variation in mean daily water levels of the Kafue River (a) the lechwe dung C:N ratios (b), lechwe dung C:P ratios (c), between March 2010 and April 2011. Mean daily water levels of the Kafue River in a) were obtained from the ZESCO hydrological gauging station at Nyimba (for detailed location see Fig. 1a). Sample numbers in the other months varied between 8-37; total 270 samples. Filled black dots in d and e) represent samples without *D. cinerea* seeds; red dots represent samples with seeds.

Figure S2 – Foliar nitrogen concentrations in living grass biomass in the main lechwe habitats termitaria (a), water-meadows (b) and floodplain grasslands (c) as well as and foliar phosphorus concentrations (d-e). Biomass samples were taken at six moments in time between May 2010 and February 2011 in 10-13 sites in termitaria, 7-10 sites in water-meadows and 8-10 sites in floodplain grasslands in Lochinvar National Park (cf. Fig. 2 Chapter 1). Missing data is indicated with the indication NA, while missing bars stand for a value of zero. Displayed are mean values and standard errors.



Summary

Ecosystems in which a high proportion of the aboveground primary production is consumed by large herbivores (both wild and domestic) are known as grazing ecosystems. In recent decades the structure of many grazing ecosystems has been altered by the spread of woody species. By changing the availability of light, water and nutrients, encroachment can have major effects on the understory layer, and hence alter the availability of forage for herbivores.

This study was performed in the Kafue Flats wetlands in Zambia, a large, seasonally inundated floodplain composed of flooded grasslands and marshes, and higher lying termitaria grasslands. The hydrological regime of the Kafue Flats has changed considerably since the construction of two dams across the river Kafue in the 1970s. Furthermore, during the past two decades parts of the floodplain area have been substantially encroached by the South American shrub *Mimosa pigra,* while the termitaria zone has been invaded by the native shrubs *Dichrostachys cinerea* and several *Acacia* species. Large herds of Kafue Lechwe (*Kobus leche* ssp. *kafuensis* Haltenorth, 1963), an endemic antelope species, graze the Kafue Flats ecosystem and migrate seasonally between the termitaria and floodplain areas.

The overall aim of this thesis is to determine the consequences of shrub encroachment for (i) soil carbon (C), nitrogen (N), and phosphorus (P) pools and availabilities, (ii) the diversity, quality and productivity of understory herbaceous plants, and (iii) the food supply of the Kafue lechwe, and its possible effects upon the size of the population. In addition to a field study, I carried out a meta-analysis of the effects of shrub encroachment on soil nutrients and productivity of understory vegetation.

The spread of the leguminous shrub *D. cinerea* in the termitaria area has had major effects on soil conditions, with N and P pools and availabilities increasing with increasing shrub cover and age. This accumulation of soil N and P was consistent with studies of other leguminous shrubs that form a high canopy. The results indicate that *D. cinerea* was not limited by shortages of soil N and P, and there was no apparently negative feedback of nutrient availability upon growth.

Encroaching woody species vary widely in their effects on understory vegetation. The meta-analysis reconciles previously conflicting results and demonstrates that the differences can be explained largely by the functional and morphological traits of different species (i.e. N-fixing ability and height of the canopy above the soil surface) and the rainfall in an area. Along a wide rainfall gradient, N-fixing trees with high canopies showed positive (i.e. net facilitative) effects on understory productivity in drier regions, but negative (i.e. net competition) in wet regions. Woody species with low canopies casting dense shade always had negative effects on understory productivity regardless of water and nutrient relations.

The effect of increasing shrub cover upon understory biomass differed between the two shrub species. Beneath *Mimosa pigra* (a low canopy species), available herbaceous biomass, plant species richness and grass cover all declined linearly with increasing shrub cover*,* while for *D. cinerea* (a high canopy species) the relationships were unimodal and only decreased plant species richness and grass cover at shrub cover above 40%. Furthermore, *D. cinerea* led to a more than doubling of foliar N and P concentrations, while *M. pigra* density had no net effect. These contrasting results indicate that there is no general pattern for encroaching woody species along cover gradients and that canopy architecture and level of encroachment have to be taken into account when assessing potential effects of shrubs on soil or understory vegetation.

The seasonal movements and changes in the nutritional status of the Kafue lechwe were strongly linked to flood height and food resources in their wet season habitat (termitaria). Animals suffered nutritional stress in the period before the annual floods receded, and recovered when the floods allowed them to migrate to the floodplain. Hence, food in the floodplain, where *M. pigra* is now encroaching, does not seem to be limiting the lechwe population. During the period of food scarcity the lechwe – although considered a strict grazer – were found to consume *D. cinerea* seedpods, with apparently beneficial effects for their nutritional status. The fact that lechwe utilized *D. cinerea* as food, and also that shrubs increased the nutritional quality of understory grasses, suggest that effect of encroachment has been less negative than previously supposed. Rather, the critical factor determining the lechwe population seems to be the timing of flooding, both its rise and fall, which influences floodplain productivity and largely determines when animals can leave the termitaria grasslands and feed on the better quality herbage of the floodplain. Hence, water management is of crucial importance for conservation of this species.

In conclusion, encroachment of the Kafue Flats ecosystem by two morphologically different leguminous shrubs has had large effects on understory vegetation. These effects depend strongly on the canopy structure of the different shrubs and their ability to fix N, as well as upon the degree of encroachment. Thus, merely quantifying the extent of woody plant invasion does not necessarily yield reliable predictions about its consequences for grazers. Although woody encroachment has reduced herbage production, the Kafue lechwe have been resilient to this decline because they were able to adapt their diet and benefit from shrubs as a dry season food supplement. These findings add to our understanding of the effects of woody plant encroachment on grassland and wetland ecosystems, and should contribute to the sustainable management and conservation of these ecosystems and their herbivores.

Zusammenfassung

Ökosysteme, in welchen Huftiere grosse Anteile der Primärproduktion konsumieren, werden als Weideland-Ökosysteme bezeichnet. In den letzten Jahrzehnten führte Verbuschung in vielen dieser Weideland-Ökosysteme zu einer Veränderung der Vegetationsstruktur. Verbuschung verändert die Verfügbarkeit von Licht, Wasser und Nährstoffen, sie kann daher einen wesentlichen Einfluss auf die Vegetation im Unterwuchs haben und somit das Futterangebot für Herbivore verändern.

Diese Studie wurde im Kafue Flats-Ökosystem, einem saisonal überfluteten Auengebiet in Sambia, durchgeführt. Das Ökosystem besteht aus Feuchtwiesen und Sümpfen sowie einem höher gelegenen, durch zahlreiche Termitenhügel gekennzeichneten Grasgebiet (Termitaria). Seit der Konstruktion von zwei Staudämmen am Kafue Fluss hat sich die Hydrologie der Kafue Flats drastisch verändert: Teile der Feuchtwiesen erlitten Verbuschung durch die invasive Strauchart *Mimosa pigra*, und die Termitaria verzeichnete eine Zunahme der Baumdichte durch *Dichrostachys cinerea* und verschiedene Akazienarten. Das Kafue Flats-Ökosystem wird von grossen Herden der endemischen Kafue-Litschi-Moorantilope (*Kobus leche* ssp. *kafuensis* Haltenorth, 1963) beweidet. Je nach Saison wandern die Litschi-Moorantilopen zwischen den Termitaria und den Feuchtwiesengebieten.

Ziel dieser Dissertation war es, den Einfluss von Verbuschung auf (i) Kohlenstoff (C), Stickstoff (N) und Phosphor (P) Pools und Verfügbarkeiten im Boden, (ii) die Artenvielfalt, Qualität und Primärproduktion der Vegetation im Unterwuchs, und (iii) das Futterangebot für die Litschi-Moorantilope sowie dessen möglichen Effekt auf die Populationsgrösse der Litschi-Moorantilope zu ermitteln. Zusätzlich zu den Untersuchungen im Feld, führte ich eine Meta-Analyse über die Auswirkungen von Verbuschung auf die Boden-Nährstoffe und die Primärproduktion der Vegetation durch.

Die Zunahme der N-fixierenden Strauchart *D. cinerea* in der Termitaria hatte einen grossen Effekt auf die Bodeneigenschaften und erhöhte N und P Pools sowie Verfügbarkeiten mit zunehmender Strauchdichte und zunehmendem Alter. Die Akkumulation von N und P im Boden war vergleichbar mit Studien, welche andere N-fixierende Bäume und Büsche mit erhobenen Baumkronen untersuchten. Meine Resultate zeigen auf, dass *D. cinerea* nicht durch einen Mangel an N und P im Boden

limitiert wird und dass die Verfügbarkeit an N und P kein negatives Feedback auf das Wachstum des Strauches hat.

Der Einfluss von Verbuschung auf die Vegetation im Unterwuchs variiert stark zwischen verschiedenen Holzgewächsen. Die Meta-Analyse ermöglichte es mir, zuvor gegensätzliche Resultate unter einen Hut zu bringen, und sie zeigte auf, dass die Unterschiede grossteils von funktionellen und morphologischen Merkmalen der verschiedenen Arten (d.h. von ihrer Fähigkeit, Stickstoff zu fixieren und von der Höhe der Baumkronen über dem Boden) sowie vom Niederschlag in einem Gebiet abhängen. Stickstoff-fixierende Holzgewächse entlang eines Niederschlaggradienten hatten positive Effekte auf das Wachstum der Vegetation im Unterwuchs in trockenen Regionen, aber negative Effekte in Regionen mit hohem Niederschlag. Holzgewächse mit niedrigen Baumkronen, welche dichte Schatten werfen, hatten immer einen negativen Effekt auf das Wachstum im Unterwuchs, unabhängig vom Niederschlag.

Zunehmende Dichten der beiden Straucharten *Mimosa pigra* und *D. cinerea* hatten einen unterschiedlichen Einfluss auf die Vegetation im Unterwuchs. Unter *M. pigra* (einer Strauchart mit niedriger Baumkrone), führte eine Zunahme der Strauchdichte zu einer linearen Abnahme der krautartigen Biomasse, der Artenvielfalt sowie der Dichte der Grasbedeckung, während der Zusammenhang unter *D. cinerea* (einer Strauchart mit erhöhter Baumkrone) unimodal war. Zudem führte eine Zunahme der Dichte von *D. cinerea* zu mehr als einer Verdoppelung der N und P Konzentrationen im Pflanzenmaterial der Gräser im Unterwuchs, während *M. pigra* keine solchen Effekte zeigte. Diese kontrastierenden Resultate zeigen, dass es kein generelles Muster gibt, wie sich Straucharten entlang eines Gradienten mit zunehmender Dichte verhalten und dass die Architektur der Baumkronen sowie der Grad der Verbuschung mitbeachtet werden muss, wenn man die potentiellen Effekte von Sträuchern auf die Vegetation im Unterwuchs abschätzen will.

Die saisonalen Migrationsbewegungen sowie Veränderungen im Ernährungszustand der Litschi-Moorantilopen waren stark von den Wasserständen in den Feuchtwiesen sowie den Nahrungsressourcen im - in der Regenzeit beweideten - Habitat (Termitaria) abhängig. In der Zeit, bevor die Wasserstände nach der jährlichen Überflutung sinken, litten die Tiere unter Mangelernährung und erholten sich erst, wenn es ihnen tiefere Wasserstände erlaubten, in die Feuchtwiesen zu migrieren. Demzufolge scheint die Nahrungsverfügbarkeit in den Feuchtwiesen, wo die Verbuschung durch M. pigra stattfindet, nicht limitierend für die Litschi-

Population zu sein. Ich stellte fest, dass die Litschi-Moorantilope während der Zeitspanne der Futterknappheit *D. cinerea* Samenkapseln frassen, dies obschon die Antilope als strikt grasfressende herbivore Art klassifiziert ist. Der Konsum von *D. cinerea* Samenkapseln wirkte sich positiv auf den Ernährungszustand der Litschi-Moorantilope aus. Die Tatsache, dass Litschi *D. cinerea* als Nahrung nutzten und dass diese Strauchart die Nährqualität des Grases im Unterwuchs erhöhte, deutet darauf hin, dass der Effekt der Verbuschung durch *D. cinerea* weniger negativ sein kann, als zuvor vermeintlich angenommen. Vielmehr scheint das Timing der jährlichen Überflutung, sowie das Steigen wie auch das Zurückgehen des Wasserpegels der kritische Faktor zu sein, welcher die Grösse der Litschi-Population festlegt. Das Timing der Überflutung beeinflusst die Primärproduktion der Vegetation in den Feuchtwiesen und bestimmt zu einem grossen Teil, wann die Antilopen die Termitaria verlassen können, um in den nahrhafteren Feuchtwiesen zu weiden. Die Wasserwirtschaft (water management) ist demzufolge von entscheidender Bedeutung für die Erhaltung der Litschi-Moorantilope in den Kafue Flats.

Abschliessend lässt sich daher folgern, dass die Verbuschung durch zwei morphologisch unterschiedliche, Stickstoff-fixierende Straucharten im Kafue Flats-Ökosystem starke Auswirkungen auf die Vegetation im Unterwuchs hat. Diese Auswirkungen hängen jedoch stark von der Baumkronen-Struktur, der Fähigkeit von Sträuchern, Stickstoff zu fixieren sowie dem Grad der Verbuschung ab. Das blosse Quantifizierung des Ausmasses an Verbuschung ist daher nicht ausreichend, um zuverlässige Voraussagen bezüglich Konsequenzen von Verbuschung für weidende Huftiere zu machen. Obschon Verbuschung die Produktion der Vegetation im Unterwuchs verringert hat, trotzt die Litschi-Moorantilope dieser Abnahme, da sie ihre Ernährung den veränderten Verhältnissen anpassen konnte und nun von den Sträuchern als Nahrungsergänzung profitiert.

Meine Erkenntnisse tragen zum besseren Verständnis der Auswirkungen von Verbuschung in Weideland und Feuchtgebieten bei und leisten daher einen hilfreichen Beitrag für eine angemessene Bewirtschaftung und Erhaltung dieser Ökosysteme und ihrer Herbivoren.

Acknowledgements

My PhD brought me to an amazing country with fascinating ecosystems, wildlife, culture and incredibly warm and welcoming people. But not only in Zambia but also at home I got to meet and know so many amazing people that supported me along the way. So if I had to do this PhD again I would start right now just to meet all of you again.

I am very grateful to Peter Edwards and Harry Olde Venterink for supervising my thesis and supporting me throughout all the highlights and lowlights this PhD brought along. Thanks a lot for believing in me. I am thankful that Julian Thompson was willing to be my co-examiner.

The two years I spend in Zambia were the best time of my PhD and I was privileged to have the support of fantastic people during my stay. I am extremely thankful to Griffin Shanungu who was housing me in Lochinvar and supported and motivated me every day I spent in Zambia. Thank you for your great friendship! In Lochinvar my close companions were Benjamin, Osten, Michael, Event and Chris. Thank you for sharing your vast knowledge about the Kafue Flats and for opening my eyes to so many important details. Your observations and questions about my work made this thesis become what it is today. I am very grateful to the Zambia Wildlife Authority (ZAWA) who granted me permission to conduct this work in Lochinvar National Park and provided a lot of support in the field. I thank all the wildlife police officers in Lochinvar as well as management staff in Monze and Chilanga. A big thank you goes to Cliff, Zeko and Albert for their help with dung collections.

I had the privilege to work with many of the former researchers in the Kafue Flats area. A special thanks goes to Gerard Ellenbroek and his wife Merian, Bob Douthwaite, Geoffrey Howard, Wendy Rees and Mike Bingham who rendered assistance both in the field and remotely via e-mail. I further extend my gratitude to the IWRM centre at the University of Zambia.

A big thanks goes to my work colleagues in Zurich who supported me mainly during the hard and long period of writing this thesis and made my life in Zurich to be about so much more than just my PhD. I especially like to thank Judith, Simon, Aud, Luciola and Jeff. Thank you for your open ears, your encouraging words and all the laughs we shared! I extend my gratitude further to Annette, Karsten, Hans-Heini, Regina, Nicky, Andrea, Lin, Jake, Iris, Ana, Dieter, Kathrin, Margot, Sonja, Steffi, Stephanie and Hans. Thanks to all my ADAPT colleagues for their fruitful collaborations over the past four years, particularly Roland Zurbrügg, Philipp Meier and Florian Köck. For their huge support and visits in Zambian I would also like to thank my friends and extended family. I could not have done it without you.

This project was founded by the Competence Centre for Environment and Sustainability (CCES) of the ETH domain.

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Publications

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Roy, B. A., T. Coulson, W. Blaser, T. Policha, J. L. Stewart, G. K. Blaisdell, and S. Gusewell. 2011. Population regulation by enemies of the grass Brachypodium sylvaticum: demography in native and invaded ranges. Ecology 92:665-675.