CHAPTER 8

8.1 CONCLUSION

Overall, my results showed that ungulate browsing may negatively influence nutrient cycling in the immediate vicinity of palatable tree species (i.e. decelerating effect) through a drastic reduction of organic matter returned to the soil rather than through changes in litter quality as has been proposed for boreal forest ecosystems (Fig. 8.1). However, (Naiman, *personal comments*) this must be better addressed through a more detailed analysis of processes involved in the nutrient cycling within the plant-browser-soil system (e.g. N denitrification, mineralization, N2-fixation, N dung content etc.). Indeed, the fact that I found less total soil N at heavily browsed sites doesn't necessarily mean that it is associated with a decreased nitrogen cycling (Pastor, *personal comments*). Nitrogen and phosphorus availabilities to plants are determined not by pool sizes but by the supply rate into those pools through mineralization of organic matter (Pastor, *personal comments*). Therefore my first hypothesis that ungulate browsing may have a decelerating effect on nutrient cycling must be tested further.

However, ungulate browsers are able to establish a positive feedback loop with highly palatable, inherent fast growing woody plant species, which produce highly decomposable litter and show high mass compensatory growth abilities (i.e. accelerating effect). These plant responses resemble those observed in grasses under ungulate grazing (Fig. 8.2). Grazers are able to induce changes in the nutrient cycle within individual plants and increase grass compensatory growth abilities promoting and sustaining the "grazing lawns" (McNaughton 1979, 1983). I demonstrated here that *Acacia nigrescens* trees are highly resilient to browsing pressure in the long-term. This suggests the presence of analogous "browsing lawns" where heavily browsed *Acacia* trees rely on different eco-physiological mechanisms and/or nutrient sources to sustain plant compensatory growth (Fig. 8.2). However, although ungulate browsing seems to be able to stimulate and maintain a fast nutrient cycling within the plant-browser system, it is unlikely that this will have the same consequences at the whole ecosystem level as shown for the "grazing lawns" (Fig. 8.2). Nevertheless, it might be possible that within the woody plant community, individual plants might affect nutrient cycling at local scales in different ways (Naiman et al. 2003). For example, there are indications that total soil N beneath heavily browsed *A. nigrescens* trees is lower than in lightly browsed sites (Chapter 4; du

Toit et al. 1990). The opposite trend was observed for *A. tortilis* (du Toit el al. 1990), soil N being still high under trees that experienced browsing damage at a waterhole site. Although waterhole sites might represent hotspots of elevated soil nutrients (Naiman et al. 2003), it is plausible that the interactions between individual woody plants and browsing intensity may influence soil nutrient concentrations beneath the tree crowns.

The study was motivated by the need to improve our understanding of the effects of ungulate browsing on ecosystem properties since most of the previous studies in African savannas have been focused on the grazing guild. Nevertheless, the study has tested predictions of prevailing hypotheses, which are based on research in boreal and temperate forests (Naiman et al. 1986; Pastor et al. 1988; Pastor et al. 1993; Persson et al. 2005). Those studies showed that large mammalian browsers through their selective feeding on preferred woody plant species are able to modify fundamental ecosystem processes such as nutrient cycling and habitat productivity.

In N-limited boreal forest ecosystems, browsers preferentially feed on fast growing palatable species in the early stages of vegetation succession. This leads to an increased number of unpalatable evergreens, which produce less decomposable litter with consequent negative effects on ecosystem nutrient cycling (Fig 8.1). It has been shown however, that litter quantity rather than leaf litter quality may also be responsible for reducing productivity in N-limited Swedish boreal forests (Persson et al. 2005). This because browsers when feeding on medium preferred “bulk food” species, and not only on highly preferred deciduous species, may not cause changes in the functional species composition of the plant community. Consequently, the reduction of organic matter returned to the soil might be the main factor responsible for the decreased microbial activity and decreased nutrient cycling rather than the chemical composition of leaf litter. These findings demonstrate that the effects of ungulate browsing on ecosystem processes are complex and depend on the interactive effects of many critical environmental factors.

Here I’ve focused my research on browser-plant-soil interactions in a semi-arid eutrophic African savanna where the set of abiotic and biotic factors is markedly different from their boreal forest counterparts. I showed that the browsing guild is responsible for dramatic changes in the population structure of a palatable *Acacia* woody species and proposed new hypotheses on how ungulate browsing may affect nutrient cycling within few meters from highly palatable woody species. Indeed, no changes in plant functional type composition were found within the vegetation community along a strong browsing gradient whereas a high number of palatable plants were recorded among heavily browsed sites. The reason for this discordance with boreal and temperate scenarios should be searched for in the main ecological factors responsible for ecosystem functioning in semi-arid southern African savannas. Abiotic drivers such as soil nutrient concentration and water availability contribute to a patchy distribution of evergreens and other unpalatable slow-growing species throughout the landscape, regardless of browsing intensity. Moreover, palatable woody species showed high resilience under high browsing intensity due to increased physical defences, increased compensatory growth abilities in adult trees, as well as high resprounting abilities in gullivers. Therefore, in an arid-eutrophic savanna it appears that fast-growing palatable woody species are the better competitors against more chemically defended, slow-growing tree species, which is contrary to the general pattern in boreal-temperate forests.

Measurements of gullivers morpho-functional traits and modelling results suggest that ungulate browsing strongly limits plant recruitment from seedling to adult size. This might be more critical for individuals of tolerant plants in their early life-history stages. They are highly damaged by browsers, likely use nutrients stored in the roots to re-sprout and need efficient mechanisms to replenish root reserves since mineralization rates are low and highly variable in semi-arid African savannas. Hence, ungulate browsing may represent a stronger selective force than fire for the expression of resistance traits in sites associated with high grazing pressure. It might be then, that in heavily browsed and heavily grazed sites (i.e. sites within few km from water sources) where fire occurs less frequently due to the low grass fuel, woody species that rely more on resistant than on tolerant traits would be favoured within the vegetation community in the long-term period.

In general, my results suggest that long-term selective browsing on stands of palatable *Acacia* trees may have a negative effect on nutrient cycling, as inferred from a general depletion of total soil N at heavily browsed vegetation sites. I suggest that soil nutrients depletion is primarily due to a drastic reduction of litter input into the soil from heavily browsed palatable trees (Fig. 8.2). This would lead in a long-term to a C deficit for microbial activity, which in turn has negative effects on soil N mineralization rates. However, more data are needed to conferm such results since I didn’t measure important nutrient cycling processes such as nitrogen mineralization, denitrification, nitrogen inputs and nitrogen released from dung. I suggest there are important indications of a positive feedback loop between browsers and their food resource, which resemble at least in part those proposed for the grazing guild (Fig. 8.2). In fact, ungulate browsing seems to be able to stimulate and maintain a fast nutrient cycling within the plant-browser system but not with the same positive consequences at the whole ecosystem level as shown for the "grazing lawns". The fast nutrient cycle is triggered by tree pruning which is likely to decrease competition between plant shoots (du Toit et al. 1990) and simultaneously increase N availability for plant sprounting which was indeed supported by the higher leaf N content found in heavily browsed trees during the growing season.

To conclude, my data show that ungulate browsing affects nutrient cycling through two different processes, (1) promoting a short-term positive feed-back loop with palatable woody plants which is triggered by tree pruning (i.e. effect similar to those observed for the "grazing lawns"), and (2) a potential negative long-tem impact due to constant browsing pressure on plant species driven by changes in quantity of organic matter returned to the soil rather than qualitative changes in plant community composition.

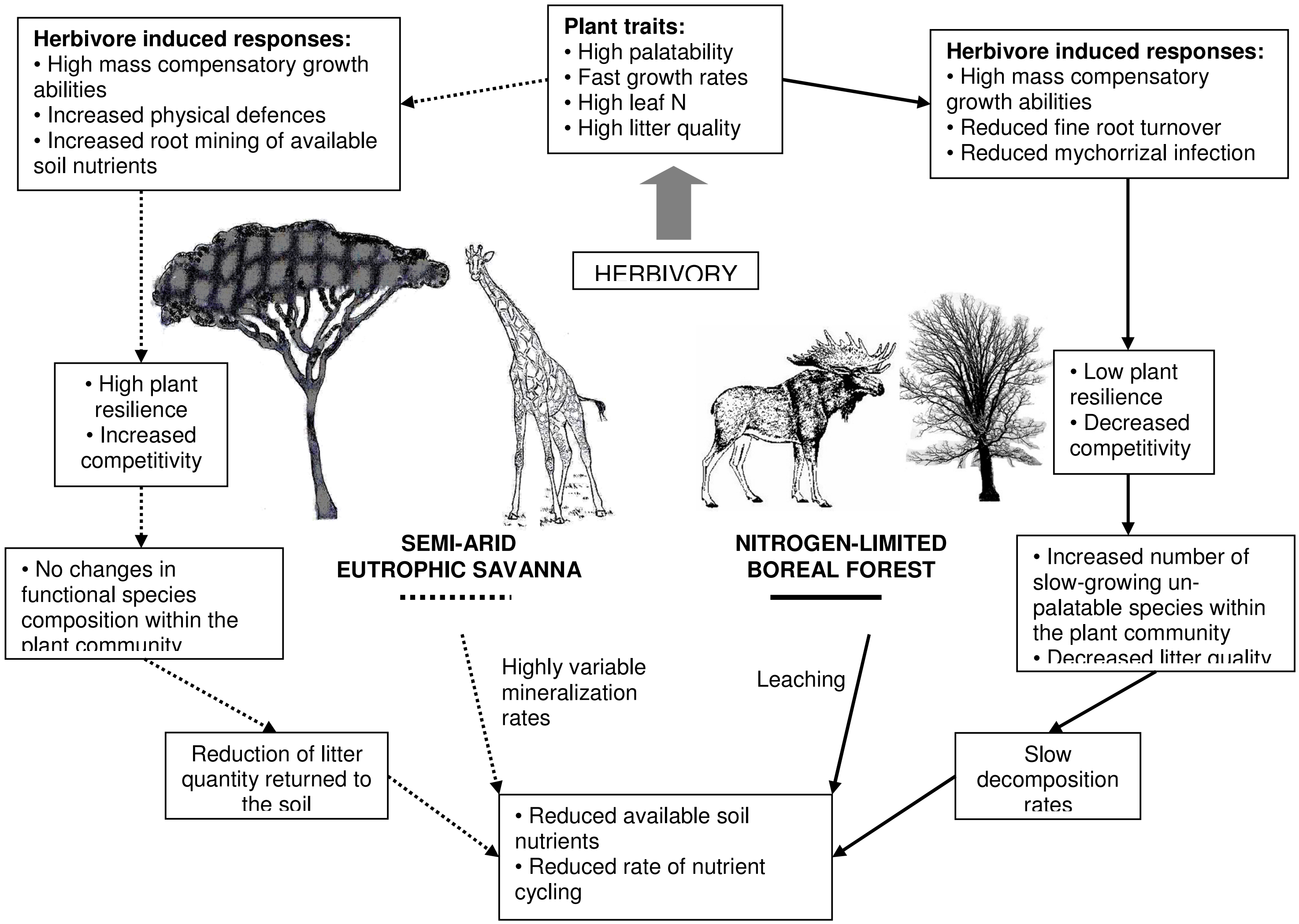

FIG. 5. Schematic of the effects of ungulate browsing on nutrient cycling in semi-arid African savannas and boreal forest ecosystems.

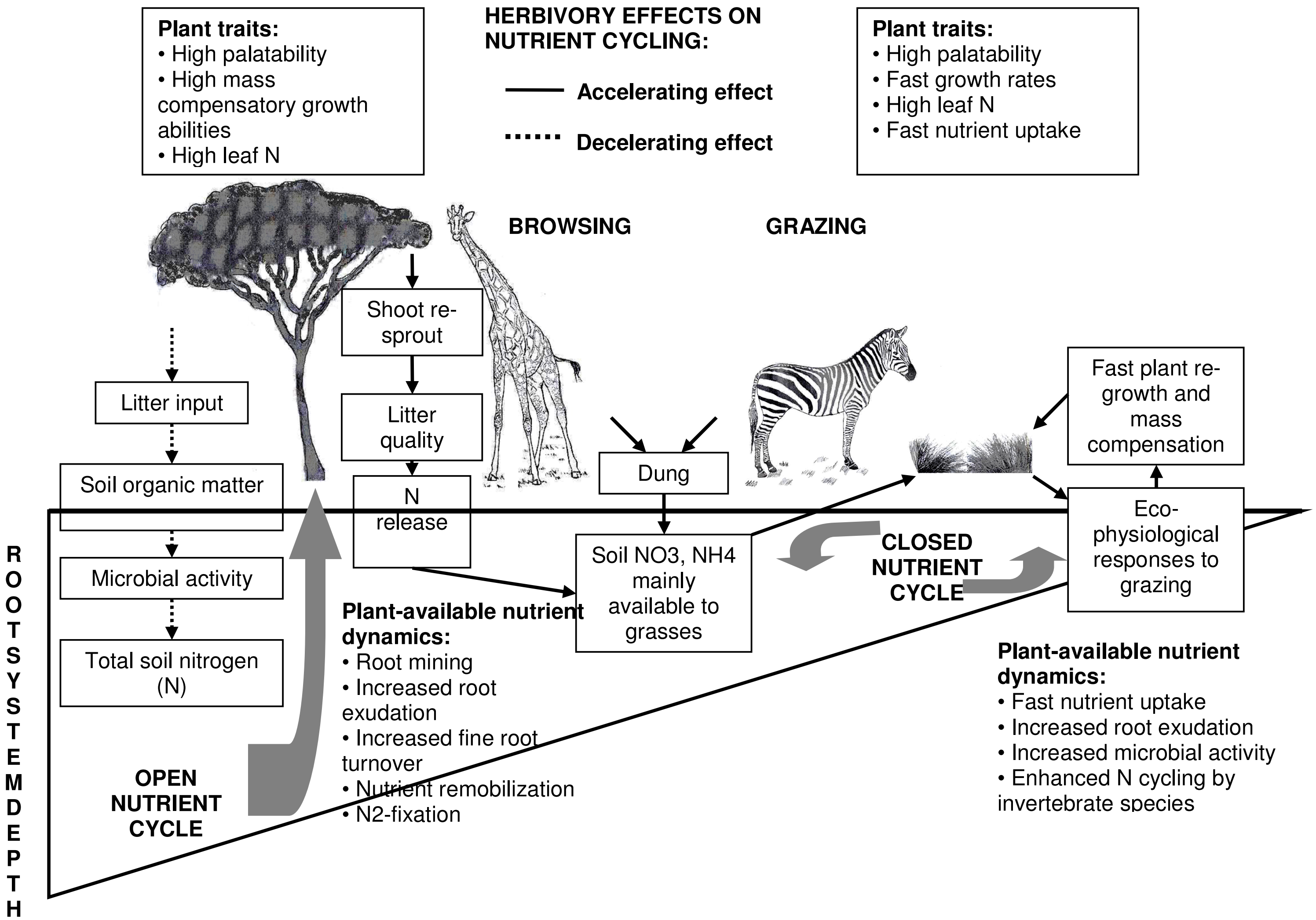

FIG. 6. Mechanistic basis on how browsers and grazers may differently affect nutrient cycling in semi-arid eutrophic savannas.

8.2 REFERENCES:

du Toit, J., Bryant, J. P., Frisby, K. 1990. Regrowth and palatability of *Acacia* shoots following pruning by African Savanna browsers. *Ecology* 71:140-154.

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

McNaughton, S. J. 1983. Compensatory growth as a response to herbivory. *Oikos* 40:329-336.

Naiman, P. J., Melillo, J. M. and Hobbie, J. E. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). *Ecology* 67:1254-1269.

Naiman, R. J., Braack, L. Grant, R., Kemp, A. C., du Toit, J. T., Venter, F. J. 2003. Interactions between species and ecosystem characteristics. In: J. du Toit, K. Rogers and H. Biggs, editors. *The Kruger experience. Ecology and Management of savanna heterogeneity.* Island Press, Washington, DC, US. pp 221-241.

Pastor, J., Naiman, R. J., Dewey, B. and McInnes, P. 1988. Moose, Microbes, and the Boreal Forest. *BioScience* 38: 770-777.

Pastor, J., Dewey, B., Naiman, R. J., McInnes, P. F. and Cohen, Y. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74:467-480.

Persson, I. -L., Pastor, J., Danell, K. and Bergström, R. 2005. Impact of moose population density on the production and composition of litter in boreal forests. *Oikos* 108:297-306.