

CHAPTER 7

Ungulate browsing and plant defensive traits: modelling changes in plant productivity and soil nutrient availability in savanna

Abstract

I propose a simple simulation model that makes predictions on the effects of ungulate browsing on changes in plant productivity and soil nutrient availability in a semi-arid eutrophic savanna. I assumed that percentage of yearly plant biomass lost as leaves and stems due to browsers is dependent upon plant defensive strategy (i.e. resistance and tolerance). Hence browser-tolerant plants experience high damage but show high compensatory growth abilities rather than relying on physical or chemical defence. If we Holding constant default parameters for the model runs, the results show that resistant plants have low nutrient requirements, reduce soil nutrient uptake, produce less compensatory biomass, and keep soil resources at higher levels than tolerant plants. On the other hand, tolerant plants have high nutrient requirements, increase soil nutrient uptake and potentially grow faster than resistant plants. However, populations of browse-tolerant plants can be maintained only at suitable nutrient supply rates (e.g. mineralization rates), which are highly variable in semi-arid African savannas. Moreover, when costs related to the increased resprouting abilities were considered for early plant life-history stages, then tolerant plants decreased productivity more than resistant plants. Modelling results partially confirm those from empirical data collected during a two-year vegetation survey in a southern African savanna where spinescent *Acacia* trees predominate within the vegetation community. However, field observations and literature show that many savanna woody species may often rely on both resistance and tolerance traits. I suggest that the existence of these functional types in semi-arid eutrophic savannas may be explained by the fact that (1) costs related to resistance traits (i.e. spines) are relatively low and amortized overall several years, and (2) tolerant traits, such as enhanced plant compensatory growth abilities, may rely on different nutrient source-sinks (i.e. N₂ fixation, plant internal N remobilization, indirect positive effects of browsers on

mineralization rates via the root system etc.) other than those provided by leaf litter or manuring by mammalian herbivores.

KEY WORDS: *Acacia*, ALLOCATE model, compensatory growth, resistance, tolerance

7.1 INTRODUCTION

Plant responses to damage induced by large mammalian herbivores have been addressed at levels ranging from tree species (Danell et al. 1985; Young 1987; du Toit et al. 1990; Edenius et al. 1993; Young and Okello 1998; Bergström et al. 2000; Oba et al. 2000), through plant communities (Jachmann and Croes 1991; McInnes et al. 1992; Liang and Seagle 2002; Augustine and McNaughton 2004) to ecosystems (Pastor et al. 1988; Pastor and Naiman 1992; Ritchie et al. 1998; Wardle et al. 2001; Bardgett and Wardle 2003). Empirical and theoretical studies have demonstrated that such responses have important consequences for primary productivity and mediate interactions between producers, consumers, and decomposers (McNaughton et al. 1988; Pastor et al. 1988, 1997; Bryant et al. 1991; Ritchie et al. 1998; de Mazancourt and Loreau 2000; Bardgett and Wardle 2003). Qualitative and quantitative plant responses to herbivory are likely dependent on levels of habitat resources (Coley et al. 1985), which influence from the “bottom-up” the type of defensive trait adopted.

Plants may enhance either chemical or physical *resistance* traits (*sensu* Strauss and Agrawal 1999) to reduce the amount of biomass removed by herbivores (Cooper and Owen-Smith 1985, 1986; Young 1987; Gowda 1996) or may show *tolerance* (Strauss and Agrawal 1999; Chase et al. 2000) by enhancing compensatory growth abilities to recover from mass loss due to herbivore damage (Dangerfield and Modukanele 1996; Oba 2000; Abu-Zanat et al. 2004; see Strauss and Agrawal 1999 for review). Differences in plant resistance and tolerance traits within vegetation communities may have important ecological and evolutionary implications (Chase et al. 2000), and it is likely that a trade-off between these two opposite defensive traits occurs depending on the interplay of key environmental constraints (Rosenthal and Kotanen 1994). Moreover, the type of defence adopted may be related to important plant eco-physiological traits, such as leaf palatability, relative growth rate or nutrient use efficiency (see Ritchie et al. 1998).

Former hypotheses, which aimed to explain patterns of plant responses to herbivory (see Stamp 2003 for review), have focused on cost/benefits of different defensive traits according to tradeoffs across plant growth-defence-reproduction

processes (Lerdau and Gershenzon 1997). We might then expect highly protected resistant plants to have high costs associated with increased mechanical or chemical defences (see Chase et al. 2000), and would grow slower than less protected tolerant plants, which rely on high compensatory growth abilities when subjected to high mass loss rates. Nonetheless, this may have consequences on plant nutrient requirements (i.e. nutrient uptake rates), which in turn affects availability of soil nutrients (Ritchie and Tilman 1995; Ritchie et al. 1998). For example, in temperate and boreal forests ungulate browsers preferentially feed on tolerant, fast-growing plants (i.e. pioneer woody species in the early stages of vegetation succession) than on more resistant unpalatable woody species (i.e. evergreens) with important implications for both plant community composition and ecosystem functioning (Pastor 1988, McInnes et al. 1992; Kielland and Bryant 1998; Ruess et al. 1998). Therefore, simulation models have been proposed in the last few decades to better predict the effects of ungulate browsing on forest structure-dynamics, as well as to support decision-making processes for forest management (Jorritsma et al. 1999; Kramer et al. 2003; Weisberg and Coughenour 2003; Tremblay et al. 2004 for review).

Whether these complex gap models were spatially explicit or individual based, great attention has been paid to key parameters, such as plant leaf area and light-use efficiency of simulated tree species to evaluate browsing effects on plant community structure and patterns of vegetation succession. However, there is a need to address how ungulate browsing can affect plant productivity and the soil nutrient pool according to opposing plant defensive traits (i.e. resistance *vs* tolerance) in ecosystems where light is not a major constraint in structuring the vegetation community. A good example is the *Acacia* savannas of eastern and southern Africa, which have co-evolved with a high density and variety of large mammalian herbivores (du Toit and Cumming 1999; Olff et al. 2002).

Since the investment in different plant defensive traits indirectly influence plant productivity and soil nutrient uptake (see Lerdau and Gershenzon 1997), a modelling approach that addresses such interactions may improve our understanding of the mechanisms affecting nutrient cycling within the plant-browser system.

Here, I propose a simple simulation model applicable to a semiarid eutrophic southern African savanna for which empirical data had been collected during a two-year survey (see Chapter 3, 4, 5 and 6). The model simulates the effects of ungulate browsing on woody plants, which alternatively show three different defensive traits: high tolerance,

high resistance and an intermediate defensive trait. The model is neither thought to simulate vegetation dynamics nor interspecific competition. The aim of the model is to quantify the effects of different plant defensive traits on changes in plant biomass and in the concentration of available soil nutrients along a strong browsing gradient.

7.1.1 Conceptual definition

Tree pruning by ungulate browsers causes mass loss in woody plant species and affects plant morpho-functional traits. This influences resource allocation patterns to different plant compartments such as roots, stems and leaves (Fig. 7.1). The amount of biomass removed also depends on the type of defensive trait adopted, which is related to important plant eco-physiological traits. For example, tolerant plants must grow quickly and allocate biomass to new leaves and stems after severe herbivore damage. This in turn modifies the use of soil resources by woody plants (e.g. plant nutrient requirements), and in a long-term period affects soil nutrient levels (Fig. 7.1). It must be noticed that the model doesn't incorporate complex plant-animal interactions, neither feedbacks within the plant-browser-soil system. Moreover aspects related to turnover rates of roots and the activities of fossorial animals were not incorporate into the model to limit as much as possible complexity. Hence the simulation model focuses on the effects of tree pruning on both changes in plant biomass and soil nutrient availability along a strong browsing gradient and its predictions must be interpreted under the above-mentioned limitations. I started considering the important theoretical framework of the model ALLOCATE, proposed by Tilman (1988), which already incorporates critical aspects and mechanisms of plant growth according to key environmental factors. ALLOCATE can make predictions on the outcomes of plant interspecific competition according to varying light and plant resource requirements, but interspecific competition was not considered in my model. Instead, I specifically focus on individual plant species, which are assumed to grow in monospecific stands.

7.1.2 Assumptions

First, light is not considered a key factor among those structuring woody vegetation communities in open eutrophic savannas (see Sinclair and Norton-Griffiths 1979; Huntley 1982). Second, the model assumes that plant growth is affected by soil nutrient availability, which in turn depends on nutrient requirements by plants (Tilman 1988).

Plant nutrient requirements are affected by nutrient supply rates, as well as by the amount of biomass removed by browsers according to varying defensive traits. Third, I assume that plant individuals grow under density independent loss rates. Finally, the model is neither spatially explicit nor individual based, and has only a vertical structure, therefore all the individuals of the same cohort experience the same nutrient availability and grow under the same environmental constraints.

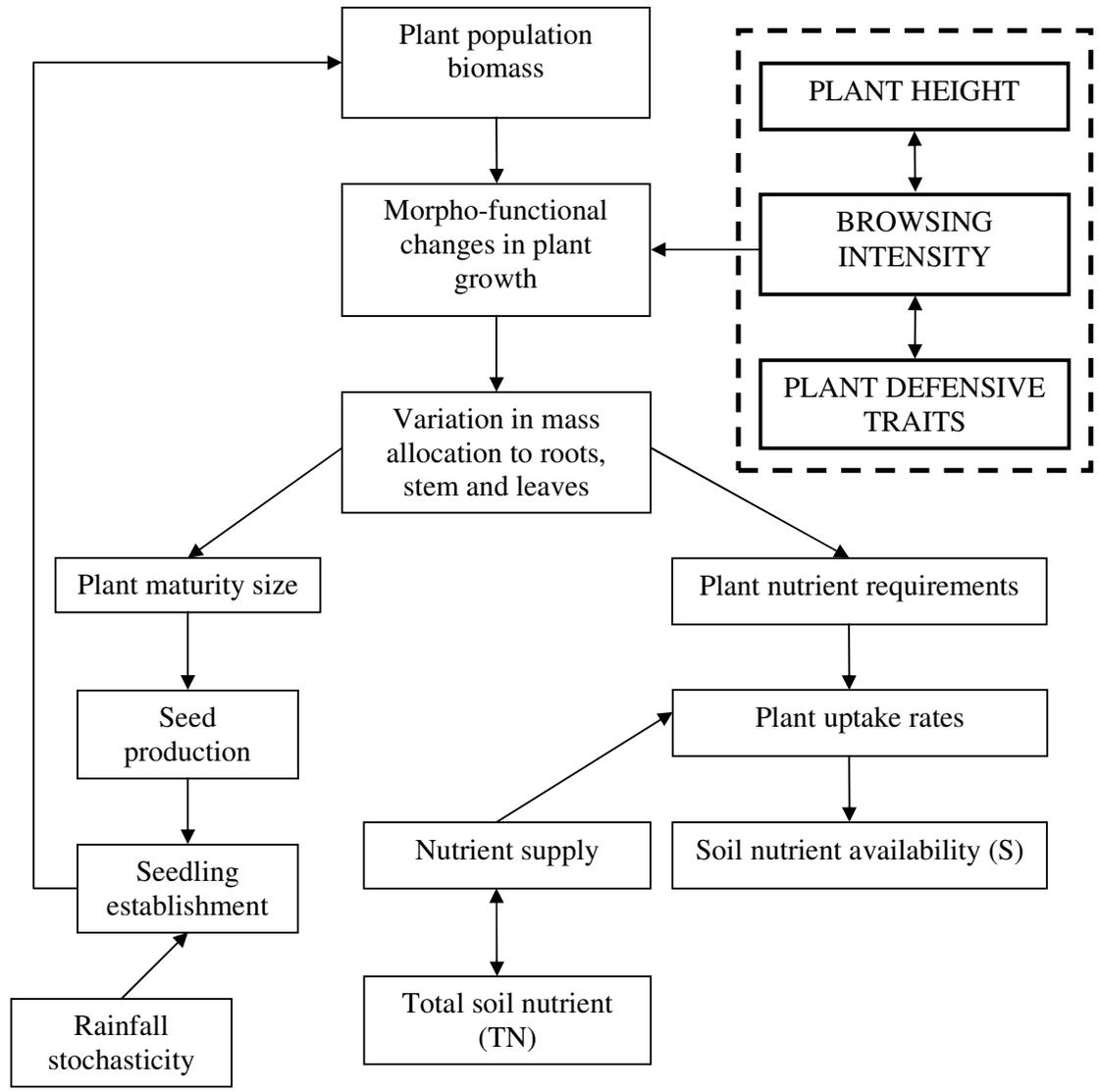


Fig. 7.1. Conceptual model of the potential effects of browsing intensity, defensive traits and plant height on changes in plant biomass and soil nutrient availability (S). Note – the above elements of the system are those that were incorporated in the model only. The influence of browsing on litter quantity, quality and decomposition (for example) were not included. Moreover important feedbacks from leaf litter which may better incorporate nutrient cycling were excluded for simplicity.

7.2 OPERATIONAL DEFINITION

Specific formulae used to simulate plant growth can be found in Tilman (1988) and are summarized below as part of the ALLOCATE model. Meanwhile, I introduced definitional and ecological rules (*sensu* Jeltsch et al. 1997) to optimize my modelling approach on ungulate browsing-woody plant interactions in a eutrophic African savanna.

7.2.1 Specific formulae of the ALLOCATE model

- A) A size-structured population with individuals germinating from seeds and undergoing continuous vegetative growth until reaching adult size was considered. Starting as seed the individual allocates biomass according to varying proportional allocation to roots, stems and leaves. Biomass to roots (BR), leaves (BL) and stem (BS) increases daily due to allocation of new photosynthate (DBt, see Table 7.1) to different plant compartments as follows:

$$BR = rAR * DBt + BR;$$

$$BL = rAL * DBt + BL;$$

$$BS = rASt * DBt + BS;$$

Here rAR, rASt and rAL are the proportional allocation, respectively to roots, stems and leaves (see Table 7.1). According to phenological traits of common *Acacia* trees growing in a eutrophic savanna (e.g. *Acacia nigrescens*, *A. tortilis*, *A. exuvialis*; see Coates Palgrave et al. 2002), I consider one simulated year including 180 days during which woody plants could actively photosynthesize before to shed their leaves.

- B) Photosynthetic efficiency is nutrient dependent and production of new photosynthate is positively correlated to leaf biomass according to the function (modified from Tilman 1988):

$$DBt = ((BL * r * C) / (C + K)) - RESP;$$

Here, DBt is the amount of photosynthate produced daily, RESP includes plant respiration rates (see below), r is the maximal photosynthetic rate, K is an half saturation constant for soil nutrients, C is the effective availability of soil nutrients (see Table 7.1) and is calculated, as follows: $C = S * (BR / BL)$. Here S is the measurable concentration of available forms of the limiting nutrient in the soil. The sum of respiration rates of leaves, roots and stem was expressed as:

$RESP = (BR*RR+BS*RS+BL*RL)$, where RR, RS and RL are the per unit biomass respiration rates for roots, stem and leaves (see Table 7.1).

Table 7.1. State variables, names and unit measure used for the simulation runs.

Symbol	Variable name	Unit measure
BR	Root biomass per individual of each cohort	g
BL	Leaf biomass per individual of each cohort	g
BS	Stem biomass per individual of each cohort	g
rAR	Proportional allocation to roots	Scaled 0 - 1
rAL	Proportional allocation to leaves	Scaled 0 - 1
rASt	Proportional allocation to stem	Scaled 0 - 1
HT	Plant height	m
DBt	Amount of photosynthate produced daily	$\text{g g}^{-1} \text{d}^{-1}$
C	Effective availability of soil resource	mg/kg
TN	Total nutrient pool in the soil	mg/kg
S	Availability of the limiting soil nutrient	mg/kg
a	Proportional rate constant defining resources supply rates	Scaled 0-1
BN	Total amount of nutrient contained in plant biomass	mg/kg
Supply	Rate of nutrient supply	mg/kg

Table 7.2. Parameter symbols, names and default values used for the simulation runs.

Symbol	Parameter name	Default value
Bseed	Seed biomass	0.02 g
RR	Respiration rates per unit of root biomass	$0.024 \text{ g g}^{-1} \text{d}^{-1}$
RL	Respiration rate per unit of leaf biomass	$0.03 \text{ g g}^{-1} \text{d}^{-1}$
RS	Respiration rate per unit of stem biomass	$0.02 \text{ g g}^{-1} \text{d}^{-1}$
NR	Nutrient content per unit biomass of root	0.003 mg g^{-1}
NL	Nutrient content per unit biomass of leaf	0.002 mg g^{-1}
NS	Nutrient content per unit biomass of stem	0.004 mg g^{-1}
NSeed	Nutrient content per unit biomass of seeds	0.004 mg g^{-1}
r	Maximal rate of photosynthesis per unit leaf biomass	$0.08 \text{ g g}^{-1} \text{d}^{-1}$
K	Half saturation constant for nutrient	0.5

C) Nutrient availability in the soil is determined by mineralization rates and rates of nutrient uptake by plants. Soil nutrients are taken up by plants in the amount required to meet the nutrient demand related to the production of stem, roots, leaves and seeds (Tilman 1988). Nutrient uptake is determined by adding nutrients required per unit biomass of roots, stem, leaves and seeds according to tree reproductive age (seeds were produced only when a plant reached adult size). Nutrient supply rates (i.e. mineralization rates) of the limiting soil resources result from the “equable” mode through which they are supplied to the soil (Tilman 1982). This represents a useful approximation of the amount of available forms of the limiting resource in the soil such as N or P. The nutrient supply is calculated according to Tilman (1988) as follows:

$$\text{Supply rate} = a \cdot (\text{TN} - \text{BN} - \text{S});$$

Here a , is the proportionality rate constant defining resource supply rates (Tilman 1982), TN is the total amount of nutrient in the soil, and BN is the total amount of nutrient in plant biomass and depends on plant uptake rates.

7.2.2 Aspects related to the plant-browser system in a semi-arid eutrophic savanna

Photosynthetic and respiration rates

To simulate plant growth in a southern African savanna, photosynthetic, as well as respiration rates for savanna woody plants were deduced from empirical data and parameterized according to average values resulting from eco-physiological studies in semi-arid environments as southern African savannas and/or sub-tropical biomes (see Medina 1982; Cresswell et al. 1982; Eamus et al. 1999; Reich et al. 1998; Hoffman and Franco 2003; Midgley et al. 2004). Nutrient content per unit plant biomass was also estimated according to studies of savanna woody species (Tolsma et al. 1987; Atkin et al. 1998; Reich et al. 1998; Schmidt and Stewart 2003; Midgley et al. 2004; see also Scholes et al. 2003, Table 7.2).

Tree height and maturity size

Based on information of feeding height stratification among savanna ungulate browsers (see du Toit 1990; Woolnough and du Toit 2001) and according to field observations on pod production, I introduced an ecological rule assuming that individual plants are able to produce seeds once they have reached 4 m in height, having then escaped from browsing

damage by the tallest browsers, namely giraffes (*Giraffa camelopardis*). Plant height is considered dependent on biomass allocated to stem, is thus proportional to the square root of stem biomass (Tilman 1988).

Seed production

I tried to estimate the number of seeds produced per year by common *Acacia* species using data from the literature. However, due to limited published information and the highly variable environmental influences on seed-set (see Wagner 1997; Brown et al. 2003; Walters and Milton 2003), I assumed (according to Tilman 1988) that current photosynthate is entirely devoted to seed production once individual plants have reached the maturity size. This represents a simplification of the model by excluding constant eco-physiological processes, such as the allocation of new photosynthate to respiration, branch and root elongation, and the replacement of biomass due to high turnover of leaves and fine roots once the individual has reached maturity size. It follows that the number of seeds is equal to the ratio DBt/seed mass. Seed biomass was estimated using literature for *Acacia* species in sub-tropical biomes and/or semi-arid environments (see Brown et al. 2003; Moles and Westoby 2003).

Rainfall and seedling establishment

Although the magnitude and seasonality of annual rainfall events may play an important role in shaping vegetation communities of African savannas (Walker and Noy-Meir 1982; Walker 1987), I assumed that savanna woody plants have evolved efficient eco-physiological mechanisms to deal with rainfall stochasticity, regardless browsing pressure or fire regime such as, for example, increased nitrogen use efficiency at increasing moisture availability (Midgley et al. 2004). Hence, plant-available moisture (PAM, see Walker 1993) was not considered a factor influencing browsing effects on woody plants with different defensive traits across the same landscape type. Instead I considered PAM to influence the chances of seedling establishment. Indeed, the number of seedlings that germinate and survive their first year is very low in semi-arid savannas, and probably only in exceptionally wet years may they escape herbivory and fire to become established as a cohort of young trees (Bond and van Wilgen 1996). Therefore, based on an evaluation of rainfall data from weather stations distributed across the Kruger National Park (see Venter et al. 2003), I assumed that wet episodes when a woody seedling may successfully establish occur in ~ wet 20% of the overall simulated years. Then the

number of seedlings established during a wet year is proportional to the total amount of precipitation occurred, which is given by a random number generator sampled from a normal distribution.

Defensive traits

As a definitional rule, three plant defensive traits (D_i) were introduced as follows: resistant plants (D_1), intermediate (D_2) and tolerant plants (D_3). Hence, in our savanna system resistant plants are protected through either physical (e.g. spines) or chemical defences (e.g. tannins). They experience low browsing pressure as we might expect from a negative correlation between amount of biomass removed and the presence of efficient either mechanical or chemical defences (Cooper and Owen-Smith 1986; Bryant et al. 1991; Milewski et al. 1991; Gowda 1996). On the other side, tolerant plants, though partially protected by thorns and/or prickles, experience high browsing pressure (i.e. high mass loss) and show higher resprouting abilities (see du Toit et al. 1990; Chapter 5) than resistant plants.

Browsing intensity

According to empirical data (Chapter 3, 4, 5 and 6; Fornara *unpublished data*), three different browsing intensity levels (i.e. browsing gradient) were identified representing different amounts of leaf and stem biomass yearly removed by browsers, as follows: R_1 = high removal, R_2 = medium removal, R_3 = low removal. Therefore, under each browsing intensity level, plants with different defensive traits experienced different yearly removal rates (see below). Moreover, the amount of mass removed was associated with tree height since the shorter individuals are vulnerable to a higher number of browser species (du Toit 1990). Three height classes were then defined as follows: HT_1 = 0-1.5 m, HT_2 = 1.5-4 m, HT_3 > 4 m. Hence, the percentage of biomass yearly removed was imposed depending upon: (1) type of defensive trait adopted, (2) browsing intensity level, and (3) tree height class (see Table 7.3 for plants in the HT_1 height class).

Mortality

The number of individuals that survive the end of each year was calculated according to different mortality rates, which are applied depending on tree height. The highest mortality rates are applied to individuals shorter than 1.5 m, since they are damaged by

the highest number of browser species and generally, mortality decreases with increasing tree height.

Table 7.3. Percentage of mass yearly removed from leaves (BL) and stem (BS) of individuals ranging between 0-1.5 m height (HT₁) along the browsing gradient (R₁ = high removal; R₂ = medium removal; R₃ = low removal) and according to different defensive traits (D₁ = resistant; D₂ = intermediate; D₃ = tolerant).

	D ₁		D ₂		D ₃	
	BL (%)	BS (%)	BL (%)	BS (%)	BL (%)	BS (%)
R ₁	20	20	35	30	50	40
R ₂	10	5	30	20	35	30
R ₃	5	2	20	10	25	15

7.3 RESULTS

Model sensitivity was tested varying in turn by $\pm 20\%$, parameter values and percentages of mass yearly removed from stem and leaves according to different defensive traits. The model was run for 100 years a single run was used for each parameter setting. This procedure has shown that the levels of variable values changed but the dynamics of the model and the effects on plant productivity and nutrient availability were not affected across defensive traits.

Only a limited number of allocation patterns to roots, leaves and stems allowed a plant population to grow and persist till the end of a simulation period of 100 years. Overall, within the range of feasible allocation patterns plant growth was possible when at least 40% of the current photosynthate was allocated to leaves ($AL = 0.4$). Regardless of defensive traits, increased browsing pressure ($R_3 < R_2 < R_1$) was positively associated with the availability of soil nutrients (Fig. 7.2 a, c, e) and negatively correlated with plant biomass (Fig. 7.2 b, d, f). This means that both tolerant and resistant plants increased productivity and depleted soil nutrients more efficiently at low than at high browsing intensities.

Among different allocation patterns (Fig. 7.3 a, b, c) tolerant plants reduced soil nutrients (S) at lower levels than resistant plants along the simulated browsing gradient (R_1, R_2, R_3). Consequently, for certain allocation patterns and at low browsing intensity (R_3 ; Fig. 7.3 a, b) populations of tolerant plants went extinct before the end of the simulated period for total exploitation of soil nutrients. This was also due to the fact that tolerant plants were able to produce a high number of offspring under low browsing pressure (see below).

The high exploitation of soil nutrients by tolerant plants in the model was primarily due to the high root:leaf ratio (BR/BL), which increased the effective availability of soil nutrient (C; Table 7.1) and in turn supported high nutrient uptake to enhance production of new leaves after browsing damage. Plants with intermediate defensive traits (D_2) appeared to be less efficient (Fig. 7.3) in reducing soil nutrients than tolerant and resistant plants for different allocation patterns considered (Fig. 7.3 a, b, c).

In this case the non-linear relationship between defensive traits was due to the different response of resistant plants (D_1), which were supposed to maintain available soil nutrients (S) at higher levels than intermediate species (D_2) since their higher efficiency in protecting leaves and the potential lower nutrient requirements. Instead, D_1 plants reduced soil nutrients more than D_2 plants (Fig. 7.3).

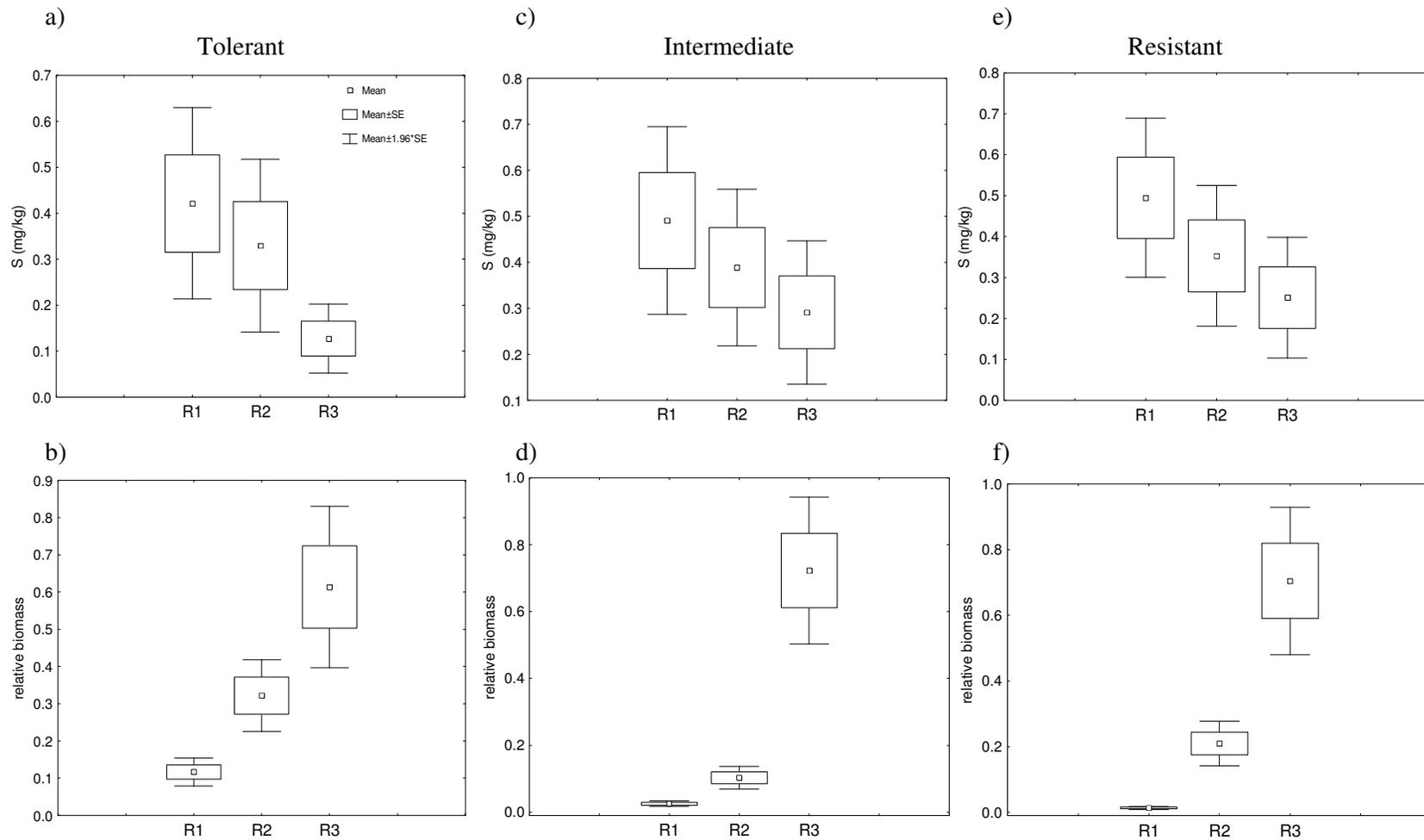
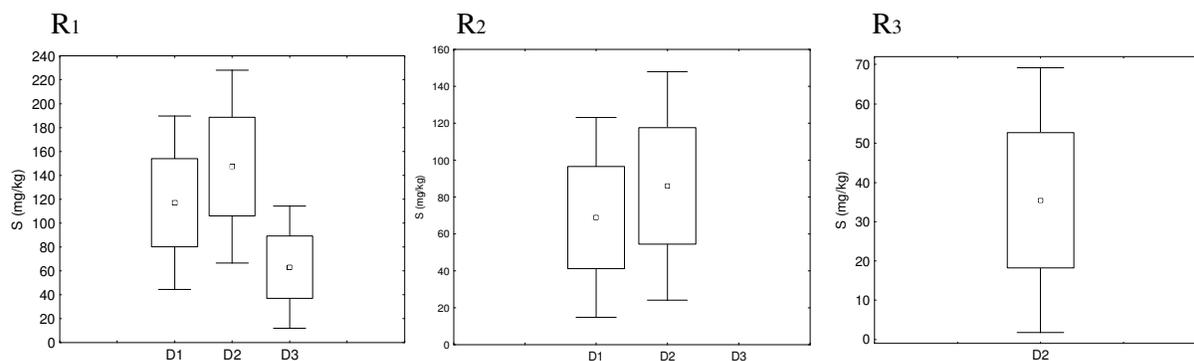
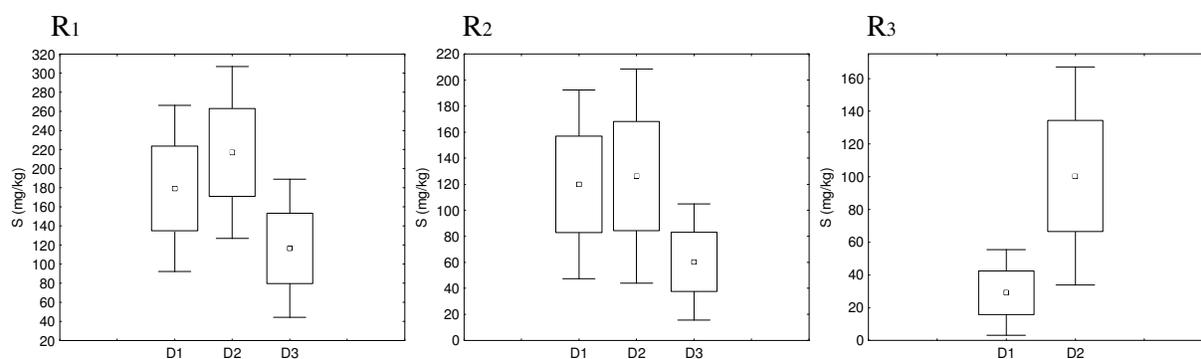


Fig. 7.2. Relative concentration of nutrient available in the soil (S) and relative biomass produced by a plant population under different browsing intensity (R₁ = high; R₂ = intermediate; R₃ = low) after a simulation period of 100 years. Individuals show respectively, high tolerance (a, b), intermediate defensive trait (c, d) and high resistance (e, f). Allocation patterns: AR=0.1, AS=0.5, AL=0.4.

a) AR = 0.3, AS = 0.3, AL = 0.4



b) AR = 0.2, AS = 0.4, AL = 0.4



c) AR = 0.1, AS = 0.5, AL = 0.4

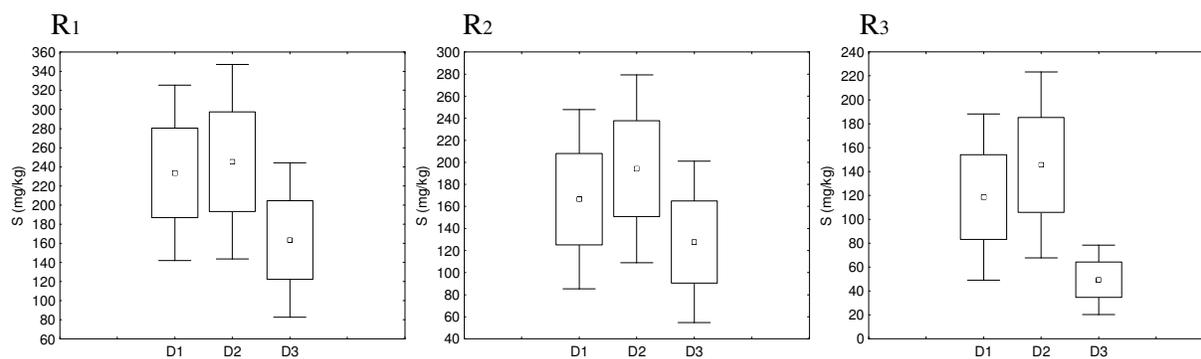


Fig. 7.3. Changes in soil nutrient availability (S) after a simulation period of 100 years according to different allocation patterns (a, b, c). S values (mg/kg) for each browsing level (R₁ = high; R₂ = medium; R₃ = low) and defensive traits (D₁ = resistant, D₂ = intermediate; D₃ = tolerant) were calculated as mean of varying nutrient concentration in the soil (TN). Rate of photosynthesis = 0.08 g g⁻¹ d⁻¹.

The mechanism responsible for such result is likely explained by the trade-off between nutrient uptake rates high for D₂ plants since they experience high mass removal and productivity represented by the amount of photosynthate produced (high for resistant plants since they experience low mass removal). Simply, high leaf protection, conserved photosynthetic tissue which in turn increased productivity (DBt) and enhanced soil nutrient uptake more efficiently than for medium defended plants whose productivity was lower (due to high leaf removal).

In my simulations both tolerant and resistant plants increase plant biomass and reduce soil nutrients more efficiently than plants with an intermediate defensive trait (Fig. 7.3). This trend is also confirmed under different photosynthetic rates and along the browsing gradient (Fig. 7.4). When default parameters were held constant, tolerant plants always increased biomass and reduced soil nutrient availability more efficiently than plants with the other two defensive traits. This because mechanisms of plant growth in the model conferred costs to resistant plants in terms of reduced soil nutrients uptake, whereas they didn't lead to growth related costs for tolerant plants. Therefore D₃ plants could potentially deplete soil nutrients and quickly grow reaching maturity size faster than individuals showing the other two defensive traits even under high browsing pressure (Fig. 7.5). However, holding plant traits constant, a first disadvantage for tolerant plants appears to be their high nutrient demand to support fast growth. Indeed, populations of tolerant plants could be only sustained at high nutrient supply rates (Fig. 7.6).

To further investigate potential costs for tolerant plants I considered (without changing default parameters) the importance of the root system assuming that below-ground compartments represent important storage organs to support regrowth after damage (Fig. 7.7). For all plant defensive traits (D₁, D₂, D₃) the increased allocation to roots (from AR = 0.1 to AR = 0.3), enhanced plant productivity (Fig. 7.7). Moreover, in some cases high resistant (D₁) and medium defended plants (D₂) with a high proportional allocation to roots (AR = 0.3) were able to produce more biomass than those tolerant plants, which allocated less biomass to roots (Fig. 7.7). Although somewhat speculative I assumed that the high browsing pressure and consequent high mass removal from tolerant plants might have a negative impact on plant growth rates in early life-history stages (i.e. seedling-sapling) when individuals likely rely on root reserves for resprouting after herbivory (see Bond and Midgley 2003). For further simulations I then assumed that at the end of each year following browsing damage, the proportional allocation to roots for saplings (0-1.5

m in height), was reduced in direct proportion with the mass loss in above-ground organs (stem and leaves). My assumption finds justification in recent studies on functional responses of seedlings and lignotubers to artificial clipping, which show that carbohydrates reserves in roots are seriously depleted after severe and multiple defoliations (Canadell and Lopez-Soria 1998; Canham et al. 1999). Hence relative to whole plant biomass, tolerant saplings were yearly experiencing higher decreases in the proportional allocation to roots than resistant saplings in order to support higher compensatory abilities (i.e. higher allocation to leaves).

When mean plant productivity (photosynthate) was simulated for saplings under high browsing pressure, and allocation costs to roots are considered (Fig. 7.8), tolerant plants were less productive than resistant plants while intermediate plants still showed the lowest production of photosynthate. Accordingly, when I simulated relative time for an individual plant to reach adult size I found that resistant plants grew faster (in net effect) and produced more biomass when compared with the other two defensive traits (Fig. 7.9).

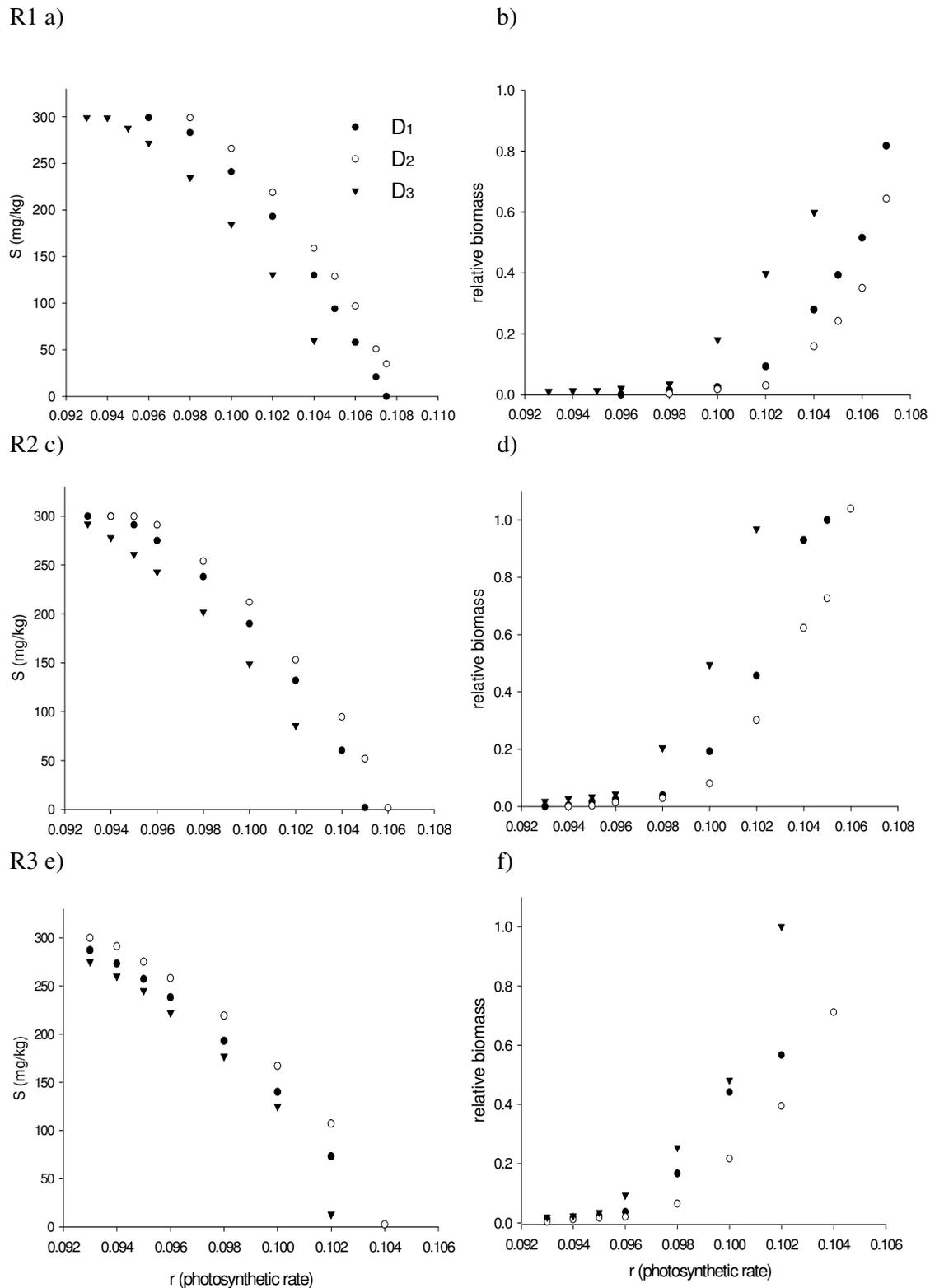


Fig. 7.4. Changes in soil nutrient availability (S) and relative biomass at increased photosynthetic rates for different defensive traits and browsing intensity levels. Allocation patterns as follows: AR=0.3, AS=0.3, AL=0.4, and total soil nutrient TN = 300.

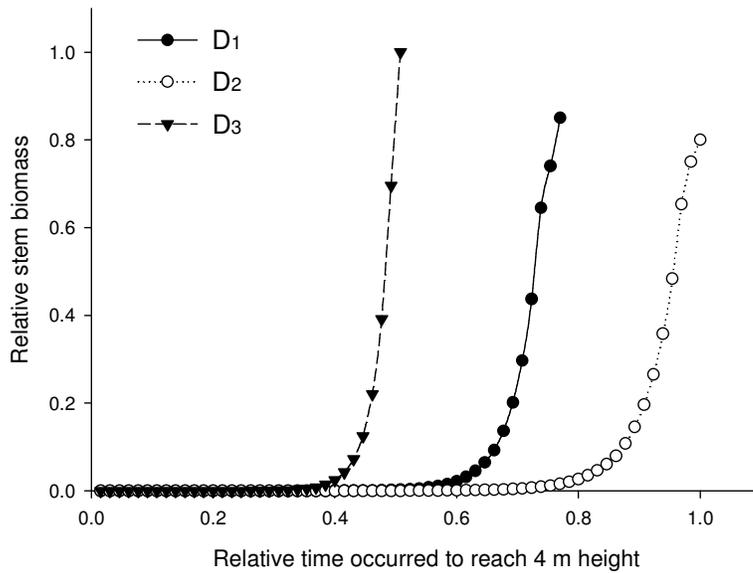


Fig. 7.5. Relative time occurred for an individual to reach adult size under high browsing (R_1) according to different defensive traits (Abbreviations as for Fig. 7.3) and not costs involved. Amount of nutrients in the soil, $TN = 300$, and allocation patterns: $AR=0.2$, $AS=0.4$, $AL=0.4$.

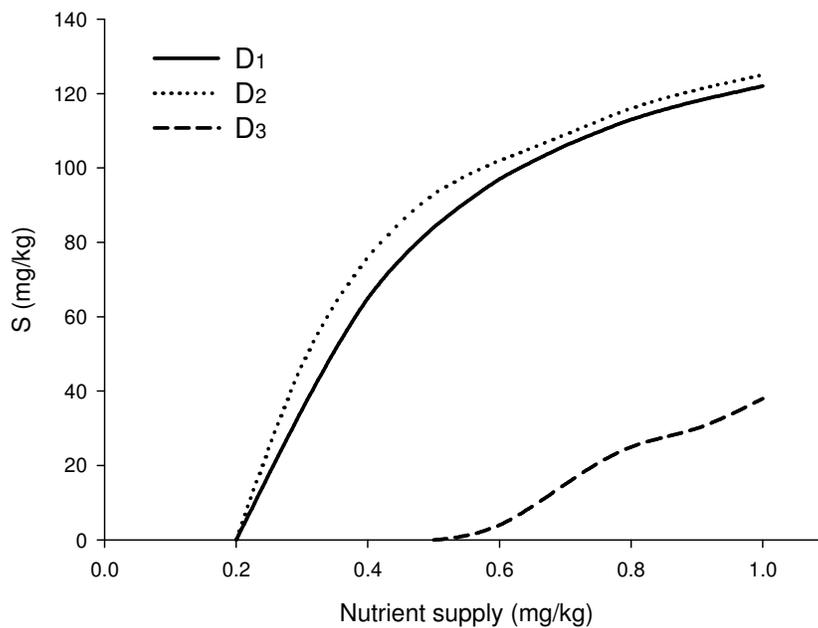


Fig. 7.6. Availability of soil resources to support plant growth after a simulation period of 100 years according to increased nutrient supply rates (i.e. mineralization rates) for different defensive traits (Abbreviations as for Fig. 7.3). R_1 , $TN=200$, $AR=0.2$, $AS=0.2$, $AL=0.4$.

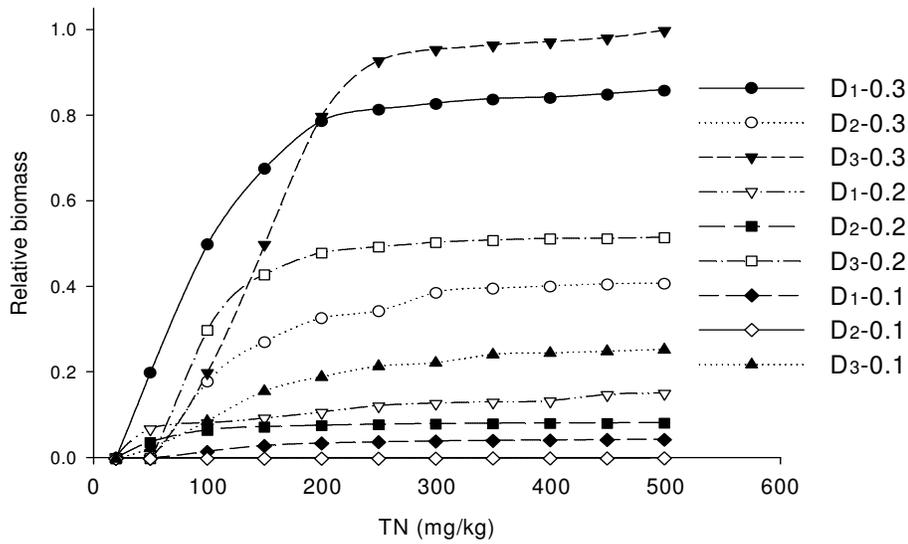


Fig. 7.7. Relative biomass produced by an individual, which alternatively shows the three defensive traits (D1, D2, D3) and grows until to reach adult size (4 m height). Allocation patterns to roots (AR) are respectively: 0.3, 0.2 and 0.1.

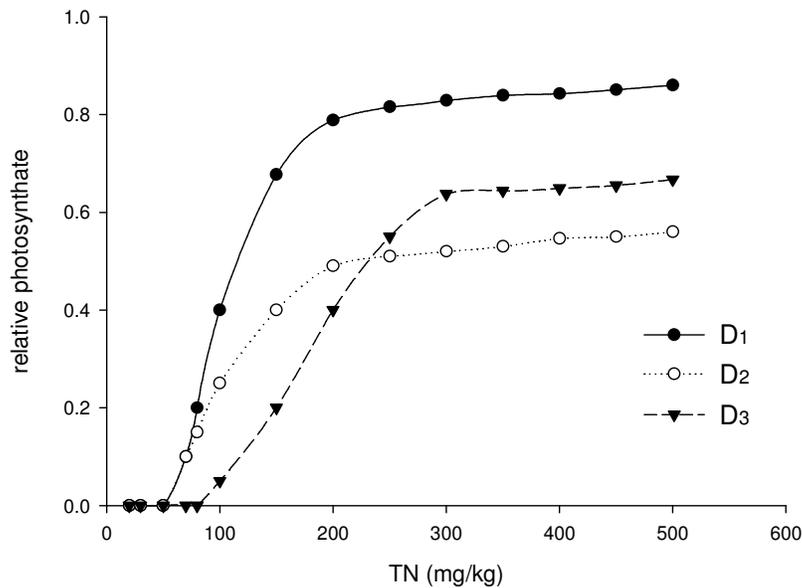


Fig. 7.8. Mean relative productivity (photosynthate) of an individual, which starts as seed and grows till 1.5 m in height. Roots are assumed to be the main storage organ to support regrowth after damage. Allocation patterns: AR=0.3, AS=0.3, AL=0.4.

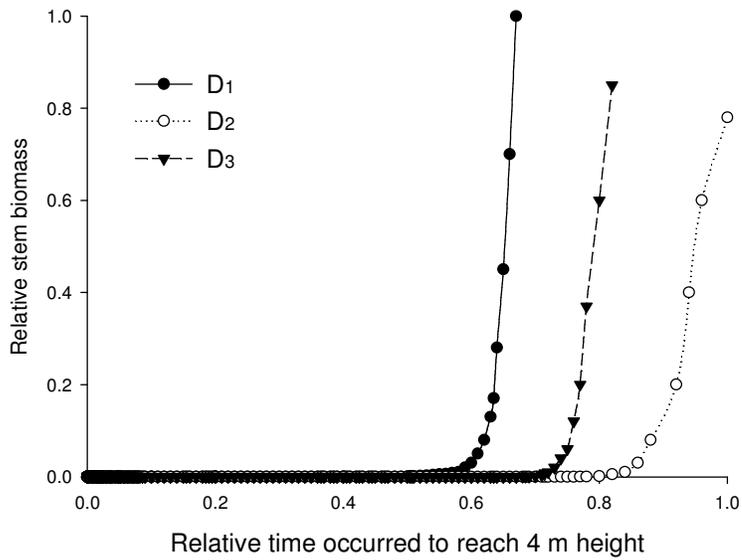


Fig. 7.9. Relative time occurred for an individual to reach adult size assuming that the proportion of biomass yearly allocated to roots is negatively correlated to the amount of biomass removed in above-ground organs (stem and leaves). TN = 300, browsing level = R1, and allocation patterns: AR=0.2, AS=0.4, AL=0.4.

7.4 DISCUSSION

7.4.1 *Tolerance vs resistance: plant biomass and soil nutrient availability*

Overall, my results show that at low browsing intensity regardless of defensive traits and allocation patterns, plants produce more biomass and deplete soil nutrients more efficiently than at high browsing intensity. Nevertheless, under high browsing intensity more nutrients are left in the soil after the simulation period of 100 years as we might expect from a positive correlation between the availability of soil resources and rates of mass loss (Tilman 1988). Comparing different defensive traits without changing default parameters in the model, I obtained two main results.

First, tolerant plants show high productivity and are able to low soil nutrients more efficiently than intermediate and resistant plants. Second, intermediate plants neither optimizing resistance nor tolerance against herbivory, under similar allocation patterns, have low productivity, need long time to reach maturity size, and finally maintain soil nutrients at high levels. Hence, plants which show a poor compromise between tolerance and resistance traits likely would be disadvantaged within a mixed plant community with individuals showing the three different defensive traits.

The mechanisms responsible involve tradeoffs across nutrient uptake rates, plant nutrient requirements, and photosynthetic efficiencies. Indeed, the increased uptake rates of tolerant plants depends on the effective availability of soil resources (in the model called 'C', see Table 7.1), which increases with their high root:leaf ratio that results when photosynthetic tissue is removed by browsers. In turn, the high plant nutrient requirements of tolerant plants contribute to increase amount of photosynthate and allow them to grow quicker than resistant plants. However, populations of tolerant plants could only be maintained in the model simulations at high nutrient supply rates (i.e. high mineralization rates), but these are highly variable and especially concentrated after rainfall events in semi-arid eutrophic savannas (Scholes et al. 2003). Moreover, although mechanisms of plant growth and nutrient use efficiency conferred costs to resistant plants in terms of reduced nutrient uptake rates, the same mechanisms did not impose costs on tolerant plants. The same findings have been suggested by Chase et al. (2000), who used an analytical approach under a similar conceptual framework to address soil resource-plant-herbivore interactions. They suggested that tolerant plants might incur costs only if an increase in tolerance also involves a strong increase in density-independent mortality.

This might occur, for example, through the use of protected storage organs and stored meristems (Marquis 1996; Stowe et al. 2000; see also Chase et al. 2000).

I attempted to evaluate costs for tolerant plants assuming in the seedling-sapling stage, the root system is the main storage organ that supports resprouting abilities (see Canadell and Lopez-Soria 1998; Canham et al. 1999; Bond and Midgley 2003). I therefore speculated that at the end of each year (after browsing damage) the proportion of mass allocated to roots was decreased in direct proportion with the biomass removed from leaves and stem. Consequently, I found that seedlings of tolerant plants produced less photosynthate (Fig. 7.8) and reached maturity size later than resistant plants (Fig. 7.9).

Such results indirectly stress the role of roots as important storage organs for surviving herbivory (and fire), especially during critical plant life-history stages as the seedling-sapling stage. Indeed, I showed that large root systems were associated with increased resprouting abilities in gullivers of two *Acacia* woody species in a semi-arid eutrophic savanna (see Chapter 6). Interestingly, gullivers of the less resistant knobthorn (*A. nigrescens*) experienced higher mortality than the more resistant umbrella tree (*A. tortilis*) after severe artificial clipping while being exposed to high browsing pressure. This confirms modelling results and suggests that mass allocation to below-ground reserves is likely more cost effective for tolerant than resistant plants since the former experience high removal rates of above-ground tissues.

7.4.2 Plant community composition and nutrient cycling

Modelling results suggest that resistant traits may strongly enhance woody species persistence under long-term browsing pressure when compared to either intermediate or tolerant traits. Indeed, resistant plants experience low mass loss rates, have more photosynthetic tissue available, and increase their productivity more than plants with intermediate defensive traits.

Nevertheless, though resistant plants grow slower than tolerant plants, they are less nutrient-dependent and may persist under high browsing pressure at relatively low nutrient supply rates. Indeed I found that highly resistant (i.e. highly spinescent) individuals of different *Acacia* woody species are very common in heavily browsed sites (see Chapter 3, 4). This also agrees with recent outcomes of the resource economics of chemical and structural defences across nitrogen supply gradients as we may expect an

increased number of spinescent species in semi-arid eutrophic savannas (see Craine et al. 2003).

Therefore there are indications that resistant plants would predominate the plant community in heavily browsed sites over long-term periods with local and/or temporary dominance of fast growing tolerant plants whenever the combination of nutrient supply and browsing rates would be favourable to sustain their populations.

However, field observations and data from literature clearly show that many savanna woody plants have developed both efficient resistance and tolerance traits in response to mammal herbivory and frequent fire regimes (Bond and van Wilgen 1996; Hoffmann 1998; Higgins et al. 2000; Midgley and Bond 2001). Indeed, many woody species are both spinescent in order to reduce intake rates of ungulate browsers (Cooper and Owen-Smith 1986; Young 1987; Mileswski et al. 1991; Gowda 1996), and are also able to recover after herbivore damage through increased compensatory growth abilities (du Toit et al. 1990; Dangerfield and Modukanele 1996; Oba et al. 2000; see Chapter 5).

For a plant showing both tolerance and resistance traits we would expect that costs related to resistance traits (i.e. spines and thorns) should be relatively low in a semi-arid eutrophic savanna. Moreover, I propose that important source-sinks of nutrients, other than nutrients recycled from leaf litter and manuring by mammalian herbivores, play a critical role in supporting plant compensatory growth abilities after browsing damage.

Physical defences may not cost a lot of resources especially when amortized overall several years but clearly, they still allow leaves to be eaten (Craine et al. 2003). Moreover, there are indications from recent studies in the Kruger National Park (see Scholes et al. 2003) that many woody species of the Mimosoideae family, which are often protected by physical defences, are able to fix nitrogen. In fact, N₂ fixation is far higher in eutrophic fine-leaved than in broad-leaved savannas on relatively poor soil (Scholes et al. 2003). Moreover, the Kruger National Park receives some of the highest atmospheric inputs of nitrogen in the world (~ 20kg/ha/yr; M. Scholes, personal communication) and some influence on some plant characteristics. This may represent an important source of nutrients to support regrowth in plants that experience high removal rates from ungulate browsers. Nevertheless, mechanisms of N remobilization (see Chapter 4, 5 and 6) and indirect positive effects of tree pruning on mineralization rates via the root system may also enhance plant compensatory growth abilities after herbivore damage (Bardgett et al. 1998; Bardgett and Wardle 2003; Ayres et al. 2004). The model, however, doesn't address efficiently how the nutrient cycling is closed and how nutrients are reimported to

the system through either external N inputs or feedbacks from the leaf litter. Therefore, the model predictions should be seen in terms of responses of woody plant species under ungulate browsing but with limited significance to what concerns potential changes in soil nutrient cycling.

It is likely that fire and browsing have different roles in maintaining species with enhanced tolerance and resistance traits at the landscape level. Undoubtedly, both disturbances select for tolerant plants with high resprouting abilities in their early life-history stages, which rely on important below-ground nutrient storage organs (Bond and van Wilgen 1996; Canadell and López-Soria 1998; Canham et al. 1999; Hoffman and Franco 2003). However, ungulate browsing may represent a stronger selective force than fire for the expression of resistance traits, such as physical defences (see Young 1987; Young and Okello 1998). It is likely then, that in heavily browsed and heavily grazed sites (i.e. sites within few km from waterholes) 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 in a long-term period. Our results suggest that the degree of tolerance and/or resistance shown by different woody species plays a key role in influencing vegetation structure in highly disturbed arid-eutrophic African savannas.

7.5 REFERENCES

- Abu-Zanat, M. W., Ruyle, G. B. and Abdel-Hamid, N. F. 2004. Increasing range production from fodder shrubs in low rainfall areas. *Journal of Arid Environments* 59:205-216.
- Atkin, O. K., Schortemeyer, M., McFarlane, N. and Evans, J. R. 1998. Variation in the components of relative growth rate in ten acacia species from contrasting environments. *Plant, Cell and Environments* 21:1007-1017.
- Ayres, E., Heath, J., Possell, M., Black, H. I. J., Kerstiens, G. and Bardgett, R. D. 2004. Tree physiological responses to above-ground herbivory directly modify below-ground processes of soil carbon and nitrogen cycling. *Ecology Letters* 7:469-479.
- Augustine, D. J. and McNaughton, S. J. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* 41:45-58.
- Bardgett, R. D., Wardle, D. A. and Yeates, G. W. 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biology and Biogeochemistry* 14:1867-1878.

- Bardgett, R. D. and Wardle, D. A. 2003. Herbivore-mediated linkages between aboveground and belowground communities. *Ecology* 84:2258-2268.
- Bergström, R., Skarpe, C. and Danell, K. 2000. Plant responses and herbivory following simulated browsing and stem cutting of *Combretum apiculatum*. *Journal of Vegetation Science* 11:409-414.
- Bond, W. J. and van Wilgen, B. W. 1996. *Fire and Plants*. Chapman & Hall, London, UK.
- Bond, W. J. and Midgley, J. J. 2003. The evolution ecology of sprouting in woody plants. *International Journal of Plant Science* 164:103-114.
- Brown, J. Enright, N. J. and Miller, B. P. 2003. Seed production and germination in two rare and three common co-occurring *Acacia* species from south-east Australia. *Austral Ecology* 28:271-280.
- Bryant, J. P., Provenza, F. D, Pastor, J., Reichardt, P. B., Clausen T. and du Toit, J. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annual Review of Ecology and Systematics* 22: 431-46.
- Canadell, J. and López-Soria, L. 1998. Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Functional Ecology* 12:31-38.
- Canham, C. D., Kobe, R. K., Latty, E. F., Chazdon, R. L. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. *Oecologia* 121:1-11.
- Chase, J. M., Leibold, M. A. and Simms, E. 2000. Plant tolerance and resistance in food webs: community-level predictions and evolutionary implications. *Evolutionary Ecology* 14:289-314.
- Coates Palgrave, K., Coates Palgrave, M., Drummond, R. B., Moll, E. J. 2002. *Trees of Southern Africa*. 3rd Edition Struik Publishers.
- Coley, P., Bryant, J. P. and Chapin, F. S. 1985. Resource availability and plant antiherbivore defense. *Science* 230:895-899.
- Cooper, S. M. and Owen-Smith, N. 1985. Condensed tannins deter feeding by browsing ruminants in a South African savanna. *Oecologia* 67:142-146.
- Cooper, S. M. and Owen-Smith, N. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68:446-455.
- Craine, J., Bond, W., Lee, W. G., Reich, P. B. and Ollinger, S. 2003. The resource economics of chemical and structural defenses across nitrogen supply gradients. *Oecologia* 137:547-556.

- Cresswell, C. F., Ferrar, P., Grunow, J. O., Grossman, D., Rutherford, M. C. and van Wyk, J. J. P. 1982. Phytomass, seasonal phenology and photosynthetic studies. In: B. J., Huntley, and B., H., Walker, editors. *Ecology of Tropical Savannas*. Springer-Verlag Berlin Heidelberg, New York. pp.101-119.
- Danell, K., Huss-Danell, K., and Bergström, R. 1985. Interactions between browsing moose and two species of birch in Sweden. *Ecology* 66:1867-1878.
- Dangerfield, J. M., and Modukanele, B. 1996. Overcompensation by *Acacia erubescens* in response to simulated browsing. *Journal of Tropical Ecology* 12:905-908.
- de Mazancourt, C. and Loreau, M. 2000. Effect of herbivory and plant species replacement on primary production. *American Naturalist* 155:735-754.
- 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.
- du Toit, J. T. 1990. Feeding-height stratification among African browsing ruminants. *African Journal of Ecology* 28:55-61.
- du Toit, J. T. and Cumming, D. H. M. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* 8:1643-1661.
- Eamus, D., Myers, B., Duff, G. and Williams, R. 1999. A cost-benefit analysis of leaves of eight savanna tree species differing leaf life-span. *Photosynthetica* 36:575-586.
- Edenius, L., Danell, K., and Bergström, R. 1993. Impact of herbivory and competition on compensatory growth in woody plants: winter browsing by moose on Scots pine. *Oikos* 66:286-292.
- Gowda, J. H. 1996. Spines of *Acacia tortilis*: what do they defend and how? *Oikos* 77:279-284.
- Higgins, S. I., Bond, W. J. and Trollope, W. S. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88:213-229.
- Hoffmann, W. A. 1998. Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* 35: 422-433.
- Hoffman, W. A. and Franco, A. C. 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically independent contrasts. *Journal of Ecology* 91:475-484.

- Huntley, B. J. 1982. Southern African Savannas. In: B., J., Huntley and B., H., Walker. *Ecology of Tropical Savannas*. Springer-Verlag Berlin Heidelberg, New York, pp.101-119.
- Jachmann, H. and Croes, T. 1991. Effects of browsing by elephants on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biological Conservation* 57:13-24.
- Jeltsch, F., Milton, S. J., Dean, W. R. and van Rooyen, N. 1997. Simulated pattern formation around artificial waterholes in the semi-arid Kalahari. *Journal of Vegetation Science* 8:177-188.
- Jorritsma, I. T. M., van Hees, A. F. M., Mohren, G. M. J. 1999. Forest development in relation to ungulate grazing: a modeling approach. *Forest Ecology and Management* 120:23-34.
- Kielland, K. and Bryant, J. P. 1998. Moose herbivory in taiga: effects on biogeochemistry and vegetation dynamics in primary succession. *Oikos* 82:377-383.
- Kramer, K., Groen, T. A., and van Wieren, S. E. 2003. The interacting effects of ungulates and fire on forest dynamics: an analysis using the model FORSPACE. *Forest Ecology and Management* 181:205-222.
- Lerdau, M. and Gershenson, J. 1997. Allocation theory and chemical defense. In: Bazzaz, F. A. and Grace, J. editors. *Plant resource allocation*. Academic Press, San Diego, CA, US, pp. 265-277.
- Liang, S. Y. and Seagle, S. W. 2002. Browsing and microhabitat effects on riparian forest woody seedling demography. *Ecology* 83:212-227.
- Marquis, R. J. 1996. Plant architecture, sectoriality and plant tolerance to herbivores. *Vegetatio* 127:85-97.
- McInnes, P. F., Naiman, R. J., Pastor, J. and Cohen, Y. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* 73:2059-2075.
- McNaughton, S. J., Ruess, R. W. and Seagle, S. W. 1988. Large mammals and process Dynamics in African Ecosystems. *BioScience* 38 11:794-800.
- McNaughton, S. J., Banyikwa, F. F. and McNaughton, M. M. 1997. Promotion of the cycling of diet-enhancing nutrients by African grazers. *Science* 278:1798-1800.
- Medina, E. 1982. Physiological ecology of neotropical savanna plants. In: B., J., Huntley and B. H. Walker. *Ecology of Tropical Savannas*. Springer-Verlag Berlin Heidelberg, New York, pp.101-119.

- Midgley, J. J. and Bond, W. J. 2001. A synthesis of the demography of African acacias. *Journal of Tropical Ecology* 17:871-886.
- Midgley, G. F., Aranibar, J. N., Mantlana, K. B. and Macko, S. 2004. Photosynthetic and gas exchange characteristics of dominant woody plants on a moisture gradient in an African savanna. *Global Change Biology* 10:309-317.
- Mileswski, A. V., Young, T. P. and Madden, D. 1991. Thorns as induced defenses: experimental evidence. *Oecologia* 86:70-75.
- Moles, A. T. and Westoby, M. 2003. Latitude, seed predation and seed mass. *Journal of Biogeography* 30:105-128.
- Oba, G., Mengistu, Z. and Stenseth, N. C. 2000. Compensatory growth of the acacia dwarf shrub *Indigofera spinosa* following simulated herbivory. *Ecological Applications* 10:113-1146.
- Olf, H., Ritchie, M. E. and Prins, H. H. T. 2002. Global environmental controls of diversity in large herbivores. *Nature* 415:901-904.
- Pastor, J., Naiman, R. J., Dewey, B. and McInnes, P. 1988. Moose, Microbes, and the Boreal Forest. *BioScience* 38: 770-777.
- Pastor, J. and Naiman, R. J. 1992. Selective foraging and ecosystem processes in boreal forests. *American Naturalist* 139:690-705.
- Reich, P. B., Walters, M. B., Ellsworth, D. S., Vose, J. M., Volin, J. C., Gresham, C. and Bowmann, W. D. 1998. Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a test across biomes and functional groups. *Oecologia* 114:471-482.
- Ritchie, M. E. and Tilman, D. 1995. Responses of legumes to herbivores and nutrients during succession on a nitrogen-poor soil. *Ecology* 76:2648-2655.
- Ritchie, M. E., Tilman, D. and Knops, M. H. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165-177.
- Rosenthal, J. P. and Kotanen, P. M. 1994. Terrestrial plant tolerance to herbivory. *Trends in Ecology and Evolution* 9:145-148.
- Ruess, R. W., Hendrick, R. L. and Bryant, J. P. 1998. Regulation of fine roots dynamics by mammalian browsers in early successional Alaskan taiga forests. *Ecology* 79:2706-2720.

- Schmidt, S. and Stewart, G. R. 2003. $\delta^{15}\text{N}$ values of tropical savanna and monsoon forest species reflect root specialisations and soil nitrogen status. *Oecologia* 134:569-577.
- Scholes, M., Scholes, R. J., Otter, L. B. and Woghiren, A. J. 2003. Biogeochemistry: the Cycling of Elements. 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. 130-148.
- Sinclair, A. R. E. and Norton-Griffiths, M. 1979. *Serengeti: Dynamics of an Ecosystem*. University of Chicago Press, Chicago.
- Stamp, N. 2003. Out of the quagmire of plant defense hypotheses. *The Quarterly Review of Biology* 78:23-55.
- Stowe, K. A., Marquis, R. J., Hochwender, C. G. and Simms, E. L. 2000. The evolutionary ecology of tolerance to consumer damage. *Annual Review of Ecology and Systematics* 31:565-595.
- Strauss, Y. S. and Agrawal, A. A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends in Ecology and Evolution* 14:179-185.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, New Jersey 360 pp.
- Tolsma, D. J., Ernst, W. H. O., Verweij, R. A. and Vooijs, R. 1987. Seasonal variation of nutrient concentrations in a semi-arid savanna ecosystem in Botswana. *Journal of Ecology* 75: 755-770.
- Tremblay, J. P., Hester, A., McLeod, J., and Huot, J. 2004. Choice and development of decision support tools for the sustainable management of deer-forest systems. *Forest Ecology and Management* 191:1-16.
- Venter, F. J., Scholes, R. J., Eckhardt, H. C. 2003. The abiotic template and its associated vegetation pattern. In: du Toit, J., Rogers, K., Biggs, H., (Eds). *The Kruger experience. Ecology and Management of savanna heterogeneity*. Island Press, Washington, DC, US, pp. 83-129.
- Wagner, D. 1997. the influence of ant nests on *Acacia* seed production, herbivory and soil nutrients. *Journal of Ecology* 85:83-93.

- Walker, B. H. and Noy-Meir, I. 1982. Aspects of the Stability and Resilience of Savanna Ecosystems. In: B. J. Huntley and B.H. Walker. *Ecology of Tropical Savannas* Springer-Verlag Berlin Heidelberg, New York, 556-590.
- Walker, B. H. 1987. *Determinants of tropical savannas*. IRL Press Oxford UK.
- Walker, B. H. 1993. Rangeland ecology: understanding and managing change. *Ambio* 22:80-87.
- Walters, M. and Milton, S. J. 2003. The production, storage and viability of seeds of *Acacia karoo* and *A. nilotica* in a grassy savanna in KwaZulu-Natal, South Africa. *African Journal of Ecology* 41:211-217.
- Wardle, D. A., Barker, G. M., Yeates, G. W., Bonner, K. I. and Ghani, A. 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecological Monographs* 71:587-614.
- Weisberg, P. J. and Coughenour, M. B. 2003. Model-based assessment of aspen responses to elk herbivory in Rocky Mountain National Park, USA. *Environment and Management* 32:152-169.
- Woolnough, A. P. and du Toit, J. P. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. *Oecologia* 129:585-590.
- Young, T. P. 1987. Increased thorn length in *Acacia drepanolobium* – an induced response to browsing. *Oecologia* 71:436-438.
- Young, T. P. and Okello, B. D. 1998. Relaxation of an induced defense after exclusion of herbivores: spines on *Acacia drepanolobium*. *Oecologia* 115:508-513.