Tree – Grass Interactions on an East African Savanna

The effects of facilitation, competition, and hydraulic lift

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Abstract

Savanna trees can either increase or decrease the productivity of understorey grasses. Trees reduce grass growth through competition for nutrients, water and light and can facilitate grass production through increased soil nutrient availability, shade and hydraulic lift. In an East African savanna in Tarangire, I studied what determines whether *Acacia tortilis* trees interfere or facilitate understorey grass growth and especially whether trees stimulate grass growth through hydraulic lift.

The availability and concentration of all major nutrients is much higher under trees compared to open grassland. This increased nutrient availability under trees changes the nutrient limitation of the herbaceous layer from nitrogen limited in open grassland to phosphorus limitation under the tree canopy. The water availability however was lower under compared to outside tree canopies although we found clear evidence of hydraulic lift. However, exuding large amounts of water into the topsoil (up to 235 l. per night per tree) by large trees through hydraulic lift, could not compensate for water competition between trees and grasses. However grasses probably have access to hydraulically lifted water which indicates that hydraulic lift reduces the severity of water competition between trees and grasses.

So the main processes regulating tree-grass interactions in this East-African savanna are water competition and increased soil nutrient availability. This balance between positive and negative effects of trees on grass growth resulted in equal grass productivity under and outside tree canopies.

Although *Acacia tortilis* trees did not increase grass productivity, they did have a positive effect on the grass quality for herbivores. Grasses growing under trees have higher nutrient and protein concentrations. Grasses from open grassland, however, have such a low quality that wildebeest cannot maintain a stable body weight by only selecting food from open grassland but need forage from under trees. Large trees are thus essential for the survival of wildebeest in Tarangire National Park.

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Chapter 1

General Introduction

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Introduction

One eighth of the world and half the area of the African continent is covered by savannas. The most important aspect of savanna ecosystems is the co-domination of two completely different life forms, trees and grasses. Savannas typically occur in (sub)-tropical regions with a strong alternation of dry and wet seasons (Scholes and Archer 1997). Especially African savannas contain a high diversity and density of mammalian herbivores (Prins and Olff 1998). Large herds of zebra, wildebeest, elephant and buffalo can still be observed in the Serengeti and Masai ecosystems of Northern Tanzania. It is still unclear how these relatively arid environments can sustain such a high density of large herbivores. To understand how these semi-arid ecosystems can produce enough biomass to feed all the herbivores it is important to understand how the two growth forms, trees and grasses interact. Especially, how trees affect the quality and productivity of grasses, the main food source for grazing mammals. The research described in this thesis is based on the hypothesis that positive interactions between trees and grasses is (part of) the explanation why African savannas can sustain such a large concentration of herbivores.

Historically, the interactions between trees and grasses are seen as competitive. Grasses reduce the growth and establishment of trees and a high tree density will reduce grass production. Several studies indeed showed that grass production is lower under trees than in open grassland (Stuart-Hill and Tainton 1989, Mordelet and Menaut 1995, Anderson et al. 2001). However during the last decade, there is increasing evidence that also positive interactions can dominate plant communities (Belsky 1994, Callaway 1995, Callaway and Walter 1997, Brooker and Callaghan 1998, Bertness et al. 1999). Several previous studies showed that in savannas, grass productivity was higher under trees compared to open grassland (Knoop and Walker 1985, Belsky et al. 1989, Weltzin and Coughenour 1990, Belsky et al. 1993). So in stead of competing with grasses, trees can also facilitate the growth of understorey plants. However, it is still unclear what determines whether trees and grasses compete for resources and when trees facilitate the growth of grasses. The main goal of this thesis is to determine which mechanisms regulate whether trees interfere or facilitate the growth of grasses.

Tree – grass interactions on savannas

Savannas are characterized by a continuous grass layer and an open discontinuous layer of trees and shrubs. So grasses can grow both under and outside tree canopies. The habitat of grasses is changed dramatically by the presence of trees. Trees affect light, nutrient and water availability of grasses. Trees can potentially increase belowcrown soil nutrient concentration, and water availability through hydraulic lift. However, trees also reduce light availability through shade, and compete with grasses for belowground resources. Separating these different effects that trees can have on grass growth is essential to be able to determine what processes regulate tree - grass competition and facilitation.

The effect of isolated savanna trees on soil nutrient availability is well documented in the literature. Both soil nutrient concentration and fluxes of C, N, P and cations are higher under tree canopies than in open grassland (Kellman 1979, Bernhard-Reversat 1982, Belsky et al. 1989, Scholes and Archer 1997). These islands of fertility around isolated savanna trees have been described for a wide range of

savannas. The accumulation of soil nutrients under tree canopies usually increases with tree age and nitrogen enrichment is often higher under leguminous trees (Belsky et al. 1989, 1993, Scholes and Archer 1997).

The effect of the trees on belowcrown grass water availability is less clear. Walter (1971) proposed that trees and grasses in savannas avoid competition for water through niche partitioning. Walter's two-layer hypothesis states that trees have sole access to water in deeper soil layers while grasses are the dominant competitor for water in the upper soil layers. There is some empirical evidence supporting the two-layer hypothesis (Sala et al. 1989, Knoop and Walker 1985, Hesla et al. 1985) but several recent studies have rejected it (Belsky 1994, Belsky et al. 1989, 1993, Weltzin and Coughenour 1990, Georgiadis 1989, Seghieri 1995). Another possibility is that trees increase water availability by exudating ground water into the topsoil through hydraulic lift (Dawson 1993, Caldwell et al. 1998). However, trees can also compete with grasses for water and thus reduce the soil moisture content (Le Roux et al. 1995).

Reduced soil moisture availability for grasses growing under tree canopies can be compensated for by increased water use efficiency due to lower temperatures in the shade (Amundson et al. 1995). But shade can also negatively affect grass production through reduced light availability which can reduce photosynthesis. The net effect of shade depends on the local climatic situation and the amount of light intercepted by the canopy.

Hydraulic lift

Increased grass productivity under savanna trees is usually related to increased soil nutrient concentration or shade under tree canopies (Belsky 1994, Scholes and Archer 1997). However, increased soil water availability due to hydraulic lift could also potentially increase belowcrown grass productivity. Hydraulic lift is the process of water movement from relatively wet to dry soil layers through the roots of plants that have access to both deep and shallow soil layers (Figure 1.1) (Richards and Caldwell 1987, Caldwell et al. 1998). Except for CAM plants, this transport takes place during the night when leaf stomata are closed and the major water potential gradient is between the deep (wet) roots and the drier surface roots present in the top soil. However for plants with a CAM photosynthetic pathway which close their stomata during the day and take up CO_2 during the night it has been shown that they exudate water during the day and take it up the during following night (Yoder and Nowak 1999). No previous study has looked at the effect of hydraulic lift on tree – grass interactions in savannas. This process could by an important feature in the water relations between trees and grasses in semi-arid savannas.

Hydraulic lift has now been reported to occur in over 50 plant species worldwide (Caldwell et al. 1998, Horton and Hart 1998) and is conjectured to be a widespread feature as long as active roots are growing in soils with marked water potential gradients and the roots permit both uptake and loss of water to occur. At the break of the wet season when water potentials in the topsoil are higher (wetter) than in deeper soil layers also 'negative' hydraulic lift or downward water transport can take place (Schulze et al.1998, Burgess et al. 1998). This shows that hydraulic lift mainly is a passive process driven by a difference in water potential.

Trees can benefit from hydraulic lift in several ways. First of all, water lost to soils through hydraulic lift during the night can be taken up by the tree the next day. In this way trees can increase their daily water uptake and more efficiently use deep soil water (Dawson 1993, Emerman and Dawson 1996). Trees usually have few roots in deeper soil layers and by continuing to use these deep tap roots during the night and temporarily storing the water in the topsoil they increase their water uptake. Deeper soil layers contain few if any nutrients and by exuding water into the topsoil and then taking it up again, trees increase their potential nutrient uptake as well (see Dawson 1998 for some evidence). Hydraulic lift might also contribute to keep mycorrhizas and rhizobium bacteria in the top soil functional during periods of drought. Higher soil moisture contents can also increase mineralization rates which has a positive effect on soil nutrient availability (Horton and Hart 1998) and plant resource status (Dawson 1998).

Day   # Night
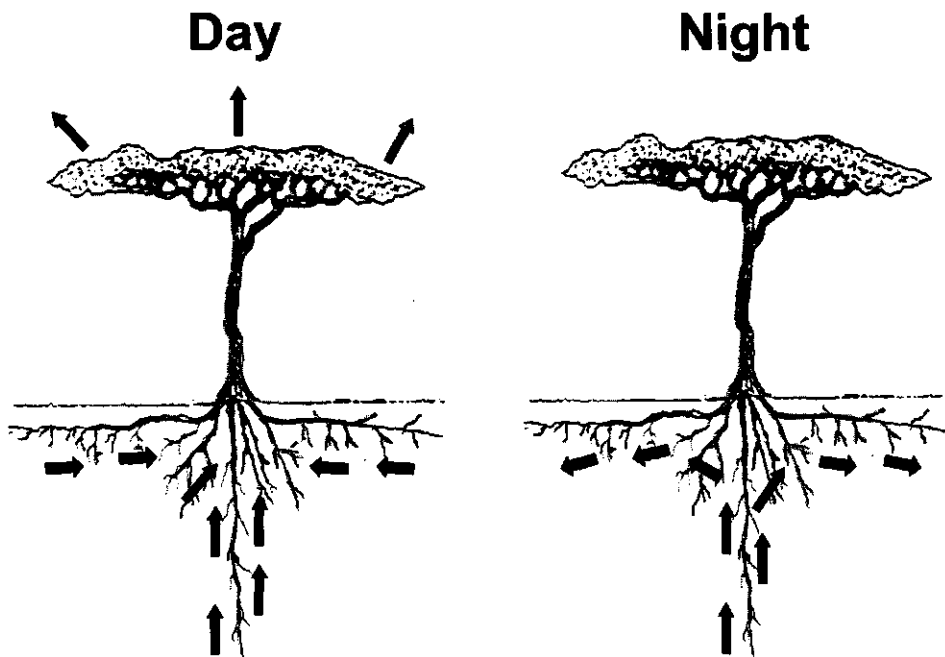
Figure 1.1. Patterns of water movement through the tree root system according to the hydraulic lift hypothesis. During the day tree roots absorb water from all soil depths which is transpired by the leaves. During the night, the transpiration is minimal and plant water potentials can rise above soil water potentials and the main water transport is from deeper soil layers through plant roots into the dryer topsoil. This nighttime process is passive, driven by a difference in soil water potential. For this thesis, hydraulic lift was studied in large *Acacia tortilis* trees.

Several authors have suggested that hydraulic lift may have substantial community and/or ecosystem effects (Caldwell et al. 1998, Horton and Hart 1998, Jackson et al. 2000, Millikin and Bledsoe 2001, Meinzer et al. 2001). In addition, recent modeling efforts suggest that the influence of hydraulic lift on ecosystem water balance (Dawson et al. *in review*, Jackson et al. 2000) and vegetation-climate

interactions (Feddes et al. 2001) can be quite significant. Despite this, there have been very few empirical studies that have demonstrated the effects of hydraulic lift on community and/or ecosystem structure or function. Of these, the first studies by Richards and Caldwell (1987) and Caldwell and Richards (1989) showed, using deuterium labeling, that groundwater hydraulically lifted by *Artemisia tridentata* can be used by the neighboring grass *Agropyron deseretorum*. Later, Dawson (1993) showed that plant species growing near sugar maple trees (*Acer saccharum*) which used more hydraulically lifted water (HLW) had higher (more favorable) leaf water potentials and stomatal conductance than plant species which did not use HLW and had no access to water lifted by the trees. This study highlighted the potential importance of the positive (facilitative) effects of hydraulic lift on the community. These previous studies show that HLW is taken up by understorey plants but whether hydraulic lift can actually increase the production of understorey plants is still unclear.

In savanna ecosystems where water availability can have a marked influence on plant functioning it is unclear how or if hydraulic lift influences or alters tree-grass interactions. In East African savannas with large, deep rooted trees and a well developed understorey vegetation, hydraulic lift could be present and if present hydraulic lift could be a potentially important process in influencing grass-tree interactions as well as community and ecosystem functioning. These aspects are explored in this thesis.

Tarangire National Park

The experiments and observations discussed in this thesis were performed in Tarangire National Park (Figure. 1.2) in Northern Tanzania. Tarangire is part of the Masai Ecosystem, an area of about 35,000 km^2 on the eastern side of the African rift valley. The western boundary of the ecosystem is the escarpment of the rift valley and it is surrounded by Serengeti and Amboseli National Park and Mount Meru and Kilimanjaro. The Masai Ecosystem is defined as the watershed boundaries of Lake Burunge and Manyara and by the migratory range of large herbivores, mainly zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) (Prins 1987, Van de Vijver 1999). The main national park in the area is Tarangire National Park which is located in the dry season range of migratory herbivore populations.

Tarangire NP (2600 km^2) was proclaimed as a game reserve in 1957 and declared as a National Park in 1969. Altitude in the park ranges from 1000 to 1350 m and it is situated between latitude 3°40' and 5°35' south and 35°45' and 37°00' East. The park has a strictly protected status and the only human activities allowed in the park are game viewing and research. The park is unfenced and animals can freely move in and out of the park. Part of the areas around the park are game controlled areas which are mainly used by pastoralists for livestock grazing and small-scale agricultural activities. These areas are also important grazing grounds for wild herbivores during the wet season. Outside the park extensive unorganised logging takes place. Especially large *Acacia* trees are used for the production of charcoal. In some areas outside the park all large trees are removed and the border of the park can be visually observed by the presence or absence of large trees.
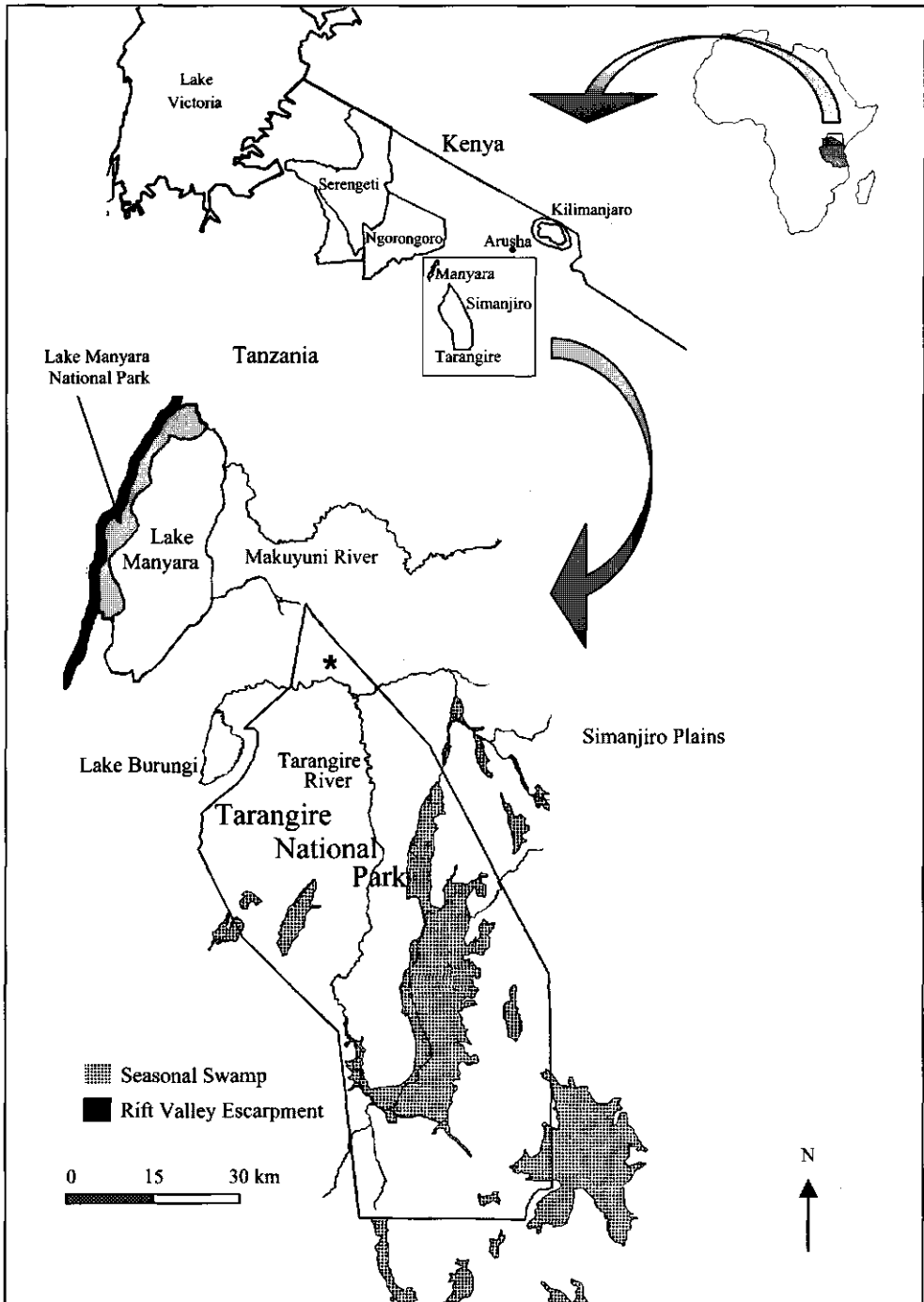
Figure 1.2 Map showing the location of Tarangire National in northern Tanzania. The main research site was located in the northern part of the park indicated by an asterisk (*)(from Van de Vijver 1999 and Voeten 1999).

The climate in Tarangire NP is semi-arid with a highly variable rainfall which is on average 650 (s.d. = 272) mm/year. The wet season occurs from November until May with most of the rain typically falling during March and April. Seasonal rainfall changed dramatically between the three years of research described in the thesis. The first season, 1998, was the wettest in 20 years with 1368 mm of rain. In 1999 rainfall was 750 mm with 75% of the rain falling in March and April. The last year, 2000, was very dry with only 350 mm (Figure 1.3).

Migratory herbivores concentrate in Tarangire NP during the dry season. In this period one of the highest concentration of large herbiovers in the world can be observed around the Tarangire river. This river is the main permanent water source in the Masai ecosystem. During the wet season animals disperse out of the park towards the Mto-wa-bu and Simanjiro game controlled areas. Therefore, Tarangire NP is intensively grazed only during the dry season. Most abundant mammal species in the area are zebra and wildebeest, other less abundant animals are African elephant (*Loxondonta africana*), African buffalo (*Syncerus caffer*), impala (*Aepyceros melumpus*), Coke's hartebeest (*Alcelaphus cokii*) giraffe (*Giraffa camelopardalis*) and eland antelope (*Tragelaphus oryx*).
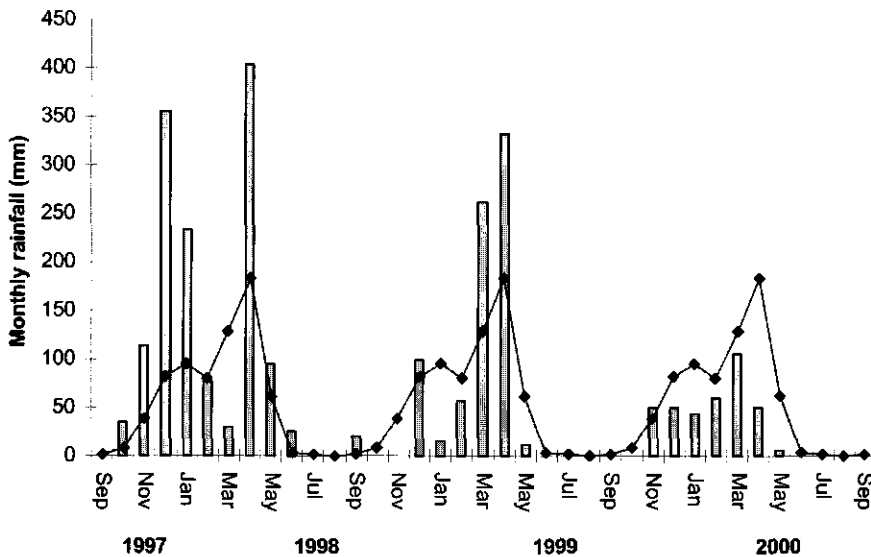
Figure 1.3 Monthly rainfall in Tarangire National Park during the three years of research described in this thesis. Bars indicate measured rainfall and line and diamonds indicate the 20 year average

The vegetation in the park is a wooded savanna with an average tree cover of 10-20 % (Van de Vijver et al. 1999). The park is dominated by two different vegetation types. A decidious savanna which is situated on the ridges and upper slopes with well drained red loam soils of Pre-Cambrian origin. The dominant trees are *Combretum* and *Commiphora* species. Secondly, the *Acacia* savanna which can be found mainly in the riverine area with soils from lacustrine origin. The research site is

located in this savanna type and the dominant tree *Acacia tortilis* is used as the research species.

Research site and species

The main research site was located in the northern part of Tarangire National park between the main gate and park head quarters (Figure 1.2). The vegetation at the site is a wooded *Acacia* savanna with a 20% tree cover. The dominant tree, *Acacia tortilis*, was used as the main research species. The common name of *Acacia tortilis*, umbrella thorn, originates from its characteristic broad-canopied flat topped form. The umbrella thorn is a member of the Leguminosae family and is capable of fixing nitrogen. *Acacia tortilis* has a very wide spread root system with both a deep tap root and extensive lateral roots (Belsky et al. 1989) and it is thus an ideal species to use for a study on hydraulic lift. At the study site 20 large isolated *Acacia tortilis* trees were selected for observations and experiments. Trees were about 10 m high and had a mean canopy diameter of 295 m^2. The trees were between 100 and 120 years old and probably established during the African rinderpest epidemic in the 1880's (Prins and Van der Jeugd 1993). Other tree species beside *Acacia tortilis* occurring irregularly in the area are *Balanites aegyptica* and *Adansonia digitata* (Baobab).

The herbaceous layer is well developed and the plant cover during the wet season is almost 100%. The herbaceous stratum is dominated by C_4 grasses and depending on the yearly rainfall the cover of herbs is between 2 and 20%. In wet years, as in 1998, herbs form an important part of the vegetation but in dry years as in 2000 all herbs die or do not resprout. Ten different grass species dominated the vegetation at the research site (see table 2.6). The distribution of these species was mainly determined by the presence of *Acacia tortilis* trees. Three different vegetation zones could be determined. A zone under trees, one around the trees and in open patches more than 50 m from any tree. *Cynodon dactylon*, *Panicum maximum*, and *Cenchrus ciliaris* dominated the vegetation under *Acacia* trees.

Outside tree canopies *Heteropogon contorits, Urochloa mosambicensis, Chloris virgata* and *Digitaria macroblephera* were the most abundant grass species. Open grassland patches were dominated by *Sehima nervosa* and *Heteropogon contoritis*. The species composition under other trees species was very similar to the vegetation under *Acacia tortilis* trees.

Outline of this thesis

The main goal of this thesis is to find out which mechanisms determine whether trees compete or facilitate the growth of understorey grasses and especially what the role is of hydraulic lift. To understand how trees affect grass productivity it is important to measure how trees affect grass resource availability. So first I studied how trees change water nutrient and light availability of the understorey vegetation. In chapter 2, the results are discussed on measurements of soil nutrient and water concentrations around trees to study how trees change plant nutrient and water availability both in space and time.

Secondly, to fully understand how trees affect the growth of grasses it is important to separate the different effects of savanna trees on understorey grasses. Four main effects of trees on the understorey vegetation were distinguished. Trees: (1)

Table 1.1 Different effects on understorey vegetation were separated by studying different tree age classes and with different experiments. Table shows which effects were absent or present under different sized trees and during different experiments. '++' indicates strong effect, '+' a weak effect and '-' no effect and '+/-' indicates unclear.

	Chapter	Shade	Soil nutrient enrichment	Belowground competition	Hydraulic lift
Large tree	2/3/5	+	++	+	+
Open grassland	2/3	-	-	-	-
Bush	2	++	-/+	+	-
Small tree	2	+	+	+	-/+
Dead tree	2	-	++	-	-
Nutrient experiment (under large tree canopy)	3	+	+++	+	+
Nutrient experiment (in open grassland)	3	-	++	-	-
Shade experiment	3	++	-	-	-
Trenching experiment	5	+	++	-	-

provide shade, (2) increase the belowcrown soil nutrient concentration, (3) compete with grasses for belowground resources and (4) exude water in the topsoil through hydraulic lift. Under large trees all four processes can be important while in open grassland none of these processes influence grass growth. In this thesis I describe experiments and observations with a range of different combinations of effects which trees have on the understorey vegetation (Table 1.1). In chapter 2, I focus on trees of different age classes and dead trees and thereafter the effect of nutrients, shade, water competition and hydraulic lift were studied by experimental manipulation.

Chapter 3 describes experiments which studied the effect of nutrients and shade on tree – grass interactions. We tested whether trees change the nutrient limitation of the herbaceous layer and whether shade increases or limits grass productivity. Chapter 4, describes measurements of hydraulic lift in large *Acacia tortilis* trees in a relatively wet and a very dry year and we tested whether understorey grasses can take up hydraulically lifted water. This was studied With a combination of continuous soil water potential measurements and stable isotopes in plant and source water Chapter 5 shows the results of a tree root trenching experiment. We prevented tree – grass root interactions to test whether trees facilitate the growth of grasses through hydraulic lift or compete with grasses for soil moisture. For herbivores not only the grass production is important but especially the grass nutritional quality. So in chapter 6 ,we studied the effect of savanna trees on forage quality and what the effects are of a decline in the number large trees on herbivore food availability and quality. In the last chapter the long term effects of tree removal on herbivore forage quality and availability are discussed and I propose a conceptual model which explains why savanna trees either reduce or increase understorey productivity.

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Chapter 2

Savanna tree influences on nutrient, water and light availability and how this affects productivity and composition of the understorey vegetation

Fulco Ludwig, Hans de Kroon, Frank Berendse and Herbert H.T. Prins

Abstract

In an East African savanna we studied herbaceous layer productivity and species composition around *Acacia tortilis* trees of three different age classes, dead trees and in open grassland patches. We measured the effect of trees on nutrient, light and water availability to study which resource determines changes in herbaceous layer productivity and composition.

Soil nutrient availability increased with tree age and size and was lowest in open grassland and highest under dead trees. The lower N:P ratios of grasses from open grassland compared to grasses from under trees indicated that productivity in open grassland was limited by nitrogen. Soil moisture contents were lower under than outside canopies of large *Acacia* trees. This indicates that water competition between trees and grasses is more important than facilitation through hydraulic lift.

Species composition of the herbaceous layer under *Acacia* trees was completely different from the vegetation in open grassland. Also the vegetation under bushes of *Acacia tortilis* was different from both open grassland and the understorey of large trees. The main factor causing differences in species composition is probably nutrient availability because species compositions were similar under situations of equal soil nutrient concentrations even when light and water availability were different. Changes in species composition did not result in differences in above ground biomass which was remarkably similar under different sized trees and in open grassland. The only exception was around dead trees where herbaceous plant production was 60% higher than under living trees.

Herbaceous layer productivity was not increased under trees by a higher soil nutrient availability because under trees grass production was probably limited by competition for water. When trees die and water competition disappears but the high soil nutrient availability remains, plant production can increase, which explains the high grass production around dead trees. So, we conclude that the two most important processes regulating tree-grass interactions in this semi-arid savanna are tree soil nutrient enrichment and belowground competition for water.

Introduction

Savanna ecosystems are characterised by a continuous herbaceous layer and a discontinuous tree layer. Several studies have focused on the effect of savanna trees on the functioning of the grass layer and have reported that different species grow under trees than in open grassland. (Belsky et al. 1989, 1993, Mclaren and Bartolome 1989, Akpo 1997). By changing resource availability trees can either increase or reduce plant productivity of the understorey. (Belsky et al. 1989, 1993, Weltzin and Coughenour 1990, Mordelet and Menaut 1995, Anderson et al. 2001). It is still unclear what determines understorey species changes and whether trees reduce or increase understorey plant productivity. It is difficult to determine this because trees affect nutrient, light and water availability of the understorey vegetation simultaneously (Scholes and Archer 1997).

Trees facilitate understorey plant growth through increased nutrient availability. A higher soil fertility under tree canopies has been reported for a wide range of savannas (Kellman 1979, Bernhard-Reversat 1982, Belsky et al. 1989, Callaway et al. 1991). However, it is still unknown how these 'islands of fertility' around isolated trees develop. It has been proposed that trees act as a nutrient pump taking up nutrients from deeper soil layers or from soil outside the canopy and depositing them under their canopy through litter fall or leaching (Kellman 1979, Scholes 1990). Other possibilities are that the trees are an effective trap for atmospheric dust or attract mammals which deposit their dung under tree canopies (Bernhard-Reversat 1982, Georgiadis 1989, Belsky 1994).

The effect of trees on soil water content is less clear than the effect of nutrients. There are some reports of increased soil moisture content under trees compared to open grassland which is probably caused by either decreased transpiration of understorey plants or hydraulic lift (Dawson 1993, Joffre and Rambal 1993). Hydraulic lift is the process of water movement from relatively wet to dry soil layers through the roots of plants that have access to both deep and shallow soil layers (Dawson 1993, Caldwell et al. 1998). Other studies showed reduced soil water availability under savanna trees due to a high tree water uptake (Amundson et al. 1995, Anderson et al. 2001). Also shade can have both positive and negative effects on below-crown plant production. Reduced light availability limits plant production but lower temperatures in the shade resulting in an improved grass water status could potentially increase plant growth (Belsky 1994, Anderson et al. 2001).

In this study, we used isolated *Acacia tortilis* trees of three different age classes, dead trees and open grassland patches, together representing five different successional stages of savannas, to investigate the effects of trees on the functioning of the herbaceous layer. We measured the effects of tree on soil water content, plant production and composition, soil and plant nutrient concentration, and light availability.

Comparing these different stages of savannas gave us a unique opportunity to study how the species composition and production of the understorey vegetation changes over time and which processes affect these changes. We distinguished four different effects of trees on the understorey vegetation as introduced in Table 2.1. We hypothesized that (a) nutrient enrichment of the soil is probably increasing with tree age and size and soil fertility is likely to be higher under dead trees than in open

grassland. However, (b) under living trees the herbaceous layer has to compete for belowground resources (both nutrients and water) while around dead trees and in open grassland herbaceous species have all the resources for themselves. (c) Hydraulic lift is more likely to occur under large than under small trees and bushes which may increase soil water availability under large trees and (d) Light availability is reduced by all living trees.

Combining these hypotheses we predict that herbaceous layer productivity is higher under large trees than under small trees and open grassland caused by a combination of a high soil fertility and hydraulic lift. Plant production around dead trees is probably higher than in open grassland because of an increased soil fertility. Bushes probably reduce plant production compared to open grassland because they provide too much shade and there is probably no increased soil fertility yet.

Table 2.1. The hypothesised effects of *Acacia tortilis* trees on the understorey vegetation and how this depends on tree stage. A minus sign indicates no effect of the tree and a plus sign indicates a weak (+) or strong (++) effect.

	Nutrients	competition for below ground resources	Hydraulic lift	Shade
Open grassland	-	-	-	-
Bush	-	+	-	++
Small tree	+	+	-/+	+
Large tree	++	+	+	+
Dead tree	++	-	-	-

Material and Methods

Site Description

The study site is located in the northern part of Tarangire National Park (4° S, 37° E, 1200m above sea level) on the eastern side of the Great Rift Valley in northern Tanzania. The soil at the site consisted of coarse sandy loams of lacustrine origin. The vegetation was wooded savanna with a tree cover of 10-20% (Van de Vijver et al. 1999). The dominant tree was the *Acacia tortilis*, the species we used for our measurements. Other tree species occurring in the area were *Balanites aegiptica* and *Adansonia digitata*. The last fire at the site occurred in 1994 (Van de Vijver, pers. comm.).

Mean rainfall over the last 20 years is 650 mm/yr (Van de Vijver 1999). The wet season is from November until May with most of the rain typically falling during March and April. During the 2 years of our observations rainfall was above average. The first season of our measurements (1997-1998) was the wettest in 20 years (1368 mm) with exceptionally high rainfall in December and January and rain continued until June. During the second season (1998-1999) rainfall was 798 mm with 75% of the rain between early March and late April and the rain already stopped early May. The study area is located in the dry season range of large migratory herbivore populations. From June until December the study site is grazed by large herds of Burchell's zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*). In the wet season most of the herbivores migrate to the Masai Steppe (Voeten and Prins 1999) and as a result from January until June (wet season) there is only occasional

grazing by impala (*Aepyceros melampus*) and herds of African elephant (*Loxodonta africana*) moving through the area.

Sampling design

In January 1998, we selected five large *Acacia tortilis* trees with a mean DBH of 72 cm (s.d. = 22) and a mean canopy cover of 286 m^2 (s.d.= 75). Trees were separated from other large trees by at least 100m and 50m from any bushes or small trees. According to Prins and van der Jeugd (1993) these trees are about 100 years old. Samples and data were collected at four different distances from the tree stem, at 25%, 75%, 125%, and 175% in which 100% is the distance from the tree stem to the canopy edge. Samples were collected in three directions (0 (north), 120 and 240 degrees) so in every direction we took 2 samples under, and 2 outside the tree canopy.

In the second season, 1999, we included four more stages of savanna succession. Five replicates of each stage were selected in the same 2*2 km area as where the large trees were located. 'Open grassland' patches were at least 100m from any tree or bush. Well developed 'bushes' of *Acacia tortilis* were about 4 m high and had no sign of tree or umbrella shape development (mean DBH=12 cm (s.d. = 3)) and average canopy cover = 13 m^2(s.d. = 6)). 'Small trees' had a clear tree form of at least 10 m high and began to form an umbrella shape (mean DBH= 38 cm (s.d. = 13), and canopy cover= 77m^2(s.d. = 21)). The last stage were 'dead trees' which were large trees which had died between 4-8 years before we started our measurements. Through information of park management, we know for three trees the exact year in which the tree died. The time of death of the other two trees was estimated by comparing the decay status of the trunks with trees of which the year of death was known. Small trees, bushes and dead trees were separated from large trees by at least 50m and from other small trees and bushes by at least 20m. The second year (1999) we only studied four of the same five large trees as in 1998, because under one of the trees a firebreak was created in September 1998.

Soil water content

To determine soil moisture content, soil samples were taken around 5 large trees and at 4 distances, as described above. In 1998, soil samples were collected twice during the wet season, at 27 February and 15 April, and twice during the dry season, at 13 June and 19 August. Samples were collected with a metal pipe (diameter = 4.2 cm) at 2 different depths from 0-10 cm and 20-30 cm. Soil water content in samples was determined gravimetrically by drying them at 100°C.

During the second season (1999) soil samples were collected just after the first rain (11 January), in middle of the wet season (23 March), and in the dry season (13 August). In 1999, in addition to large trees we also collected samples under bushes and small trees, for both stages halfway the canopy and the stem. Around dead trees we could not collect samples in relation to the canopy so we sampled at 2 and 5 m from the stem, which is under the original canopy, and at 10m which must have been outside the original canopy. Sampling under each bush, small and dead tree was replicated in North and South direction and samples were taken at 2 depths, from 0-10 cm and 20-30 cm. In August, at each open grassland patch, two samples were collected at both soil depths. To achieve a more detailed understanding of the effect of

large trees on soil water availability, we analysed soil water content around large trees on 3 additional days in the dry season of 1999 (on 3 June, 22 June and 13 July). These soil samples were taken at 25% and 175% of the canopy radius of large trees following the same procedure as described above.

Soil nutrient concentration

A part of each soil sample collected in August 1999 in the top layer (0-10 cm) was sun-dried and analysed for total and available N and P, available K and soil organic matter. Total N and P concentrations were determined using a modified Kjeldahl procedure with Selenium as a catalyst (Novozamski et al. 1983). After digestion, N and P concentrations were measured colorimetrically with a continuous flow analyser (Skalar SA-4000). Available K^+, NO_3^- and NH_4^{3+} were analysed by extracting 3 g soil in 30 ml of a 0.01 M CaCl solution. After extraction, NO_3^- and NH_4^{3+} concentrations were analysed colorimetrically with a continuous flow analyser and K was analysed with an atomic absorption spectrophotometer (Varian Spectra AA-600). Soil organic matter was analysed by loss on ignition. Available PO_4^{3-} was analysed following the Bray method (Bray and Kurtz 1945) 1 g soil was extracted in a 0.03 M NH_4F and 0.025 HCl solution. After extraction, PO_4^{3-} concentration was analysed colorimetrically with a continuous flow analyser.

Plant nutrient concentration

N:P ratios in plant tissue are good indicators to determine whether N or P is limiting the production of the vegetation (Koerselman and Meuleman 1996). In order to test whether grasses growing under trees are limited by different nutrients, green fully extended young grass leaves were collected under different trees. In June 1998, we collected grass leaves under 5 large trees at 4 different distances from the stem at 25%, 75%, 125%, and 175% of the canopy radius. In April 1999, we again collected grass leaf samples around large trees at the same distances and under small trees and bushes and around dead trees. The samples around dead trees were divided in grasses growing between 1 and 3 m and between 4 and 6 m from the tree. Grasses were sundried and analysed for total N and P concentration using a modified Kjeldahl procedure (see soil samples). Different grass species were collected around each tree stage because of differences in the vegetation composition. We collected samples of the grass species *Cynodon dactylon, Panicum maximum, Setaria verticillata, Urochloa mosambicensis, Chloris virgata, Cenchrus ciliaris,* and *Heteropogon contortis.* Only, one species, *Cenchrus ciliaris,* could be collected at all the different distances and tree sizes. At each tree stage and distance at least 10 grass samples were collected.

Herbaceous layer biomass and species composition

Species composition of the understorey vegetation was recorded at peak biomass in May 1999. Plots of 2*2 m were situated at the same spots where soil samples were taken. For each plot the aerial cover of all plant species was visually estimated. Nomenclature was according to Clayton and Renvoize (1982). At the same time we also measured peak standing biomass of the herbaceous layer. At the same place

where we determined species composition, plots of 70 by 70 cm were clipped by hand to ground level. Plant material was separated into grasses and non-grasses, dried in the sun for several days and weighed.

Light availability with hemispherical photographs

To determine light availability, in July 1998, at the end of the growing season hemispherical (or fish-eye) photographs were made under large *Acacia* trees using a lens with a 180 degree view, which produces a circular projection of the sky hemisphere. Pictures were taken 1.5 m above the ground where light was intercepted by the tree and not by the herbaceous layer. Pictures were taken under 5 large trees at 4 different distances from the stem at 25%, 75%, 125%, and 175% of the canopy radius in the 4 compass directions. After scanning, pictures were analysed with the computer program Hemiphot (Ter Steege 1994). From the pictures first the leaf area index was calculated and thereafter direct and diffuse light intercepted by the tree for every single day in a year. Finally, values are expressed as "total site factor" (Anderson 1964). The "total site factor" is the fraction of total (both diffuse and direct) radiation relative to the amount of radiation above the tree canopy that will penetrate into the herbaceous layer at the site a picture was taken.

Statistical Analysis

All data were statistically analysed with SPSS 7.5 for Windows. The soil water content, plant nutrient concentration, and light availability data of 1998 were analysed with a GLM with distance to large trees as a covariable, trees as a random (block) factor, and compass direction as a fixed factor. In case of the soil water content, depth was taken as an additional fixed factor.

As our experimental set-up in 1999 did not allow for one single analysis for all data, we first analysed whether different successional stages had an effect on soil and plant nutrient concentration, soil water content and herbaceous biomass. We thus compared data collected in open grassland, under bushes, and under small trees, at two meter from dead trees and at 25 % of canopy radius of large trees. The effect of tree stage was analysed with a GLM with tree growth stages (small, large and dead trees, bushes open grassland) and compass direction as fixed factors and in case of the soil water content, soil depth as an additional fixed factor. Thereafter we separately tested the effects of distance to large trees and to dead trees with distance to the tree as covariable.

Results

Soil water content

In general, soil water content was lower under than outside the canopies of large *A. tortilis* trees (Figure 2.1). On all dates in 1998 except in the middle of the heavy rains in April there was a significant effect of distance to the tree on soil water content (Table 2.2). During the wet season of 1999, in January and March, distance to large trees had no effect on soil water content,. but during the first two months of the dry season, in June and July, soil water content was again lower under than outside large
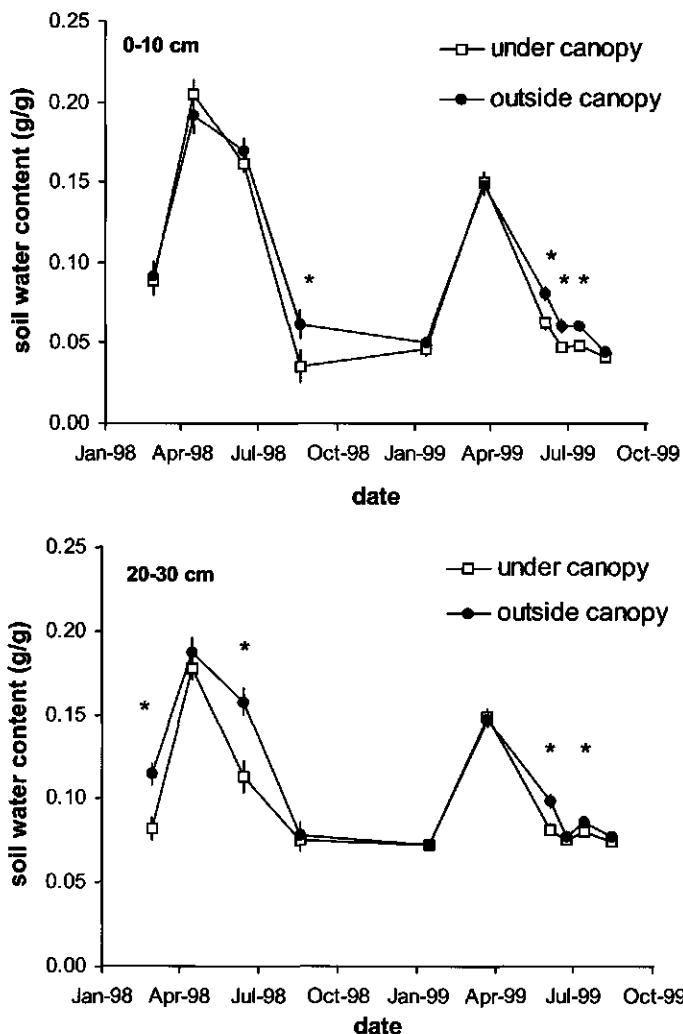
Figure 2.1. Average soil water contents (±s.e.) under and outside canopies of large *Acacia tortilis* trees at two different depths at 0-10 cm (A) and 20-30 cm (B). Soil samples were taken during a period of two seasons. Only data from 25% and 175% compared to the tree canopy edge (= 100%) are presented. Soil water content at 75% and 125% from canopy edge was always in between the values at 25% and 175%. Asterisks indicate a significant effect of trees on soil water content on that individual date (Tukey HSD test; $P<0.05$)

tree canopies. Later in the dry season, in August, soils were too dry to distinguish any differences between under and outside canopies.

There was no effect of tree size or stage on soil water content in the early wet season (January) of 1999 (Figure 2.2). In the middle of the wet season, in March 1999, soil water content was higher under large trees and lower close to dead trees with intermediate values under bushes and small trees. Three months into the dry

season, in August, there was no effect of tree stage on soil water content; probably because soils were already very dry. Soil water content at 5 and 10 m from dead trees was similar to the values at 2 m (data not shown).

Soil nutrient concentrations

Acacia trees had a strong effect on soil nutrient concentration (Figure 2.3). In general, the older the tree the higher the soil nutrient concentration and the highest concentrations were found in soils close to dead trees. The largest differences were observed for the available nutrient concentrations. Available NO_3^- concentration was more than 10 times higher under large and dead trees than in open grassland. Differences were smaller for K^+ and PO_4^{3-} but there was still a significant effect of tree age on concentrations of these nutrients (Table 2.3)

Table 2.2 Analysis of variance using a general linear model showing the effect of *Acacia tortilis* trees on soil water content. In three separated analyses, we tested the effect of tree stage at comparable distances from tree stems (bushes, small, large and dead trees and open grassland[†]), the effect of distance from large and the effect distance form dead trees on soil water content. In 1999 we took samples under all tree stages and in 1998 only under large trees. Interactions which were not significant are not shown.

	df	4 dates 1998 F	28/2/98 F	15/4/98 F	13/6/98 F	19/8/98 F	3 dates 1999 F	14/1/99 F	23/3/99 F	13/8/99 F
Large trees										
Distance to stem	1	13.74***	6.145*	0.01	16.42***	6.39*	0.57	0.99	0.13	3.21
Tree	4	57.86***	62.58	21.42***	16.15***	17.53***	27.93***	33.12***	18.34***	18.38***
Depth	1	0.64	0.70	8.58**	36.11***	27.37***	37.36***	60.33***	0.01	116.01***
Date	2/3	98.12***					381.61***			
Depth*distance to stem	1	3.29	9.70**	2.27	9.28**	3.538	0.13	0.56	0.01	0.09
Tree stages										
Tree stage	3/4						14.81***	1.41	35.61***	0.89
Depth	1						33.91***	7.08**	2.63	51.48***
Date							168.81***			
Depth*tree stage	3/4						1.37	2.13	0.57	1.119
Date*tree kind	2						18.03***			
Dead trees										
Distance to dead tree	1						0.09	0.21	0.28	0.06
Depth	1						5.14*	0.04	0.13	23.38***

* P<0.05, ** P<0.01, *** P<0.001
† open grassland was only included on 13/8/99

Under large trees, nutrient concentrations were the highest close to the tree stem and gradually reduced with increasing distance from the stem. Outside canopies of large trees, nutrient concentrations were still higher than in open grassland and similar to the soils under bushes and small trees (Figure 2.3). There was also a significant effect of distance to dead trees on nutrient concentrations, with higher values under than outside the original canopies (Table 2.3). The effects of tree stage and distance to large and dead trees on soil total N and P concentration were quantitatively similar to the effects of available nutrients but the differences were smaller (Table 2.3).
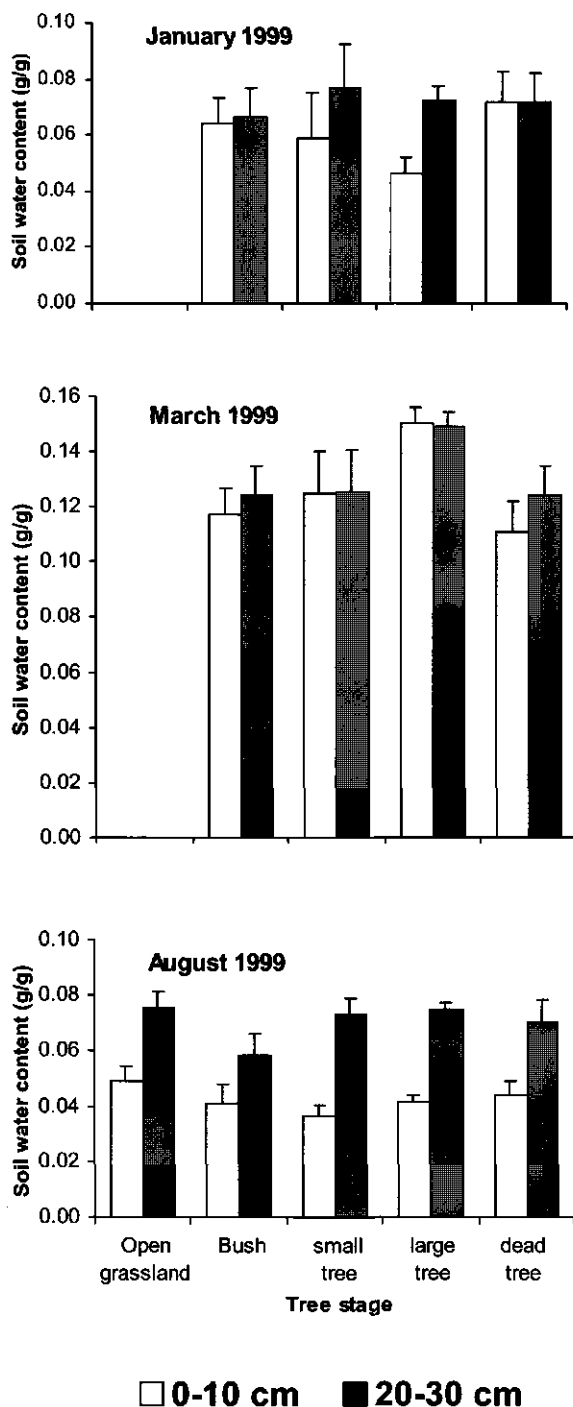
Figure 2.2. Average soil water content (±s.e.) at two different depths in open grassland, under bushes, small and large (25% from canopy edge) *Acacia tortilis* trees and at 2 m form dead trees. Soil samples were taken in the wet season in January and March and in the dry season in August of 1999. For statistics see table 2.
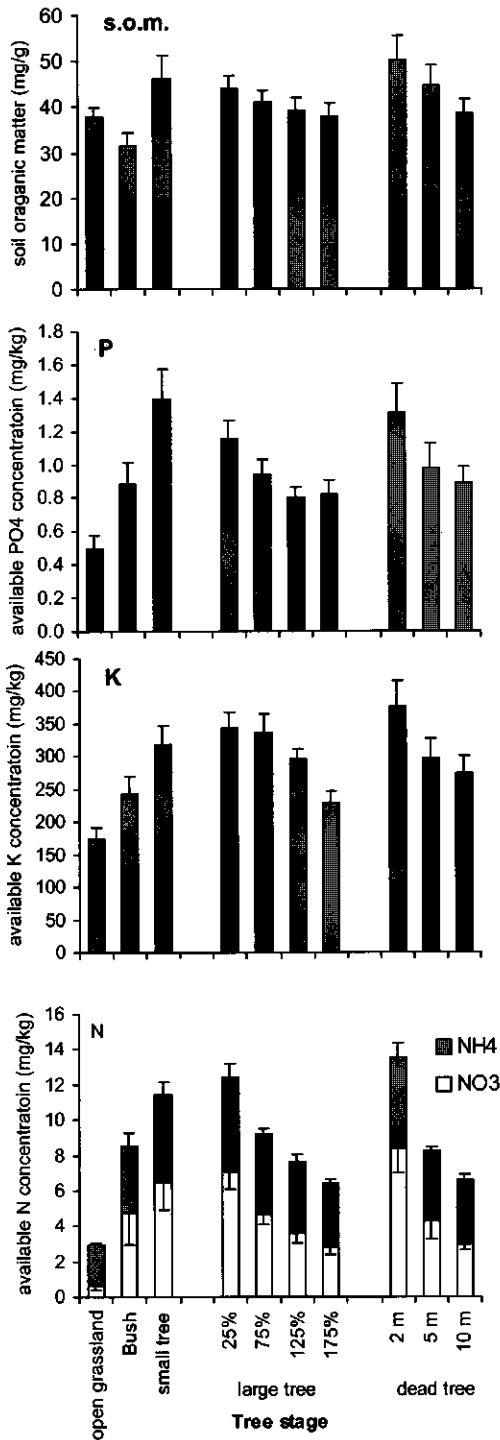
Figure 2.3 Average (±s.e.) soil organic matter (s.o.m.) and available N, P and K concentration in soil samples taken at different distances from large *Acacia tortilis* trees, under bushes and small trees and in open grassland. Available nitrogen concentration is separated in NH_4^+ and NO_3^- concentration. Distances from large trees are expressed relative to the canopy edge (edge = 100%). For statistics see table 3.

Light availability

Under large tree canopies, photosynthetic active radiation was about 50% of the light available in open grassland (Figure 2.4). Relative light availability (total site factor) was significantly affected by distance from the tree stem (df=1, F=273, P<0.001) while compass direction had no effect on light availability (P>0.05).

Plant nutrient concentrations

In June 1998, two weeks into the dry season, grass leaf N concentrations were significantly higher under than outside canopies of large trees (Table 2.4). The opposite trend was observed for P with a higher concentration outside large tree canopies. These opposite trends resulted in large differences in N:P ratios. Under tree canopies the values fluctuated around 12 but outside the canopy the ratio was only about 6.

In 1999, again grass N concentrations were much higher under than outside large tree canopies but this year there was no difference in P concentration. N:P ratios were again higher under than outside canopies of large trees.

Table 2.3. Analysis of variance using a general linear model showing the effects of *Acacia tortilis* trees on different nutrient concentrations and soil organic matter (s.o.m). In three separate analyses we tested the effect of tree stages (open grassland, bushes and small, large and dead trees), distance from large trees and distance from dead trees.

	df	Total N F	Total P F	Available K F	Available NO_3^- F	Available NH_4^{3+} F	Total available N F	Available PO_4^{3-} F	s.o.m. F
Effect of tree stage	4	6.704***	6.249***	8.371***	5.715***	3.198*	6.211***	6.294***	3.566*
Distance from large trees	1	23.22***	22.80***	20.03***	21.19***	1.024ns	23.22***	22.80***	11.70***
Distance from dead trees	1	15.56***	6.528*	6.41*	17.54***	3.395+	14.82***	8.634**	15.61***

ns = not significant, + P<0.10, * P<0.05, ** P<0.01, *** P<0.001

There was also a clear effect of tree stage on grass nitrogen concentrations. Grass nitrogen concentration were the highest under large trees and the lowest under bushes, with intermediate values for dead and small trees (Table 2.4). Trees size had no effect on grass P concentration. The N:P ratios followed the same trend as N concentrations with higher values under large trees and lower values under bushes.

Herbaceous layer production

The amount of aboveground biomass of the herbaceous layer was very similar under living trees and in open grassland patches (Figure 2.5). However, close to dead trees there was more biomass than around other tree stages (P=0.056; Table 2.5). Aboveground biomass at 2 m from dead trees was almost 900 g/m^2 while under bushes, small and large trees it was only around 550 g/m^2. The amount of above ground biomass around dead trees reduced with increasing distance from the stem.
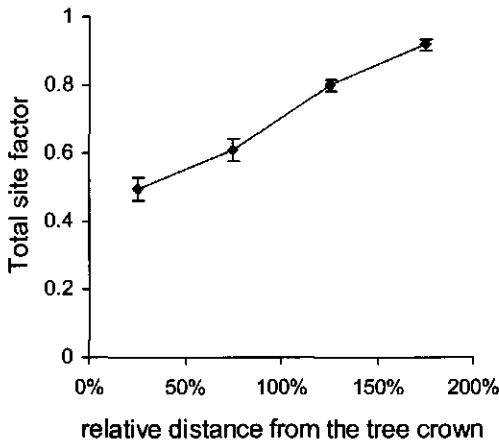
Figure 2.4. Relative light availability around canopies of large *Acacia tortilis* trees. Values are expressed as total site factor (±s.e.) which is the fraction of total PAR that will penetrate into the herbaceous layer compared to the amount of radiation above the tree canopy. Distances are expressed relative to the canopy edge (edge = 100%).

Around large trees the amount of biomass was similar under and outside canopies. Both the amount of grass and herb biomass was higher around dead trees than under living trees and in open grassland. However, when herb and grass biomass were analysed separately there was no significant effect of tree stage on plant production (Table 2.5).
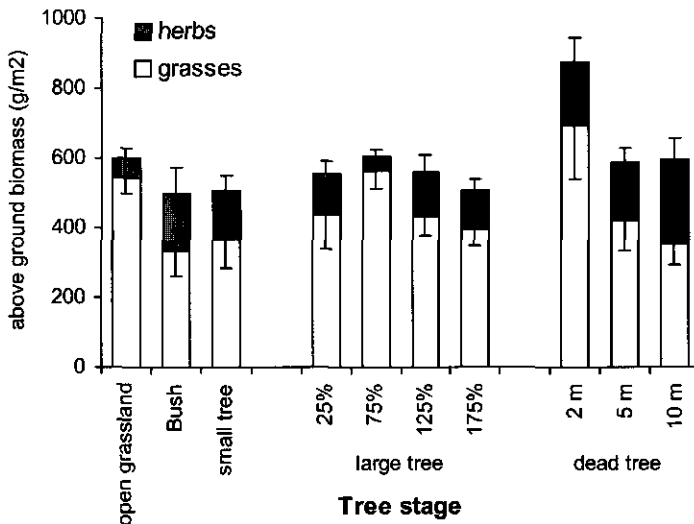

Figure 2.5. Average aboveground grass (-s.e.) and herb (+s.e.) biomass at different distances from large and dead trees of *Acacia tortilis*, under bushes and small trees and in open grassland. Biomass was determined at the end of the growing season in May 1999. Distances from large trees are expressed relative to the canopy edge (edge = 100%). For statistics see table 5.

Table 2.4. Mean leaf N and P concentrations of grasses collected at different distances from large and dead trees and under bushes and small trees and results of an analysis of variance using a general linear model for N and P concentration and N:P ratio. The effect of tree stages, distance from large tree and distance from dead trees was tested in three separate analyses. Presented are degrees of freedom (df), F values and level of significance.

Nutrient Concentration		1998 N concentration (mg/g)	1998 P concentration (mg/g)	1998 N:P ratio	1999 N concentration (mg/g)	1999 P concentration (mg/g)	1999 N:P ratio
Bush					28.9	3.86	7.88
Small tree					34.8	3.98	9.08
Large tree	25%	30.2	2.50	12.69	36.1	3.47	10.43
	75%	29.1	2.49	11.87	33.1	3.46	9.73
	125%	24.4	3.92	6.78	26/0	3.28	8.43
	175%	23.6	3.84	6.49	24.7	3.57	7.58
Dead tree	1-3 m				32.4	3.59	9.11
	4-6 m				27.1	3.89	7.44
Statistics	df	F	F	F	F	F	F
Effect of tree stage	3				8.54^{***}	0.773^{ns}	7.92^{***}
Distance from large trees	1	4.291^{*}	4.605^{*}	17.62^{***}	41.48^{***}	1.201^{ns}	44.26^{***}
Distance from dead trees	1				16.62^{***}	0.183^{ns}	7.35^{*}

ns = not significant, * $P<0.05$, *** $P<0.001$

Herbaceous layer composition

In open grassland the vegetation was dominated by the grasses, *Sehima nervosum* and *Heteropogon contortis* (Table 2.6). The herb cover at open grassland patches was less than 10%, which was much lower than under trees. Under bushes, *i.e.* youngest *Acacia,* the abundance of the open grassland species, *S.nervosum* and *H.contortis,* was much lower and these grass species were replaced by the grasses *Urochloa mosambicensis.* and *Cenchrus ciliaris.* Also herb species like *Solanum incanum, Sida cordifolia* and *Achyranthus aspera* appeared in the herbaceous layer under bushes. The species composition of the vegetation was similar under small trees and bushes. The open understorey vegetation of large trees was different from the vegetation under small trees or grassland. Herb cover was much lower than under small trees and the vegetation under large trees was dominated by the grasses *Cynodon dactylon, C.plectostachius* and *Panicum maximum.* These grass species were subordinate or absent in the vegetation under small trees and bushes. Just outside the canopy zone of large trees, the vegetation was different than under the canopies but similar to the vegetation under bushes and small trees.

Table 2.5. Analysis of variance using a general linear model of total, grass and herb production around different sized trees in May 1999. In three separate analyses we tested the effect of different tree stages (bushes, small, large and dead trees and open grassland,) and the effect of distance from either large or dead trees

	df	Total production F	grass production F	herb production F
Tree stage	4	$2.503^{†}$	1.805	1.908
Distance from large tree	1	0.471	0.692	0.172
Distance from dead tree	1	5.652^{*}	2.942	0.66

† $P=0.056$, * $P<0.05$,

The vegetation around dead trees was very species-rich. Compared to large trees, cover of the two *Cynodon* species was lower under dead trees but cover of the grass species *Urochloa mosambicencis* and especially the herb *Solanum incanum* was higher.

Discussion

Understorey species composition

Isolated *Acacia tortilis* trees clearly altered the species composition of the grass layer in this semi-arid savanna. A change of species composition under isolated trees compared to open grassland has also been reported in several other studies, however, what exactly causes these species changes remains unclear (Tiedemann and Klemmedson 1977, Belsky et al. 1989, 1993, Scholes and Archer 1997). Most previous studies only compared large trees to open sites but we also included smaller *Acacia* trees. In contrast to our expectations, the species composition under bushes and small trees was not a transition state from open grassland to large trees because different species dominated the vegetation under these smaller *Acacias*. Interestingly, the species composition of the herbaceous layer under bushes and small trees was similar to the vegetation just *outside* large tree canopies. Soil nutrient concentrations were also similar outside large trees and under bushes and small trees. This suggests that soil nutrient concentration is the driving factor behind the species changes and not water or light availability because these are different under bushes and outside large trees.

In addition to changing grass species composition, trees also had a large effect on the occurrence of herbaceous dicots. While in open grassland and under large trees only 10-20% of the vegetation was covered by herbs, under bushes and small trees this was 40 to 50%. Shade might be an important factor here determining the occurrence of herbs under bushes. In a shade experiment performed at the same site it was shown that herbs are more tolerant to shade than open grassland grasses (Ludwig et al. 2001; chapter 3). When *Acacia* trees start to grow, the first major environmental change for understorey herbaceous species is shade and this light reduction probably

Table 2.6 Species composition of the herbaceous layer at different distances from large and dead trees and under bushes small trees and in open grassland. Presented are the average cover in percentage for herbs and the most dominant grass species.

Species	Open grassland	bush	small tree	large tree				dead tree		
				25%	75%	125%	175%	2 m	5 m	10 m
Urochloa mosambicensis	7%	15%	16%	1%	6%	24%	20%	8%	9%	11%
Heteropogon contortis	35%	16%	6%	-	4%	25%	16%	-	4%	9%
Cynodon dactylon	0%	7%	11%	25%	16%	1%	2%	23%	11%	6%
Cenchrus ciliaris	1%	12%	5%	10%	19%	6%	2%	15%	11%	8%
Panicum maximum	1%	1%	0%	19%	11%	2%	2%	10%	18%	8%
Sehima nervosumi	31%	5%	2%	-	1%	3%	11%	-	0%	6%
Cynodon plectostachius	-	-	-	17%	12%	2%	-	5%	2%	-
Digitaria macroblephera	3%	1%	1%	-	-	6%	9%	-	3%	8%
Eragrostis superba	12%	3%	3%	-	-	5%	1%	-	1%	2%
Setaria verticillata	-	3%	2%	3%	9%	-	-	4%	1%	1%
Other grasses	3%	4%	12%	8%	13%	10%	18%	3%	1%	6%
Herbs	9%	38%	55%	21%	19%	24%	33%	42%	41%	46%

causes the open grassland species to disappear which are replaced by herbs. Under large trees there is also shade but here the vegetation is dominated by *Cynodon* and *Panicum* grasses. Here the high soil nutrient concentration becomes important because these grass species typically occur on fertile soils (Prins 1996, Durr and Rangel 2000). Nutrient concentrations are high enough for *Cynodon* and *Panicum spp.* under large trees but not yet under most small trees.

Effect of trees on nutrient availability

The clearest and probably most important effect of *Acacia* trees on the understorey vegetation is through increased nutrient availability. All measured soil nutrient concentrations increased significantly with tree size and age and nutrient concentrations around dead trees were slightly higher than under large trees. The higher soil fertility around dead trees may have been caused by extra input of organic nutrients into the soil after trees die but also under trees that died eight years before our measurements, soil nutrient concentrations were still high. This indicates that soil fertility under dead trees remains high for several years. This is consistent with a study in a North American savanna by Tiedemann and Klemmedson (1986) who found increased soil nutrient concentrations compared to open sites even 13 years after tree removal.

In almost all previous studies in savannas, nutrient concentrations were higher under isolated trees than in open grassland (Kellman 1979, Belsky et al. 1989, Anderson et al. 2001). Although this 'island of fertility' under savanna trees is a well-known phenomenon, the mechanism through which the soil is enriched by the tree is still unclear (Georgiadis 1989, Scholes and Archer 1997). At our site, it is unlikely that herbivores played an initiating role in enriching the soil because they are too large to graze under bushes and already under these young *Acacia's* the soil is more fertile than in open grassland. Large herbivores could, however, increase the rate of nutrient enrichment under large trees.

According to the 'nutrient pump' hypothesis trees collect nutrients from deeper soil layers and laterally from areas beyond the canopy, which are then deposited below the canopy through litterfall and leaching (Bernhard-Reversat 1982, Scholes and Archer 1997). If nutrients are collected from outside canopies this would result in an impoverished area around trees. However, this is not the case with the *Acacia* trees we studied, just outside the canopy the soil is still more fertile than in open grassland which indicates that *Acacia* trees also increase nutrients available for grasses on a landscape scale. Nutrients like P and K are thus likely to come from deeper soil layers while N enrichment may be caused by N-fixing bacteria associated with *Acacia* trees. These nutrients end up in the topsoil through litterfall and canopy leaching. Soil enrichment outside canopies is less likely to come from litterfall which suggests that also root litter plays a role in enriching the soil.

Due to the increased soil nitrogen concentration, understorey grass leaves were richer in nitrogen than grasses growing outside tree canopies. In 1998 but not in 1999 grass P concentrations were lower under than outside tree canopies. These opposite trends of N and P concentrations resulted in large differences in N:P ratios. Outside tree canopies the ratio was about 6, according to Koersmelman and Meuleman (1996) this clearly indicates N limitation. Under the tree, however, the ratio was about 12, according to the theory from wetland ecosystems this would still

indicate N limitation but it is closer to the critical value of 14 indicating P limitation (Verhoeven et al. 1996, Aerts and Chapin 2000). A nutrient addition experiment at the same site indeed indicated that outside *Acacia* trees grass production was limited by N while under the trees there was a slight increase of production after P addition (Ludwig et al. 2001, chapter 3). N:P ratios of grasses growing under bushes and small trees were intermediate between large trees and open grassland suggesting that the understorey of *Acacia* trees changes gradually from a N limited to a P limited vegetation.

Herbaceous layer productivity

While *Acacia* trees changed the species composition of the understorey vegetation, this did not affect the productivity of the herbaceous layer. Both under living trees and in open grassland the herbaceous biomass at the end of the growing season was about 550 g/m^2. Also in an additional study at the same site grass biomass was almost equal under and outside large trees on 7 separate dates over 2 seasons (Ludwig et al. 2001; chapter 3). Under dead trees, however, the aboveground biomass was 60% higher than under living trees.

Increased production under savanna trees compared to open sites is usually attributed to a higher soil nutrient concentration (Belsky 1994, Scholes and Archer 1997). In this study nutrient concentrations also dramatically increased from open grassland to large trees but the productivity of the understorey vegetation remained equal. This indicates that resources other than nutrients were limiting plant growth under trees. Both low water availability and reduced radiation due to shade could have limited herbaceous layer productivity under *Acacia* trees. Photosynthetic active radiation under canopies of large trees was reduced up to 50% of values in open grassland. When enough water and nutrients are available, in the (early) wet season, shade may limit grass productivity but during the dry season when water limits plant growth, shade and associated lower temperatures can increase plant productivity. An experiment around large trees indeed showed that shade reduced grass production during the wet season and increased plant growth during the dry season. The total productivity, however, was not affected by shade (Ludwig et al. 2001; chapter 3).

It is more likely that soil moisture in stead of shade limited plant growth under *Acacia* trees. Trends of lower soil moisture contents near the tree stem observed in this study were consistent with soil water potential measurements performed under the same trees (chapter 4). These same measurements showed that hydraulic lift occurs in large *Acacia* trees. However, hydraulic lift did not result in increased soil moisture content because trees take up more water than they exudate (chapter 4). A lower soil moisture content under large trees could also be caused by a higher water uptake of grasses but we consider this as unlikely because with equal grass biomass under and outside trees canopies, understorey grasses probably use less water because of their lower transpiration rate due to shade (Amundson et al. 1995). So, probably the production of the understorey vegetation of large trees was not increased although there was a higher nutrient availability because soil water availability limited the productivity.

This all changes when trees die. Then grasses do not have to compete anymore with trees for soil moisture and a high soil fertility remains. So, grasses around dead trees have plenty of nutrients available and are less limited by water than grasses under living trees which explains the high herbaceous biomass around dead trees.

Also the N:P ratios of grasses growing near trees were lower than under large trees indicating that grass production becomes limited by nitrogen again. So, although soil nutrient concentrations (especially N) were higher under dead than under large trees, grass growth became limited again by nitrogen due to a higher grass productivity.

Conclusions

Our results show that the main cause that species compositions are different in open grassland and under *Acacia* trees but productions are similar, is that different resources limit production. In open grassland, nutrients (mainly N) are limiting grass production while under trees water is the limiting factor. The lower water availability under large trees and the high herbaceous layer productivity around dead trees indicate that plant production in the understorey of large trees is limited by water. This is in contradiction to our hypothesis, and shows that competition for water between trees and grasses seems to be more important than hydraulic lift. So, the most important processes shaping tree-grass interactions in this semi-arid savanna are soil nutrient enrichment by trees and below ground competition for water. An increased nutrient concentration under trees causes the vegetation changes of the herbaceous layer while water competition limits the grass productivity under older and larger trees.

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Chapter 3

The effects of nutrients and shade on tree-grass interactions in an East African savanna

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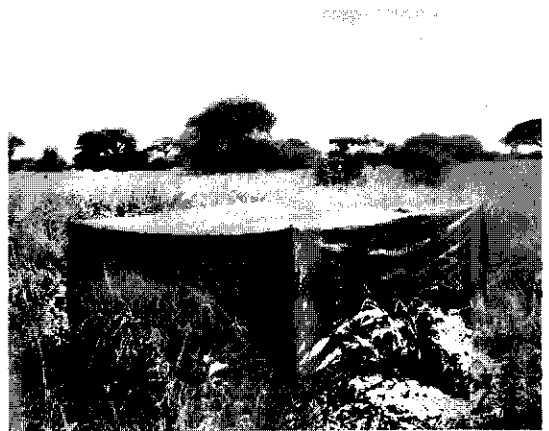
Abstract

Savanna trees have a multitude of positive and negative effects on understorey grass production, but little is known about how these effects interact and when the net result is positive or negative. Here we report on a fertilisation and shading experiment carried out in a Tanzanian tropical dry savanna around *Acacia tortilis* trees. In neither of the two years of study did grass production differ between plots from under the canopy and in open grassland. Fertilisation treatments however, indicate that trees do change the nutrient limitation of the grass layer, from an N-limited system in the open field to a P-limited system under the tree. The N:P ratios of grass leaves gave a reliable indication of the nature of nutrient limitation, but only when assessed at the end of the wet season. Mid-wet season nutrient concentrations of grasses were higher under the tree canopy than outside the tree canopy, suggesting that factors other than nutrients limit grass production. A shading experiment indicated that light may be such a limiting factor during the wet season when water and nutrients are sufficiently available. However, in the dry season when water becomes scarce, the effect of shade on plant production became positive. We conclude that whether trees increase or decrease production of the herbaceous layer depends on how positive effects (increased soil fertility) and negative effects (shade and soil water availability) interact and that these interactions may significantly change from the wet into the dry season.

Introduction

Dry tropical savannas are characterised by a continuous grass layer and a discontinuous tree layer. Whether the grasses are growing under or outside the tree crown affects all of their major resources. Trees and grasses compete for light, nutrients and water, but the tree can also increase the soil fertility (Belsky et al. 1989, Vetaas 1992) and water availability (Dawson 1993). This interplay between positive and negative effects of savanna trees on grass growth explains why both positive (Weltzin and Coughenour 1990, Belsky 1994) and negative (Stuart-Hill and Tainton 1989, Mordelet and Menaut 1995) net effects of isolated savanna trees on understorey productivity have been reported. Increased fertility of the below-crown soil is described for a wide range of savannas, both wet and dry, and on different continents (Kellman 1979, Bernhard-Reversat 1982, Belsky et al. 1989, Weltzin and Coughenour 1990, Callaway et al. 1991, Campbell et al. 1994). The relative increase in nitrogen concentration under savanna trees is often much higher than for phosphorus and this is especially the case under nitrogen fixing trees such as *Acacia* species (Callaway et al. 1991). These changes in soil nutrient concentration are likely to affect the nutrient limitation of grasses but this has never been actually demonstrated. In this study we tested which nutrient, N or P, limits grass production both in open grassland and under the tree canopy, in relation to effects of shade.

Higher grass productivity under savanna trees is often attributed to an increase in soil fertility. In several situations, however, increased below-crown soil fertility did not result in higher grass productivity under tree canopies (Anderson et al. 2001, Callaway et al. 1991). Other authors have suggested that increased below-crown productivity is caused by shade (Weltzin and Coughenour 1990, Belsky 1994, Amundson et al. 1995). Shade may improve the water relations of grasses due to lower temperatures. Light limitation may not be a major factor because most savanna trees only intercept about 50% of the sunlight which in tropical regions may not be severe enough to limit plant production (Belsky 1994). Experiments testing for the effect of shade on grass production show both negative (Tiedeman and Klemmedson 1977, Monk and Gabrielson 1985, Anderson et al. 2001,) and positive effects (Eriksen and Whitney 1981, Samarakoon et al. 1990). These contradictory effects of shade could be partly explained by seasonal changes. We hypothesise that reduced light intensities caused by shade may limit plant production during the wet season, when other resources as water and nutrients are plentiful. When water becomes limiting during the dry season, reduced water stress caused by shade will increase plant production.

It has been suggested that N:P ratios of the vegetation are a good indicator whether N or P is limiting plant growth (Koerselman and Meuleman 1996). Elemental ratios have been widely used in aquatic ecology to establish the nature of nutrient limitation (Rhee 1978, Smith 1982). Koerselman and Meuleman (1996) showed that N:P ratios can also be used in terrestrial wetland ecosystems. N:P ratios of the vegetation higher than 15 indicate P limitation while ratios under 12 imply nitrogen limitation. When the N:P ratio is between 12 and 15 there is co-limitation or K is limiting plant production (Koerselman and Meuleman 1996). This theory that the N:P ratio of the vegetation directly indicates which nutrient is limited (N or P) has never been tested in tropical ecosystems. This concept could be very useful in tropical regions where proper fertilisation experiments are hard to perform and little is known about nutrient limitation of natural vegetations.

Here, we report the results of an experiment in a dry tropical savanna in Tanzania in which *Acacia tortilis* is the dominant tree species. *Acacia tortilis* is a N-fixing species which has been reported to increase below-crown productivity in savannas in Kenya (Belsky et al. 1989, Wetlzin and Coughenour 1990, Belsky 1994). We investigated whether trees also increased grassland productivity in other East African savannas and if so whether this higher productivity is caused by shade and/or nutrients. To test which nutrient, N or P, limits grass production we fertilised plots with N, P or both under and outside the tree crown. As *Acacia* trees especially enrich the soil with nitrogen we expect phosphorus limitation under the canopy and nitrogen limitation in open grassland. We also covered plots with shade cloth and followed grass production under shaded conditions during several periods over the year to test whether effects of shade differ between dry and wet seasons.

Site Description

The experimental site was located in the northern part of Tarangire National Park (4° S, 37° E, 1200m above sea level) on the eastern side of the Great Rift Valley in northern Tanzania. The soil at the site consisted of coarse sandy loams of lacustrine origin. The vegetation was wooded savanna with a tree cover of 10-20%. The dominant tree is the *Acacia tortilis* the species we used for our experiments. Other tree species occurring irregularly over the area are *Balanites aegiptica* and *Adansonia digitata*. The herbaceous layer is well developed and the plant cover during the wet season is almost 100%. The herbaceous stratum is dominated by C_4 grasses with different species growing under (*Cynodon dactylon, Panicum maximum,* and *Setaria verticillata*) and outside (*Heteropogon contorits, Urochloa mosambicensis* and *Chloris virgata*) tree canopies.

Mean rainfall over the last 20 years is 650 mm/yr (Van de Vijver 1999). The wet season is from November until May with most of the rain typically falling during March and April. During the 2 years of our experiments the rainfall was above average. The first season (1997-1998) was the wettest in 20 years (1368 mm) with exceptionally high rainfall in December and January and the rain continued until June. During the second season (1998-1999) rainfall was 798 mm with 75% of the rain between early March and late April. In 1999 the rain already stopped early May. The study area is located in the dry season range of large migratory herbivore populations. From June until December the site is grazed by large herds of Burchell's zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*). In the wet season most of the herbivores migrate to the Masai Steppe (Voeten and Prins 1999) and as a result from January until June (wet season) there is only occasional grazing by impala (*Aepyceros melampus*) and herds of African elephant (*Loxodonta africana*) moving through the area.

Materials and Methods

Experimental design

For the experiments we used five large *Acacia tortilis* trees which are all approximately 100 years old (Prins and Van der Jeugd 1993). Trees with termite hills or large bushes in their understorey vegetation were avoided. Each tree was isolated with a minimum distance from other trees of 60-80 m. The trees had an mean DBH of

59 cm and a canopy diameter of 15 to 20 m. To investigate the effect of N and P on grassland productivity we carried out an experiment with a full factorial design both under the tree canopy and in open grassland with N and P addition as factors and the five trees as blocks. In addition, in open grassland one extra control plot and two plots covered with 55% shade cloth were established. Shade cloth was placed 150 cm above the ground. and was also placed around the plot to prevent direct sunlight during the early morning and late afternoon. Plots were 2 by 3.5 m and were situated 2 m from the tree stem under the canopy and 15-20 m from the stem for the open grassland plots.

Plots were fertilised with calcium nitrate (200 kg N $ha^{-1}yr^{-1}$) and/or calcium hydrogen phosphate (80 kg P $ha^{-1}yr^{-1}$). One third of the yearly dose of each nutrient was applied 3 times during each growing season. The nutrients for each plot were dissolved in 6 l of water and equally distributed over the plot. Control plots were only given water. Every plot thus received a total amount of 18 litres of water per year. This is less than 3 mm of rain and is thus negligible for plant growth. During the 1997-1998 growing season plots were fertilised in February, April and May and during the 1998-1999 season in December, February and April.

Production measurements

Each 2*3.5 m plot consisted of 6 subplots of 70 * 70 cm. Initially we assumed that an important part of the biomass was grazed by large herbivores so plant production was measured with removable chain-link fence exclosures. On day one, the first sub-plot (70*70 cm) was hand clipped to ground level; on the same day an exclosure was placed around the next subplot. After 6-8 weeks the vegetation inside the exclosure was clipped and the exclosure was moved to the next subplot. On the same day this procedure was repeated by first clipping a plot outside the exclosure and 6-8 weeks later harvesting inside the exclosure. By comparing the biomass outside the exclosure and the biomass inside the exclosure 6-8 weeks later we intended to measure plant production over this period. However there was no significant difference in biomass between plots inside and outside the exclosures on any of the dates ($P > 0.10$) so the biomass data of the two sub-plots clipped on the same day were lumped together and consequently above ground biomass instead of production is presented in the figures.

Aboveground biomass was harvested twice during the first wet season on March 12th, May 1st and at the start of the dry season June 23rd, 1998. Exclosures were removed from the plots after the last harvest of the first season and installed again after the first harvest of the second season. During the second year significant rainfall only started in March so the first 2 harvests on January 13, March 11 were before the rains. The next harvest on May 8 was at the end of the wet season and the last one on August 5 was 3 months into the dry season. At the final harvest in August 1999 we only collected the biomass inside the exclosures. In 1998 and 1999 we harvested sub plots on exactly the same locations. This caused no problems because during the dry season large grazers and termites remove almost all above ground herbaceous biomass and the vegetation regrows again after the onset of the rains. The harvested vegetation was sorted to grasses and non-grasses and dried in the sun and weighed.

N:P ratios

To test whether N:P ratios indicate nutrient limitation grass leaves from the fertilisation experiment were collected on June 21, 1998 and April 4, 1999 and analysed for N and P concentrations. Within each plot, young fully extended grass leaves were collected separately for each dominant grass species. Under the tree canopy we collected samples of *Cynodon dactylon*, *Panicum maximum* and *Setaria verticillata*. Outside the canopy samples of *Urochloa mosambicensis*, *Chloris virgata*, *Cynodon dactylon*, *Cenchrus ciliaris* and *Heteropogon contortis* were collected. Grasses were sun dried and analysed for total N and P concentration using a modified Kjeldahl procedure with selenium as a catalyst (Novozamsky et al. 1983). After digestion, N and P concentrations were measured colorimetrically with a continuous flow analyser (Skalar SA-4000, The Netherlands).

Data analysis

Data were statistically analysed using the General Linear Models (GLM) procedure for analysis of variance with SPSS 7.5 for windows. Whether total or grass production differed between under tree canopies and in open grassland was tested with a repeated measures analysis. As we expected nutrient addition to have its clearest effect at the end of the wet season (June 1998 and May 1999), biomass data on these dates were analysed separately for nutrient addition effects. The effect of trees (block factor), canopy and N and P fertiliser (fixed factors) on total herbaceous and grass and herb biomass was first analysed for all data from one harvesting date. Then plant biomass data from open grassland and under the tree canopy were analysed separately to test whether N or P limited plant production under tree canopies and in open grassland.

   The effect of tree canopies and N and P fertiliser on grass leaf N and P concentration and N:P ratio was analysed in the same way as the biomass data. GLM of leaf nutrient concentrations and ratios was followed by a Tukey's honestly significant differences test to detect differences between fertiliser treatments.

   The effect of shade was tested by using a repeated measures GLM in which shaded plots were compared with the control plots outside the tree. The effect of shade was also analysed separately for each harvesting date because there was a significant date x shade treatment interaction.

Results

Biomass production

During the 1997-1998 season, peak biomass in the control plots, with no nutrients added, was 650 g/m^2 but during the second season it was only around 400 g/m^2. A repeated measures analysis showed that aboveground total or grass biomass was not different under tree canopies and in open grassland (F= 2.11, P>0.10) (Figure 3.1). At the end of the first growing season in June 1998 nutrient addition had no effect on the aboveground biomass both under trees and in open grassland (Figure 3.2, Table 3.1). However, at the end of the second growing season in May 1999 both N and P had a significant effect on total biomass but there were no significant interactions between canopy and nutrient addition (Table 3.1). When the data were analysed separately for under and outside the tree canopy it became clear that N significantly increased total

Table 3.1. Analysis of variance using a general linear model of total and grass biomass. The first table represents data at the end of the first growing season in June 1998. The second table is for data from May 1999 at the end of the second growing season. The effect of N and P addition was tested on data from under the canopy and the open grassland together (overall effect) and separately. Canopy effect indicates difference between biomass under the tree canopy and in the open grassland. Trees were analysed as a block factor and all the other factors were fixed.

Effect	Total biomass						Grass biomass					
	Overall effect		Tree canopy		Open grassland		Overall effect		Tree canopy		Open grassland	
	Df	F	Df	F	df	F	df	F	df	F	df	F
1998												
N	1	0.679	1	1.073	1	0.058	1	0.632	1	2.318	1	0.040
P	1	0.271	1	1.491	1	0.065	1	0.750	1	0.291	1	0.544
Canopy	1	1.837	-		-		1	1.433	-		-	
Tree	4	4.385**	4	6.050***	4	1.623	4	6.802***	4	7.489***	4	2.263
N*p	1	0.046	1	0.205	1	0.400	1	0.530	1	0.131	1	1.737
Canopy*N	1	0.476	-		-		1	1.220	-		-	
Canopy*P	1	0.892	-		-		1	0.037	-		-	
Canopy*N*P	1	0.573	-		-		1	1.392	-		-	
Error	32		12		16		32		12		16	
1999												
N	1	4.079†	1	0.071	1	11.804**	1	4.895*	1	0.420	1	11.576**
P	1	6.441*	1	5.165*	1	2.397	1	2.330	1	3.501‡	1	0.248
Canopy	1	0.829	-		-		1	0.673	-		-	
Tree	4	3.342*	4	5.180*	4	0.744	4	2.184	4	5.840*	4	0.726
N*p	1	0.849	1	0.001	1	3.148	1	0.283	1	0.022	1	1.557
Canopy*N	1	2.618	-		-		1	1.809	-		-	
Canopy*P	1	0.770	-		-		1	0.959	-		-	
Canopy*N*P	1	0.808	-		-		1	0.534	-		-	
Error	32		12		16		32		12		16	

and grass biomass in open grassland while P increased total plant biomass under the tree canopy. At all intermediate dates N and P addition had no effect on the total or grass biomass (data not shown). Also 3 months into the dry season in August 1999 nutrient addition did not effect total or grass biomass.

Shade already had an effect by the end of the first season (Figure 3.1). In June 1998 the biomass in the shaded trea tment was 2/3 of that in full sunlight. During the second year plant production in the shade was lower during the wet season but continued for longer into the dry season so that by August 1999, three months into the dry season, biomass was equal in shaded and control plots in open grassland (Figure 3.1)

Grass nutrient concentration

At the end of the first wet season in June 1998, N concentrations were significant higher in the grass leaves collected from plots under the tree canopy than outside the tree crown while P concentrations were lower (Figure 3.3, Table 3.2). This resulted in a significantly higher N:P ratio under the tree crown compared to ratios of grasses from outside the tree. Under the tree canopy, nutrient addition had no significant effect on the leaf nutrient concentrations during the first season. In open grassland,

Table 3.2. Analysis of variance using a general linear model of leaf N and P concentration and N:P ratio in June 1998 and April 1999. The effect of N and P addition was tested on data from under the canopy and the open grassland together (overall effect) and separate. Canopy effect indicates a difference in nutrient concentration between grasses from under tree canopies and open grassland. Trees were analysed as a block factor and all the other factors were fixed. Effect of species could not be detected in the overall analysis because different species were collected under tree canopies and in open grassland.

| | N:P ratio | | | N concentration | | | P concentration | | |
| | Overall effect | Tree canopy | Open grassland | Overall effect | Tree canopy | open grassland | Overall effect | Tree canopy | Open grassland |
Effect	df F	df F	df F	df F	df F	df F	df F	df F	df F
1998									
N	1 14.61***	1 1.47	1 2.46	1 0.15	1 0.65	1 2.25	1 19.56***	1 0.05	1 1.73
P	1 7.20**	1 0.14	1 0.02	1 0.22	1 0.04	1 11.43**	1 10.50**	1 4.41†	1 3.64
species	-	2 4.98*	2 2.00	-	2 5.45**	2 2.56	-	2 25.92***	2 1.70
canopy	1 144.1***	-	-	1 76.99***	-	-	1 35.32***	-	-
tree	4 3.67**	4 3.51*	4 2.68	4 4.10**	4 5.57**	4 2.91	4 7.55***	4 4.81*	4 3.13*
N*P	1 2.06	1 1.89	1 2.01	1 0.70	1 1.36	1 6.61*	1 1.77	1 0.21	1 1.28
Canopy*N	1 2.85	-	-	1 1.26	-	-	1 15.16***	-	-
Canopy*P	1 6.97*	-	-	1 0.01	-	-	1 10.29**	-	-
Canopy*N*P	1 0.90	-	-	1 0.02	-	-	1 0.241	-	-
error	60	34	14	60	34	14	60	34	14
1999									
N	1 12.47***	1 0.56	1 13.54**	1 16.32***	1 2.75	1 13.95**	1 0.24	1 0.01	1 4.76*
P	1 40.31***	1 7.61*	1 30.34***	1 0.056	1 0.57	1 0.23	1 28.79***	1 4.71*	1 21.46***
Species	-	3 10.77***	5 4.06*	-	3 10.10***	5 5.91**	-	3 8.18**	5 6.64**
Canopy	1 0.50	-	-	1 75.47***	-	-	1 19.67***	-	-
Tree	4 2.20	4 0.122	4 0.89	4 2.92*	4 33.89***	4 1.46	4 2.03	4 2.06	4 1.54
N*P	1 2.49	1 0.015	1 1.14	1 0.01	1 0.086	1 1.23	1 0.07	1 0.05	1 1.62
Canopy*N	1 8.54**		-	1 6.65*	-	-	1 0.53		-
Canopy*P	1 5.79*		-	1 0.12	-	-	1 1.90		-
Canopy*N*P	1 .709		-	1 0.051	-	-	1 0.05		-
Error	63	19	17	63	19	17	63	19	17

* $P<0.05$, ** $P<0.01$, *** $P<0.001$, † $P = 0.054$. interactions between species and N or P were never significant

nitrogen addition reduced the P concentration of the grasses and this resulted in a higher N:P ratio.

In April 1999 in the middle of the second wet season, below crown grasses showed significantly higher N and P concentrations than grasses from outside the canopy but the N:P ratios were not different under and outside the tree crown. N fertilisation under the tree canopy had no effect on leaf N or P concentrations. P addition increased the leaf P concentrations and consequently reduced N:P ratios of grasses under the canopy. In open grassland both N and P fertilisation had an effect on the leaf nutrient concentration. N addition increased leaf nitrogen concentration and P fertilisation resulted in a higher P concentration of the grasses. The N:P ratios were reduced as a result of P fertilisation and increased by N addition.
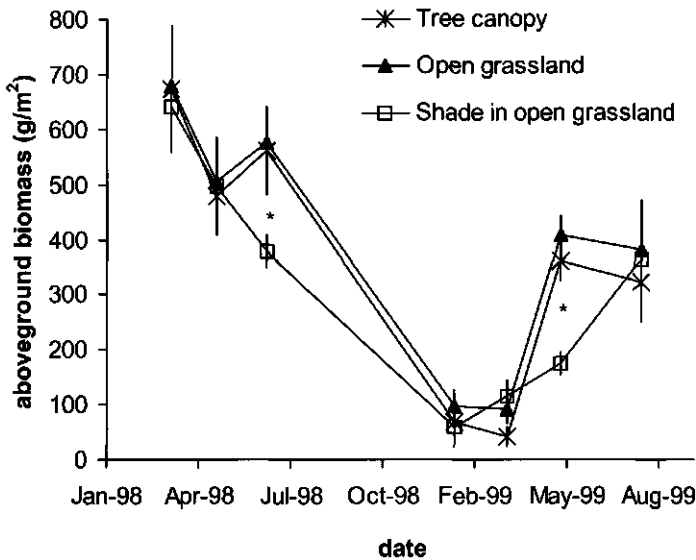
Figure 3.1. Average aboveground biomass of the herbaceous layer (±SE) in control plots under canopies of *Acacia tortilis* trees and in open grassland, compared to plots in open grassland shaded with 55% shade cloth. Asterisks (*) indicate a significant effect of shade on aboveground biomass (P<0.05) on that individual date tested with the GLM procedure for analysis of variance. A repeated measures analysis using data from all dates showed a significant effect of shade on aboveground biomass (F=5.61, df=1, P<0.05). Biomass in control plots under tree canopy and in open grassland was not significantly different (P> 0.05)

Discussion

The effect of trees on grass production

The effects of savanna trees on grass production has recently received a lot of attention and a variety of positive and negative effects have been reported (Belsky 1994, Mordelet and Menaut 1995, Scholes and Archer 1997, Anderson et al. 2001). Still, little is known about how the mechanisms of positive and negative effects of trees on grass production interact and when this culminates in a positive or negative net effect of savanna trees on grass production. In the experiment reported in this paper, apparently the positive and negative effects of the tree were in balance and herbaceous biomass never differed between under and outside the tree canopy, during either the dry or wet season. This contrasts with other observations in East Africa that report increased production under savanna trees (Weltzin and Coughenour 1990, Georgiadis 1989, Belsky et al. 1993, Belsky 1994). Nevertheless we did find that savanna trees have important effects on the kind of nutrient limitation and that shade had both positive and negative effects on grass production.
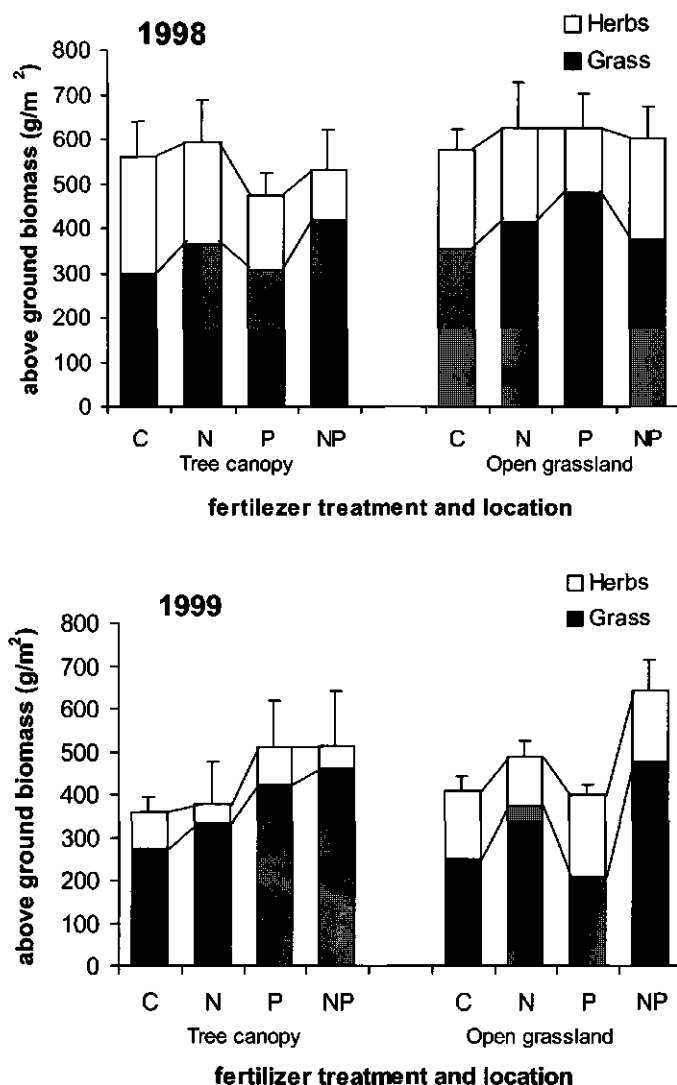
Figure 3.2 The effect of fertilisation on herb and grass biomass at the end of the wet season in June 1998 and May 1999 both under tree canopies and in open grassland; plots were fertilised with Nitrogen (N), Phosphorus (P) and a combination of both (NP) and compared with a control (C) treatment. Bars represent averages + SE of total biomass.
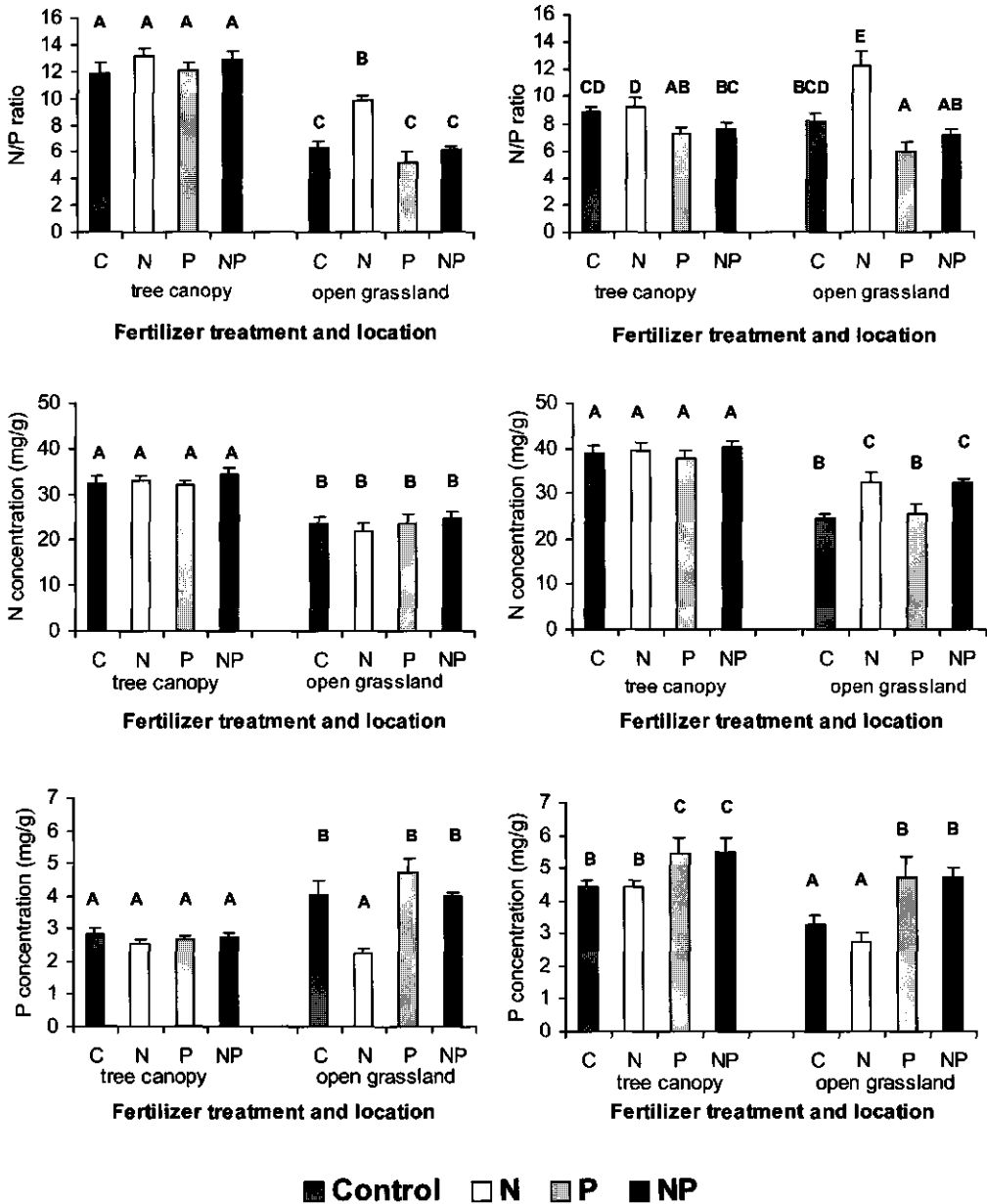
Control ☐ **N** ▦ **P** ■ **NP**

Figure 3.3. The effect of fertilisation on N and P concentration and N:P ratios (+SE) in grass leaves. Grass leaves of several species were collected in plots fertilised with N, P and NP and compared with a control treatment both under tree canopies and in open grassland. Grasses were collected at the end of the first wet season in June 1998 and in the middle of the second wet season in April 1999. Bars with the same letter are not significantly different (Tukey-HSD, P>0.05). Abbreviations as for figure 3.2.

The effect of nutrients

It is well known that savanna trees have a major positive effect on soil nutrient concentration but very little is known about how this translates into nutrient limitation of the understorey vegetation (Belsky et al. 1989, Frost and Edina 1991, Campbell et al. 1994). Our experiments show that trees can change the nutrient that limits the production of the grass layer. In open grassland, productivity increased only when nitrogen was added while it increased only in response to phosphorus addition under tree canopies. This change from nitrogen to phosphorus limitation is not surprising under a nitrogen-fixing species as *Acacia tortilis*. However, the described nutrient limitation was significant only at the end of the second wet season of the experiment in 1999. It has been shown before that fertilisation experiments do not always show an effect during the first growing season (Berendse et al. 1988). During the second season we only found an effect at the end of the wet season because this was the only period when enough soil moisture was available for nutrients to become limiting. Three months into the dry season in August 1999 the effects of nutrients had disappeared, probably because a larger part of the vegetation had senesced in the fertilised plots. In a similar savanna in southern Kenya, Belsky (1994) reported strong nutrient limitation in open grassland but not under the tree canopy. Outside *Acacia tortilis* trees, grass production was strongly affected by NPK addition. The different nutrients were not added separately in this field study but a pot experiment showed that N was limiting production in open grassland (Belsky et al. 1993). The latter results are consistent with our study.

Although total plant production was not affected by the presence of trees in our study, grass N and P concentration were higher under the tree canopy than in open grassland, in the middle of the second wet season. These increased grass nutrient concentrations indicate that more nutrients are available in the below-canopy environment. These higher concentrations are not accompanied by a higher production under the tree and suggest that factors other than nutrients limit the production of grasses under canopies.

N:P ratios

Koerselman and Meuleman (1996) recently proposed to use the N:P ratio in plant tissues as an indicator of the type of nutrient limitation, based on data from European wetland ecosystems. We tested whether N:P ratios in grasses of tropical savannas may also indicate the nutrient limitation of the herbaceous vegetation. At the end of the first growing season, mean N:P ratios in open grassland control plots were 6, clearly indicating N limitation, while below crown grasses had an average ratio of about 12. This indicates relatively low supply of phosphorus although using values from European wetlands this still indicates N limitation (Wassen et al. 1995, Koerselman and Meuleman 1996, Aerts and Chapin 2000). The results from the fertilising experiment showing that the grass under the canopy are limited by P suggesting that a N:P ratio of 12 indicates P limitation in this ecosystem. This implies that savanna grasses have a relatively lower N requirement than wetland plants. This could be caused by a higher nitrogen use efficiency of C_4- compared to C_3-plants (Long 1999).

While the different N:P ratios under and outside the tree at the end of the first growing season match the results of the two-year fertiliser experiment, the N:P ratios in the second growing season did not. In the middle of the second growing season,

N:P ratios in the control plots were almost equal under and outside the tree canopy. This difference between the years is striking and may be explained by the different time of collection within the season. In the second year, plant leaves were collected in early April, in the middle of the growing season while in the first year we collected the leaves in June at the end of the growing season. We conclude that N:P ratios are a promising tool to determine quickly the nutrient that limits plant growth in tropical dry savannas. However before it can be widely used, both the N:P ratios indicating nutrient limitation and the most favourable time of collection should be determined more precisely.

The effect of shade

In temperate areas shade is usually seen as a factor reducing plant production. In dry areas shade may also have a positive effect due to reduction in temperature and evapotranspiration (Eriksen and Whitney 1981, Wilson 1989). Our experimental results however clearly show that 55% light reduction decreases the plant production during the wet season. This indicates that in the wet season production under the tree canopy may be light limited. As suggested above, factors other than nutrients limited grass production under tree canopies and during the wet season this is most likely to be light as plenty of water is available. During the dry season, from May until August 1999, the biomass in the control plots remained the same but the grasses in the shaded plots continued to grow. This resulted in almost equal biomass both in shaded and full sun conditions in August, three months into the dry season. This increased production is probably caused by a higher water availability as a result of decreased evaporation and increased water use efficiency due to lower plant transpiration. Although during the dry season, artificial shade had a positive effect on grass production, under the trees grasses did not increase their biomass during the same period. In other experiments (chapter 2 & 4) we found less water available in the below-crown soil compared to grassland outside the tree, especially during the first two months of the dry season. Apparently, the positive effect of shade (more water availability) was overshadowed by tree water uptake.

Conclusions

Contrary to our expectations, *Acacia* trees did not affect grass production compared to open grassland plots but trees did change the understorey vegetation from an N limited to a P limited system. The grass nutrient concentrations were also higher under the tree and this indicates a better food quality for herbivores. Thus, although the grass production was not increased by the trees, herbivores may thus still benefit from the presence of A.*tortilis* trees through increased food quality (see chapter 6). During the wet season, grass growth under tree canopies is limited by light and phosphorus and in open grassland plant production is limited by nitrogen. During the dry season the effect of shade on plant biomass seems to be beneficial. Nevertheless, the understorey vegetation probably did not benefit from tree shade in the dry season due to water competition between trees and grasses. Whether savanna trees increase or decrease the production of the understorey vegetation depends on how positive effects of increased soil fertility and reduced temperature and negative effects of shade and reduced soil water availability interact.

Acknowledgements

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Chapter 4

Hydraulic Lift in *Acacia tortilis* trees on an East African savanna

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Abstract

Recent studies suggest that savanna trees in semi-arid areas can increase understorey plant production. We hypothesized that one of the mechanisms of facilitation between trees and grasses in East African savannas is through hydraulic lift. Hydraulic lift (HL) in large *Acacia tortilis* trees was studied during the first three months of the dry season during a relatively wet year (1998) and a very dry year (2000). In 1998, we found distinct diel fluctuation in soil water potential (ψ_s), with increasing values during the night and decreasing again the following day. These fluctuations in ψ_s indicating HL were found up to 10 m from the tree. This indicated that mature *Acacia* trees can lift water over an area of more than 300 m^2 and it was estimated that each tree can lift between 70 and 235 liters of water each night. In 2000, during a drought when ψ_s declined to well below –4.5 MPa, we found little evidence of HL. We believe that these observations indicate that there may be a lower limit to when HL can occur that could be caused by root death, the lack of new root growth, or poor root-soil contact.

The contrasting findings we observed where HL occurred in wetter years and did not in drier years, was consistent with $\delta^{18}O$ values in soil, rain and groundwater. Because the isotopic values of winter rainfall was similar to groundwater, the isotope data by itself could not provide conclusive evidence for HL. However, during 1998 the $\delta^{18}O$ values of water in the upper soil layer resembled ground- and root-water throughout the dry season, while in 2000 $\delta^{18}O$ of upper soil water was highly enriched and very distinct from groundwater (caused by evaporation from the upper soils). The $\delta^{18}O$ of water extracted from the xylem of the grasses showed that when they were growing near trees they had values similar to the groundwater. This could be because they either use water from deeper soil layers or use hydraulically lifted water provided by the tree; this was not seen in the grasses growing outside of the tree canopies.

Although HL occurred under *Acacia* trees, ψ_s was still lower under trees when compared to outside tree canopies. This is probably because trees (and grasses) take up more water from the upper soil layers than is exuded by the tree itself. This limits the beneficial effect of HL for the understorey grasses. Based on our data in two very different years, it appears that competition between grasses and trees for water in this East African savanna may be more important than facilitation through HYDRAULIC LIFT, although both processes take place at the same time.

Introduction

The Earth's savanna ecosystems are associated with seasonally-dry or semi-arid climatic zones and are characterized by broadly spaced trees and shrubs within a continuous grass layer. Savanna trees may facilitate and/or interfere with the growth of understorey grasses (Callaway et al. 1991, Belsky 1994, Scholes and Archer 1997) and therefore influence savanna structure and function. Because water is seasonally limiting, competition for water has long been considered to be especially important in shaping the interactions between trees and grasses in savannas. In fact, Walter's (1971) two-layer hypothesis explains the co-occurrence between savanna trees and grasses through the spatial separation of rooting niches and the differential utilization of below ground resources like water. Here, large trees have sole access to water in deeper soil horizons while grasses use water primarily in the top soil, therefore making them competitively superior when the upper soil layers are moist. Although some evidence supports Walter's two-layer hypothesis (Hesla et al. 1985, Knoop and Walker 1985, Sala et al. 1989), several recent studies reject this theory (Seghieri 1995, Le Roux et al. 1995, Mordelet et al. 1997, Higgins et al. 2000).

To date, a process that has not been considered when explaining the co-occurrence of trees and grasses in savannas is hydraulic lift. Hydraulic lift is the process of water movement from relatively wet to dry soil layers through plant roots (Richards and Caldwell 1987, Caldwell et al. 1998). This transport takes place most commonly during the night when the leaf stomata are closed and the major water potential gradient is between the deep (wet) roots and the drier surface roots in the top soil. Presently, the data suggest that this process is passively driven by differences in water potential (Caldwell et al. 1998). However, there is growing evidence that water transport might also be actively regulated by aquaporins within the root membrane; this opens up the possibility that active processes may also play a role in hydraulic lift (Agre 1998, Jackson et al. 2000, Kaldenhoff et al. 1998)

Trees can benefit from hydraulic lift in several ways. First of all, water lost to soils through hydraulic lift during the night can be taken up by the tree the next day. In this way trees can increase their daily water uptake and more efficiently use deep soil water (Dawson 1993, Emerman and Dawson 1996). Deeper soil layers contain few if any nutrients and by exuding water into the topsoil and then taking it up again, trees increase their potential nutrient uptake as well (see Dawson 1998 for some evidence of this). Hydraulic lift may also have important effects on plant communities and ecosystems in that hydraulically lifted water (HLW) that moves into the soil from deeply rooted trees can also be taken by up by the understorey vegetation (Dawson 1993, Caldwell and Richards 1989). Moreover, higher soil moisture contents can increase mineralization rates and may even help to maintain mycorrhizae which both have positive effects on soil nutrient availability (Richards and Caldwell 1987, Horton and Hart 1998) and plant resource status (Dawson 1998).

Hydraulic lift (HL) has been demonstrated in over 30 species with most of the reports from plants native to North America (Caldwell et al. 1998, Yoder and Nowak 1999, Millikin and Bledsoe 2001) and Australia (Burgess et al. 1998). We conjectured, that in African savannas with large, deep rooted trees and a well developed understorey vegetation that hydraulic lift could be present and if present a potentially important process in influencing grass-tree interactions as well as community and ecosystem functioning. *Acacia tortilis*, a dominant savannas tree, is known to have both very deep tap roots and far reaching lateral roots (Belsky et al.

1989, Belsky 1994). These trees could potentially re-distribute ground water over a large area in the top soil. Several studies report higher grass production under *Acacia* trees compared to open sites (Belsky et al. 1989, Belsky et al. 1993, Weltzin and Coughenour 1990, Georgiadis 1989). These positive effects of the tree on the understorey grasses were mainly attributed to higher soil nutrient availability and shade found under these trees (Belsky 1994, Scholes and Archer 1997). However, HL could also increase grass productivity under *Acacia* due to higher soil moisture and its effects on soil and plant nutrient availability.

We investigated if hydraulic lift occurred in large *Acacia tortilis* trees inhabiting a semi-arid savanna in East Africa, and if so, the extent to which it influenced seasonal patterns of soil moisture within the rhizosphere in a relatively wet and a very dry year. If HL is present, we also wanted to know whether the subsidized soil water provided by trees via HL was taken up by understorey grasses. We investigated the role of HL in the tree-grass interactions, by measuring soil water potential continuously at several distances from *Acacia* trees during the first three months of the dry season in two contrasting rainfall years. It is during the dry season that we expected the beneficial effects from hydraulic lift, if present, to be most important because (a) there are differences in water potential between different soil layers, and (b) the understorey vegetation is still alive and thus potentially able to take up HLW. Hydraulic lift and the use of HLW by plants was also determined by measuring stable oxygen (δ^{18}O) and hydrogen (δ^2H) isotope ratios of different water sources and of the plants on our sites as used previously by Dawson (1993).

Materials and Methods

Site Description

The experimental trees were located in the northern part of Tarangire National Park (4° S, 37° E, 1200m above sea level) on the eastern side of the Great Rift Valley in northern Tanzania. The soil at the site consisted of coarse sandy loams of lacustrine origin. The vegetation was wooded savanna with a tree cover of 10-20%. The dominant tree species, *Acacia tortilis,* was used for our measurements. The herbaceous layer is dominated by C_4-grasses with different species growing under and outside tree canopies (table 4.1) and the plant cover during the wet season is almost 100% (Ludwig et al. *in review a*). Concentrations of all major nutrients were higher in the belowcrown soil than in open grassland. However, aboveground biomass of the herbaceous layer was not different under and outside tree canopies (Table 1).

For the measurements we selected three large *Acacia tortilis* trees which are all approximately 100 years old (Prins and Van der Jeugd 1993). Trees with termite hills or large shrubs in their understorey were avoided. Each tree was isolated, with a distance from other trees of at least 100 m and a minimum of 50 m from small shrubs. The trees had an average diameter at breast height of 59 cm (± 11) and a canopy diameter of 15 to 20 m. Mean rainfall over the last 20 years is 650 mm/year (± 272 mm) (Van de Vijver 1999). The wet season occurs from November until May with most of the rain typically falling during March and April. The first year of our study, 1998, our measurements were made after the wettest season in 20 years with 1368 mm of rain. During this year the rain continued until mid-June. The year 2000 was very dry with only 350 mm of rain, and during this year the rain stopped in late April.

Psychrometer installation and measurement

In 1998, soil thermocouple psychrometers (TP; Wescor, Inc., model PST 55, Logan, UT, USA) were installed at four different distances from each tree (1.25, 2.5, 5 and 10m) and the four cardinal compass directions. Prior to installation each TP was individually calibrated. TP's were installed at a depth of 40 cm because at this depth diel temperature fluctuations are small enough to be corrected for by a calibration model (Brown and Bartos 1982). All 16 TP's around an individual tree were linked to one data logger (Model CR 7, Campbell Scientific Inc., Logan, Utah; after Dawson 1993) and soil water potential was measured every 30 or 60 minutes for at least a 4 day period. Around each tree we collected three series (nine series in total) of data over a 3 month period. In both years, measurements began two weeks after the last significant rainfall event (> 1 mm) and continued up to almost 3 months into the dry season.

Table 4.1 Differences in abiotic and biotic environment under and outside canopies of large *Acacia tortilis* trees. Soil total N and P and available N (NO_3^-+ NH_4^{3+}) concentration, maximum yearly biomass of the herbaceous layer and light availability were determined under canopies at 3 m from the stem and outside tree canopies at 15 m from the stem (data from chapter 2 & 3).

| | Soil properties | | | | Understorey Vegetation | | | Light |
	total N (mg/g)	total P (mg/g)	available (mg/kg)	biomass 1998 (g/m^2)	biomass 1999 (g/m^2)	Dominant grass species	Relative light availability
Under tree canopy	1.64	0.27	12.36	674	552	*Panicum maximum, Cynodon dactylon*	50%
Outside tree canopy	1.16	0.22	6.39	680	508	*Urochloa mosambicencis, Heteropogon contortis*	92%

In 2000, we again installed TP's at the same four distances from the same trees but this time only in two (N and S) instead of 4 directions because we had fewer psychrometers available. We started measuring soil water potential 2 weeks after the last rain and continued up to 2 months later. In total we collected 6 series of data.

The average daily variation in soil water potential was calculated as maximum ($\psi_{s,max}$) minus minimum soil water potential ($\psi_{s,min}$) during a 24 hour period corrected for the overall trend by subtracting the absolute value of the measurements at 12.00 am at the beginning ($\psi_{s,0.00}$) and the end of the day ($\psi_{s,24.00}$). Thus, daily fluctuation = $(\psi_{s,max} - \psi_{s,min}) - |(\psi_{s,0.00} - \psi_{s,24.00})|$.

Isotope sampling

Variation in the oxygen and hydrogen stable isotope composition of source waters can be used to determine the zone of active water uptake by plant roots (Ehleringer and Dawson 1992) and has been used to look at water uptake by understorey plants growing near trees that conduct HL (Dawson 1993). In order to document these same sorts of phenomena in this savanna system, we collected soil, rain and ground water samples and determined their O and H stable isotope composition. Groundwater was obtained from bore (well) holes at the Tarangire park head quarters about 500m from the experimental trees and at Tarangire Safari Lodge, 5 km from the site. Water collected from both bore holes came from a depth of about 20 m. Soil samples were

collected at a depth of 35 – 45 cm near each psychrometer after a series of soil water potential measurements had been made. Samples were collected between 7 and 9 am in the morning.

In 2000, in addition to soil samples we also collected tree root and stem samples for the determination of plant water sources following the methods outlined by Dawson and Ehleringer (1993). All samples were collected within a three-day period of each other (7–9 June 2000) approximately 30 days into the dry season. Soil samples were collected at four distances (1.25, 2.5, 5, and 10 m) from the tree in two different compass directions. At the same distances we also collected the basal, non-green culms of the grasses, *Cynodon dactylon* and *Cenchrus ciliaris* (expect at the 1.25 m location because at this location there was not enough grass to sample for water source determination). From each *Acacia* tree we also collected samples of woody stems and roots at the same locations on each plant.

Water was extracted from soil and plant tissue using a cryogenic vacuum distillation apparatus (Ehleringer et al. 2000). For the oxygen stable isotope analyses, 500 µl of the extracted water was injected into airtight 10 ml Na-glass vials, fitted with butyl rubber septa and then flushed with 2000 or 3000 ppm CO_2 in He. The vials were left at room temperature (~23°C) for 48 hours; during this period the $\delta^{18}O$ in the CO_2 within the head space of the vial equilibrates with the $\delta^{18}O$ in the H_2O sample (see Dugan et al.1985). After 48 hours CO_2 in the head space was analyzed for its oxygen isotope ratio with a Finnigan MAT Delta^{plus} XL isotope mass spectrometer (IRMS) interfaced with a GasBench II and PAL-80 autosampler. Details of this method can be found in Tu et al. (2001). For hydrogen stable isotope analyses, the same water samples were placed within airtight 1 ml vials and using the same autosampler a 0.7 µl sub-sample was injected onto hot (900°C) Cr within a sealed furnace (the Finnagan MAT H/Device) inline with the sample inlet and bellows on the IRMS and a dual-inlet analysis for the stable hydrogen isotope ratio ($\delta^{2}H$) performed.

All $\delta^{18}O$ and $\delta^{2}H$ values are expressed in delta notation (‰) relative to the international standard, V-SMOW, as:

$\delta = (R_{sample} - R_{standard})/R_{standard} \times 1000$

where R = the $^{18}O/^{16}O$ or $^{2}H/H$, and the unit 'δ' is expressed in part per thousand (‰) notation (Ehleringer and Dawson 1992).

Results

Soil water potentials

In 1998, under each of the three trees, we found distinct diel fluctuations in soil water potential (ψ_s) indicating hydraulic lift. An example of the data from one of three trees is presented in Figure 4.1 & 4.2; the soil water potential around the other two trees showed similar patterns. Around two of the trees daily fluctuations in ψ_s were measured up to 10 m from the tree (Figure 4.3). Fluctuation varied from less than 0.05 MPa up to 0.5 MPa on several occasions and were on average between 0.05 and 0.2 MPa (Figure 4.3). These daily fluctuation in ψ_s are indicative of the cycles of water exudation and uptake by plants with roots undergoing HL (Caldwell et al. 1998). We also observed a great deal of variation in the magnitude of the fluctuations observed at

the same distance from the tree during the same period. For example, at 1.25 m around one of the trees (see July 28- August 3, 1998 period, tree 3, Figure 4.1A) the southern exposure showed no diel fluctuations in ψ_s and maintained a relatively high ψ_s (-1.0 to –1.3 MPa) while the drier northern exposure showed much lower overall ψ_s (-4.1 to – 4.5 MPa) and also daily variation of $\pm$ 0.5 MPa indicative of HL. Eastern and western exposures also showed signs of HL, but with smaller magnitude than the northern exposure and at higher average water potentials (between –2.3 and –3.5 MPa).

Hydraulic lift in *A. tortilis* was observed to occur over a wide range of ψ_s from –0.2 MPa, down to –4.5 MPa and in 1998 almost all of our sensors showed a clear and consistent hydraulic lift signal below –3.0 MPa. The dryer the soil was the larger the day/night differences were and therefore the more hydraulic lifted water there was in the soil profile (see Williams *et el.* 1993 and Emerman and Dawson 1996). This is shown in our statistical analysis as a weak, but significant, correlation between average ψ_s and the day/night In the drought year, 2000, we found little or no evidence of HL, but average ψ_s was much lower than in 1998 (Figure 4.5). In this very dry year, some of our psychrometers continued to measure ψ_s down to –7.0+ MPa, few, showed day/night differences in ψ_s typically found where trees were displaying HL. Most of the fluctuations in ψ_s were random and showed no increase during the night and reducing again during the following day as would be expected during HL. Even at the relatively higher ψ_s that we measured (between –1.0 and –2.0 MPa), there was no evidence of HL, when in 1998 we had almost always observed HL at these same soil water potentials.

Stable Isotopes

$\delta^{18}O$ and δ^2H values of precipitation were highly variable (e.g., +1.5 to –3.9 ‰ for $\delta^{18}O$ and +22‰ to –21‰ for δ^2H respectively; Figures 4.6 & 4.7). As expected from most meteoric waters, $\delta^{18}O$ and δ^2H were also strongly correlated (Ehleringer and Dawson 1992). For this reason we only discuss the $\delta^{18}O$ form here on in this paper. Most of the isotopic variation we observed is explained by the type of rainfall event; for example, water collected during a heavy rainfall event had more depleted $\delta^{18}O$ with values around –3.7‰ while all other, lighter, rainfall events showed more enriched (higher) values (Figures 4.6 & 4.7). The $\delta^{18}O$ of water collected from both bore holes (e.g., ground water) showed nearly identical isotopic values (-3.8‰) to heavy rainfall and these values did not change between 1998 and 2000. In 1998 soil water $\delta^{18}O$ under all trees was between –3.2‰ and –4.0‰. There was no significant effect of distance from the tree on the isotope values of soil water (P>0.1) and these values are undistinguishable from ground water and also the same as heavy rainfall.

In hot, dry environments, it is common that soil water becomes more enriched (higher $\delta^{18}O$) when exposed to surface evaporation (see Dawson and Ehleringer 1998). However, at our sites, the $\delta^{18}O$ of the soil water remained constant from 2 weeks after the last rainfall event until three months into the dry season. Soil water potential during this period declined, however, from –0.3 to –4.0 MPa. Taken together these data suggest that *both* HL and soil water depletion by the plants growing at these sites was occurring (table 4.2).
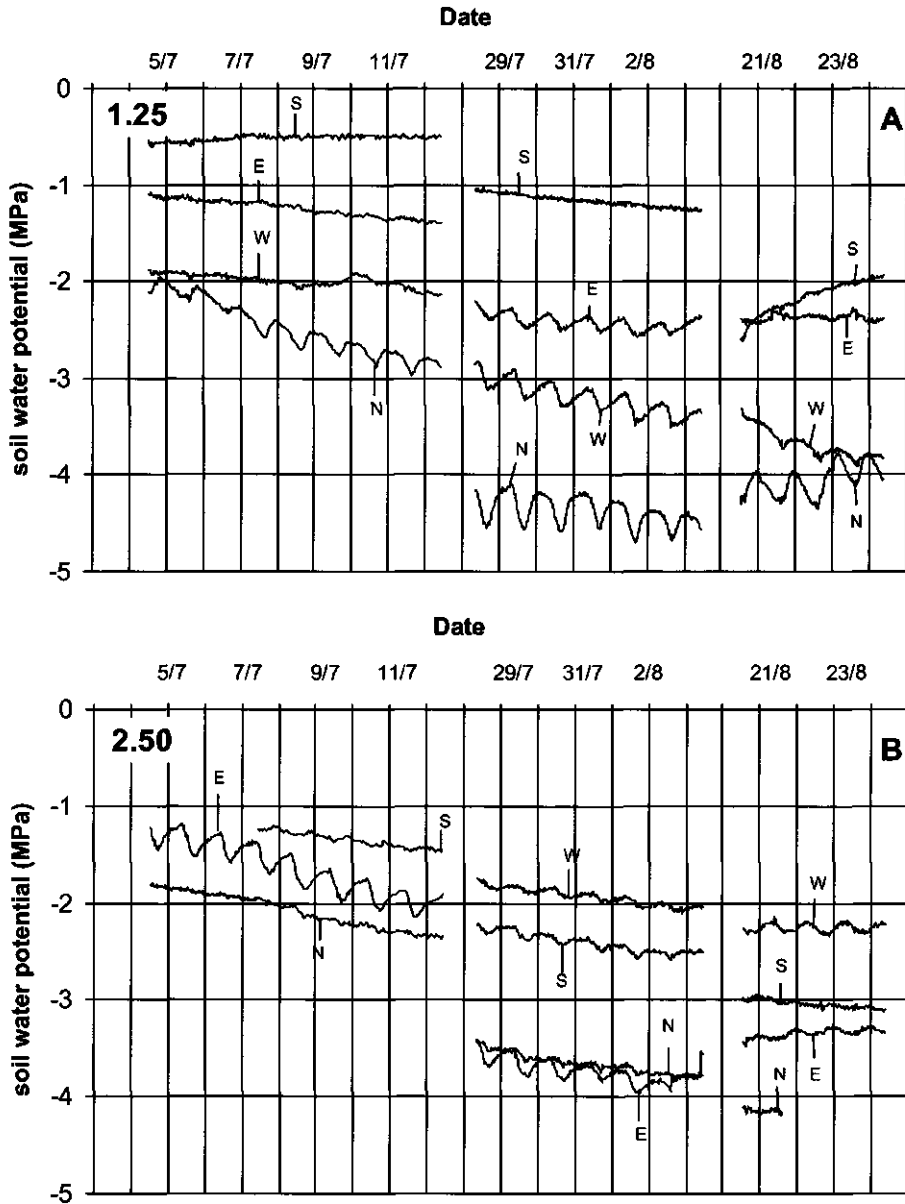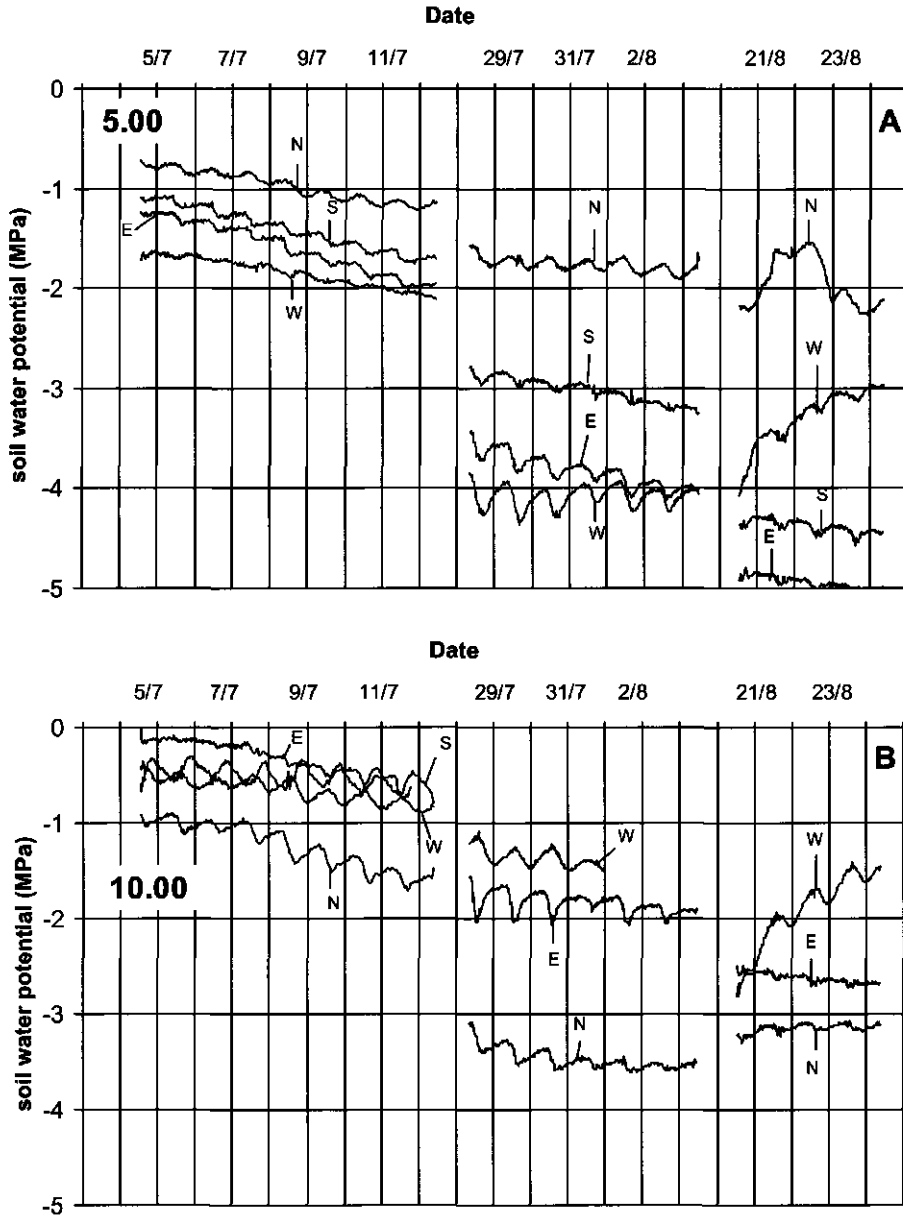
Figure 4.1 Time course of soil water potential (ψ_s) measured under a large *Acacia tortilis* tree (Tree 3) during the dry season of 1998. ψ_s was measured at **(A)** 1.25m. **(B)** 2.50 m. from the tree stem. Each figure represents the temperature corrected data of four individual soil psychrometers installed at a 40 cm depth in the four cardinal compass directions indicated by the letter next to each line. Under each tree, three sets of data were collected starting two weeks after the last rainfall event until three months into the dry season. Vertical lines indicate midnight (12.00 am).

Figure 4.2 Time course of soil water potential (ψ_s) measured under a large *Acacia tortilis* tree (Tree 3) during the dry season of 1998. ψ_s was measured at **(A)** 5.00 m and **(B)** 10.00 m from the tree stem. Each figure represents the temperature corrected data of four individual soil psychrometers installed at a 40 cm depth in the four cardinal compass directions indicated by the letter next to each line. Under each tree, three sets of data were collected starting two weeks after the last rainfall event until three months into the dry season. Vertical lines indicate midnight (12.00 am).
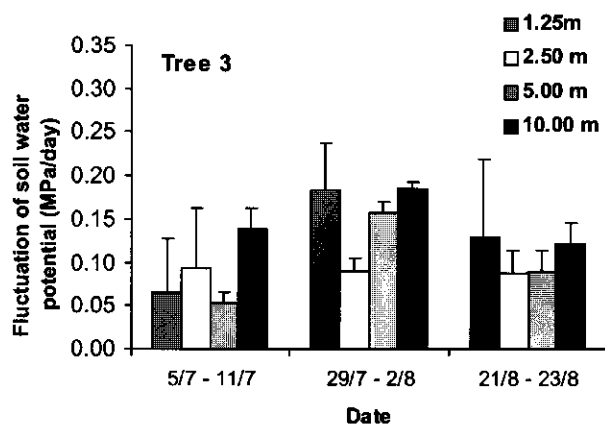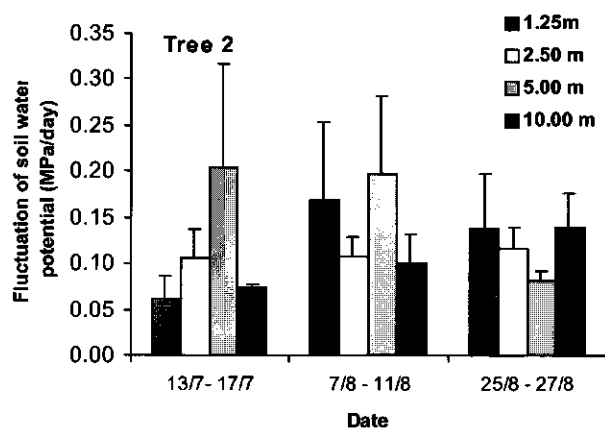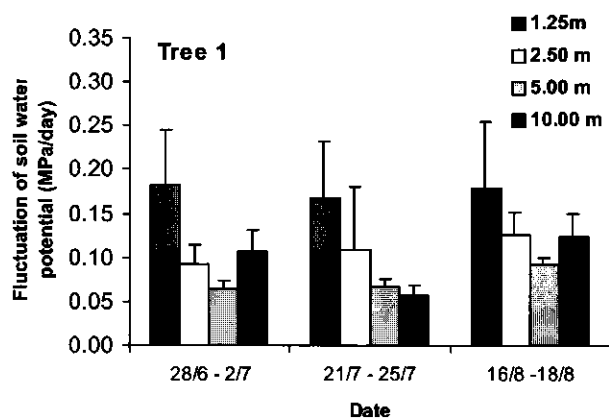
Figure 4.3 Average daily fluctuation in soil water potential (ψ_s) measured at four different distances from three large *Acacia tortilis* trees. ψ_s was measured during three different periods within the first three months of the dry season of 1998. Each bar represents the average (+ s.e.) of four psychrometers.
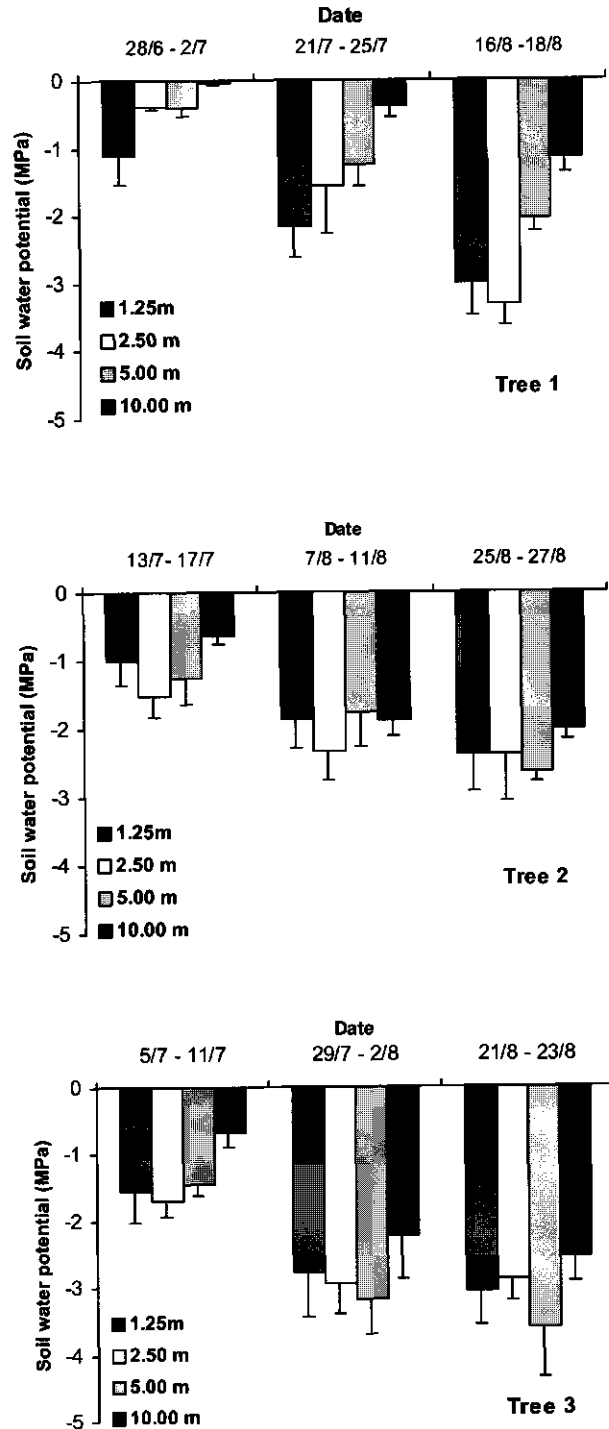
Figure 4.4 Average daily soil water potential (ψ_s) measured at four different distances from three large *Acacia tortilis* trees. ψ_s was measured during three different periods within the first three months of the dry season of 1998. Each bar represents the average (+ s.e.) of four psychrometers.
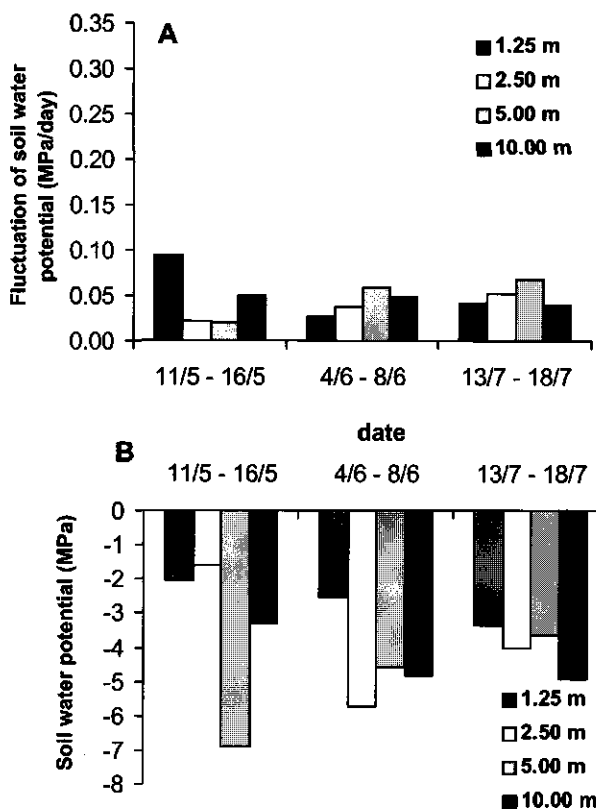
Figure 4.5 Average daily fluctuation in soil water potential (ψ_s) (A) and average soil water potential (B) measured at four different distances from a large *Acacia tortilis* trees. ψ_s was measured during three different periods within the first three months of the dry season of 2000. Each bar represents the average of two psychrometers.

In 2000, the $\delta^{18}O$ of soil water under *Acacia* trees was clearly different from the ground water; these soil water values suggested that evaporation from the upper soil layer was occurring and that HL was not. All soil water $\delta^{18}O$ values were between +1.0‰ and −1.0‰ while groundwater remained at -4‰, as in 1998. The isotopic signature from tree roots was similar to that of the groundwater suggesting that trees used this water source exclusively in 2000 (Figure 4.7). Tree stems showed slightly enriched $\delta^{18}O$ values which could reflect either an evaporative enrichment within the stems (see Dawson and Ehleringer 1993, 1998) or uptake from both the groundwater and some other (shallow) water source. Grasses growing near the tree (at 2.50 m) showed similar isotopic values as tree roots and groundwater. The $\delta^{18}O$ values of xylem water from the grasses sampled at 5 and 10 m distances away from the tree all increased. In all cases the $\delta^{18}O$ values of grasses were lower, however, when compared with the values of all other rainfall (Figure 4.7). This suggests, as with the tree stems, that tissue water was either enriched or there was uptake of a second water source that we did not measure.
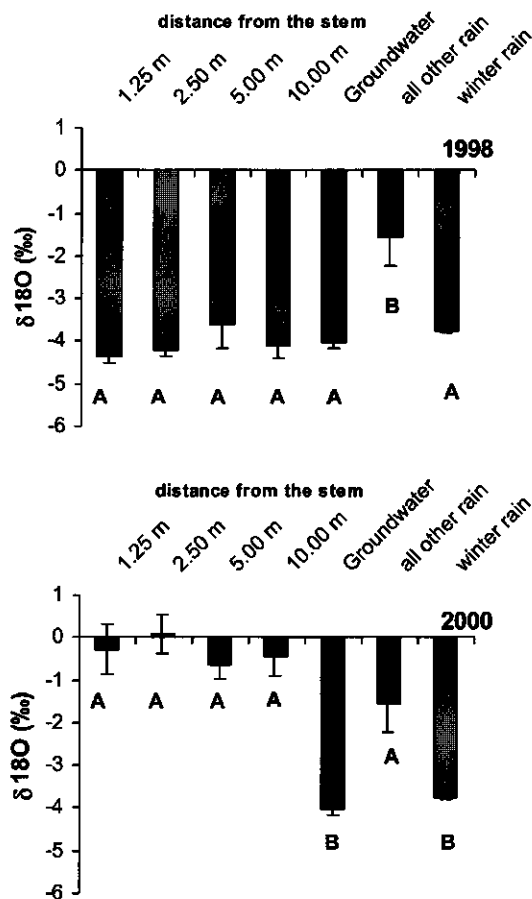
Figure 4.6 Average (± s.e.) stable oxygen isotopic composition of water sources (rain and ground water) and soils collected at 40 cm (± 5 cm) depth at different distances from large *Acacia tortilis* trees in 1998 and 2000. In 1998 soil samples were collected at different times during the first three months of the dry season. In 2000, soil samples were collected from 7 until 9 June, one month into the dry season. Bars with the same letter are not significantly different (LSD-test, P>0.05).

Discussion

Hydraulic lift has not been reported before in *Acacia* spp. or for an African plant. Our results indicate, however, that hydraulic lift does occur in *Acacia tortilis* trees in Tanzania, a country with vast areas of arid and semi-arid savanna ecosystems in which HL might be an important process. Under all of the trees we studied we found distinct diel fluctuations in soil water potentials in 1998. During the night ψ_s increased and decreased again the following day. These fluctuations are similar to those first reported by Richards and Caldwell (1987) for the shrub *Artemisia tridentata* and then in several other studies on a diversity of temperate and arid zone woody plants (Dawson 1993, 1996, Yoder and Nowak 1999, Burgess et al. 2000, Millikin and Bledsoe 2001). All of these studies, and the study presented here concluded that day/night fluctuations in ψ_s probably result from hydraulic lift. These conclusions were further supported by other data derived from stable isotope analysis (Dawson 1993), experimental manipulations (Caldwell and Richards 1989, Williams et al. 1993) and sapflow (Burgess et al. 2000) .

Acacia tortilis trees are known to have a very wide spread root system (Belsky 1994) and here we showed that these roots can redistribute water within the soil
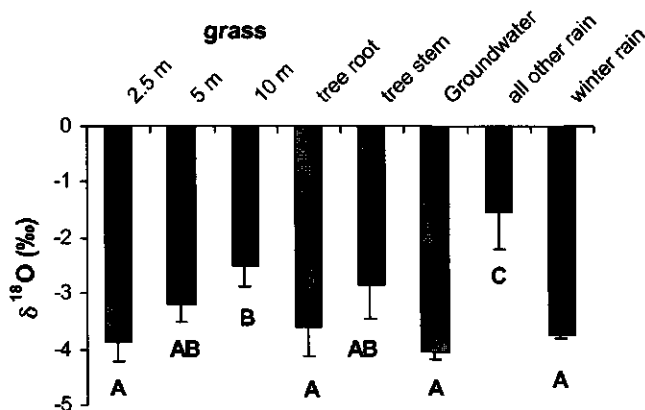
Figure 4.7 Average (± s.e.) stable oxygen isotopic composition (‰) of water sources (rain and ground water) and tree and grass samples. Grass samples were collected at different distances from large *Acacia tortilis* trees. Samples were collected from 7 until 9 June 2000, 1 month into the dry season. Bars with the same letter are not significantly different (LSD-test, P>0.05).

profile. Our data indicate that *Acacia* trees can lift a significant amount of water into the rhizosphere and up to at least 10 m from the base of the tree. These findings suggest that a single individual might influence an area around itself of at least 314 m^2. Emerman and Dawson (1996) calculated that a sugar maple tree can lift between 50 and 150 l of water per night and these trees seemed to only lift this water into the rhizosphere a short distance (up to 2.5 m) from the base of the tree. While the magnitude of day-night differences in ψ_s were lower under *Acacia* compared with sugar maple trees, HL occurred within an area 16-times larger. Using an average diel change in ψ_s of 0.15 MPa (from data in Figure 4.3) and the model developed by Emerman and Dawson (1996), we estimate that the volume of water lifted into the rhizosphere around an individual *Acacia* tree would have been between 70 and 235 l each night. These estimates are highly variable and this is very likely due to the patchy nature of HL around *Acacia*. Despite this, the data suggest that a considerable amount of water can be redistributed into the large rhizosphere volume under *A tortilis* where the trees themselves and other shrubs and grasses would have access to it.

Table 4.2. Average $\delta^{18}O$ in soil water and average soil water potential at four different distances from tree 3. Data are from three different periods within the dry season from 4 weeks after the last rainfall event until 2½ months into the dry season. The data shows that soil water $\delta^{18}O$ values stay stable while soil water potential drops from –1 to –3.5 MPa

period	$\delta^{18}O$ of soil water (‰)				soil water potential (Ψ_s) (MPa)			
	1.25m	2.50 m	5.00 m	10.00 m	1.25m	2.50 m	5.00 m	10.00 m
5/7 - 11/7	-4.2	-3.2	-4.3	-4.1	-1.56	-1.69	-1.45	-0.69
29/7 - 2/8	-4.1	-3.7	-1.2	-3.9	-2.79	-2.94	-3.18	-2.25
21/8 - 23/8	-4.9	-4.2	-3.9	-4.6	-3.07	-2.88	-3.61	-2.54

Soil water potential data: limits to hydraulic lift

We observed day-night difference in ψ_s indicating HL over a very broad range of ψ_s from -0.20 down to –4.6 MPa. There are three other studies that report HL starting at ψ_s around –0.20 (see Millikin and Bledsoe 2001) and stopping ψ_s between –4.0 and –

4.5 MPa. (Williams et al. 1993, Yoder and Nowak 1999, Millikin and Bledsoe 2001). We also found evidence of large differences in the magnitude of HL under the same tree at identical distances from the stem. In several cases the areas of the rhizosphere where measurements indicated no HL showed higher ψ_s compared with areas demonstrating strong diel differences. In addition, zones of the rhizosphere showing HL also showed a greater drop in ψ_s over time. We take all of these patterns as indicating that the roots that showed HL were also the roots which were actively extracting the bulk of the soil water used in transpiration and that ultimately these zones within the rhizosphere became areas where the greatest soil water depletion occurred. We believe that some of the variation we observed in the magnitude of HL is explained by how we placed our sensors in the soil. The sensors placed close to active roots not only indicated that HL occurred, but it was around these same sensors that the soil was dried-down to lower moisture contents due to root water uptake (see Figure 4.1 & 4.2). In contrast, the sensors that were installed away from active roots, show no HL and the soil only dries out due to evaporation. Our data also indicate that roots take up more water during the day than they exudate at night, a phenomenon observed in other HL studies (Williams et al. 1993, Caldwell et al. 1998). This also indicates that HL does not necessarily always lead to a higher ψ_s in a plant rhizosphere. That is, HL and water uptake together lead to more dynamic changes in the rhizosphere, but also greater potential resource depletion in the same area of the soil. This might limit the extent to which the understorey vegetation can benefit from hydraulic lift.

In 2000, a year with very little rainfall, we saw very little evidence of HL under *Acacia* (Figure 4.5). Between May and July the ψ_s was extremely low (down to −8.7 MPa) with very few diel fluctuations observed. We believe that this could indicate that there indeed may be real limits to when (under what conditions) HL can occur. Our data indicate that when ψ_s drops to between −5.0 and −7.0 MPa HL does not operate. In part this may be due to the fact that plants may never have produced new roots during the rainy season because soils were too dry; in some species new roots are known to show the greatest HL (Dawson 1998, Midwood et al. 1998). This is supported by our data that indicate that even when ψ_s was relatively high in 2000 (−1.0 to −3.0 MPa), there was little indication that HL occurred.

Alternatively, it is equally plausible that roots in the very dry topsoil (a) might have had very poor contact with the soil which would significantly reduce the efficacy of root water exudation, (b) may have simply died, or (c) fine roots may have cavitated (see Jackson et al. 2000). Any or all of these would lead to little or no HL.

Ecologically, if HL confers a benefit to the plant, we might expect HL to occur under a diversity of conditions, not only during a relatively wet year. During wet years it appears that water availability does not limit tree growth but perhaps in savanna ecosystem nutrients might (see Belsky 1994). Through HL the tree can obtain water present in deeper soil layers to facilitate uptake of nutrients from the topsoil (Dawson 1993, 1998, Caldwell et al. 1998, Horton and Hart 1998). This would lead to an increased growth rate during wet years. In contrast, in dry years, it is more likely that survival and not growth is selectively favored in long-lived species like *Acacia*. If so, during a drought trees may sequester what water they do obtain for survival and thereby as a consequence HL is "shut down" or "regulated" by the turnover and formation of young roots (see above and in Caldwell et al. 1998). Whether membrane proteins also play a role in the regulation of HL is still unknown (Jackson et al. 2000).

However, a study with transgenetic plants with reduced activity of aquaporins showed that these membrane proteins play in role in root water uptake (Kaldenhoff et al. 1998). This opens up the possibility that aquaporins may also play a role in regulating HL.

Stable isotope data

Our stable isotope data are consistent with the conclusions drawn from our 1998 soil water potential data that HL did occur in this wetter year but did not occur in the drier year (2000; Figures. 4.5 & 4.6). However, because the isotopic values of ground- and rain-water were so similar, the stable isotope data by itself could not provide conclusive evidence for the absence or presence of HL. Isotopically uniform soil profiles as we observed in 1998 are not uncommon and have been observed in several studies in Australia (Turner et al. 1987, Farrington et al. 1996, Burgess et al. 2000, S. Zencich, pers. comm.) where true soil development is poor and profiles are largely sand. Under these conditions, Burgess et al. (2000) suggested that a uniform soil water isotope profile might be, at least in part, caused by the redistribution of soil water by tree roots through hydraulic redistribution. Our data indicates that this may indeed be the case under *Acacia*. In 2000 when there was no redistribution of soil water via HL, $\delta^{18}O$ values of topsoil water were highly enriched due to evaporation from these upper soil layers (compare the data in Figure 4.6 A to B). Isotopic enrichment of topsoil water due to evaporation is a common observation in drying soils (Allison et al. 1983, Le Roux et al. 1995). So, in 2000 the main process affecting the isotope composition of the topsoil water probably was evaporation resulting in higher $\delta^{18}O$ values. In 1998, however it was hydraulic lift which affected the isotope composition resulting in similar $\delta^{18}O$ values in topsoil and groundwater. For example, in 1998 the soil water isotope values were constant at $-4.0‰$ $\delta^{18}O$ throughout the dry season. This "maintenance" of a constant soil water isotopic value could be via exudation (HL) of the groundwater by tree roots.

Tree-grass interactions

In 2000, both grasses and trees did not take up water from the soil layer (25-35 cm) we analyzed water from. Trees appear to take up ground water (i.e., the isotope values of ground and tree root water were essentially identical). The isotopic values of grass water were also much lower than values found in the topsoil suggesting that grasses use water which originates from deeper soil layers. This water is either accessed (a) by direct uptake from the deeper soil layers or (b) indirectly via uptake of hydraulically lifted water supplied by the tree. The $\delta^{18}O$ value of grasses growing at 2.5 m from the tree match that of deep ground water in this system. However, at 10 m from the tree the grass values are closer to what the shallower soil water $\delta^{18}O$ values are (towards the 'all other rainfall' values). This suggests that grasses under trees either switch their water uptake to a lower soil layer which may decrease competition with the trees and/or they take up water exuded into the rhizosphere by the tree. These conclusions are in contradiction with the two-layer hypothesis. (Walter 1971, Walker and Noy-Meir 1982, Sala et al. 1989). This theory explains the co-occurrence of tree and grasses in savannas by water resource partitioning. Grasses are assumed to be the dominant competitor of the two in the topsoil. Trees have exclusive access to deeper soil layer but are competitively inferior to the grasses in the upper layer. However, our

data indicates that grasses under trees use deeper water, either directly or lifted by the tree, than grasses outside canopies. So the co-occurrence of grasses and trees should not be explained by niche separation but could be caused by facilitation through HL.

In this study although we have clear evidence of HL, it is also true that average soil water potential was lower close to trees compared to further away from them. Also in a different study where we measured soil water content over 2 years, under trees we found a lower soil moisture content compared to outside canopies both during dry and wet seasons (Chapter 2, Figure 2.1). Lower soil water content under trees was probably due to the fact that both trees and grasses use water from the same soil layer and thus compete for water. Data from a two year study at the same site has shown that grass production under trees was almost equal to grass production outside *Acacia* tree canopies (Ludwig et al. 2001, chapter 3, Figure 3.1). So hydraulic lift did not result in higher grass productivity probably because roots of *Acacia* trees take up more water than they exudate.

From a methodological perspective, it is also true that spot measurements or average lower soil moisture content does not necessarily mean that water was less available to plants. Due to increased turnover of water through HL, the availability of soil water *per day* might be equal under and outside trees. In the nutrient literature it is a well known phenomenon that the nutrient turnover is a clearer indication of nutrient availability than concentration values alone indicate; the same could be true for water. With HL, average soil water content can be low but because new water is added to the soil every night, water availability may be high enough to permit continued plant function. So although HL did not result in a higher soil water content under trees compared to outside canopies HL may indeed ameliorate competition between trees and grasses.

In conclusion, the occurrence of HL under *Acacia* trees suggests facilitation of the understorey grasses, while other data indicate competition between trees and grasses for soil water. So, what may be most interesting about the data shown here is that both facilitation and competition take place at the same time. Under what circumstances water competition or facilitation through HL is the most important process shaping tree-grass interaction in savannas is still unclear and needs further investigation.

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Chapter 5

Competition between trees and grasses for water overwhelms the effects of hydraulic lift

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Abstract

In a semi-arid savanna ecosystem in East Africa we conducted a field experiment to study the effects of hydraulic lift on tree–grass interactions. Under large *Acacia tortilis* trees, which were known to show hydraulic lift, we experimentally tested whether trees facilitate grass production through hydraulic lift or compete with grasses for belowground resources. Trenching around trees to prevent tree-grass interaction lead to an increased water content in the topsoil. Higher soil moisture availability in trenched plots resulted in an increased grass biomass production relative to the un-trenched control plots indicating that trees and grasses were competing for water in the topsoil. Stable isotope analysis of plant and source waters in the un-trenched control plots showed that grasses which compete with trees use a greater proportion of deep water compared with grasses in trenched plots. This indicates that either grasses use hydraulically lifted water provided by *Acacia* trees or grasses take up deep soil water directly by growing deeper roots when competition with trees occurs. We conclude that the positive effects of hydraulic lift for neighboring species is limited in this savanna system and that facilitative effects of hydraulic lift will usually be overwhelmed by water competition in (semi-) arid areas.

Introduction

A continuous grass layer interspersed with trees and shrubs of varying density characterizes savanna ecosystems. Interactions between the grasses and woody species in savannas has been a focus of much discussion and some research during the last few decades, but definitive experiments that demonstrate how plant-plant interactions are influenced by the severe drought that typify savannas have been few. Traditionally, the co-occurrence of trees and grasses in savannas is explained by niche partitioning. Walter (1971) proposed that trees have sole access to water in deeper soil layers while grasses are the dominant competitor for water in the upper soil layers. He termed this model of co-existence, the two-layer hypothesis. Though there is some evidence supporting the two-layer hypothesis (Hesla et al. 1985, Knoop and Walker 1985, Sala et al. 1989) recent studies have rejected it (Le Roux et al. 1995, Seghieri 1995, Mordelet et al. 1997) in light of the growing evidence that trees may facilitate understorey grass production (Callaway 1995, Belsky et al. 1989, Belsky 1994, Weltzin and Coughenour 1990). Especially in East African savannas, grass productivity can be higher under trees (Belsky et al. 1989, Weltzin and Coughenour 1990) which is often attributed to increased soil nutrient concentrations found beneath trees (Belsky 1994). However, since water is often the main factor limiting productivity in semi-arid savannas, we hypothesized that there may also be beneficial effects on grass production from water that is hydraulically lifted into the rooting zone of the grasses by the trees.

Hydraulic lift is the process of water movement from relatively wet to dry soil layers through the roots of plants that have access to both deep and shallow soil layers (Richards and Caldwell 1987, Caldwell et al. 1998). Except for CAM plants, this transport takes place during the night when leaf stomata are closed and the major water potential gradient is between the deep (wet) roots and the drier surface roots present in the top soil (Richards and Caldwell 1987, Yoder and Nowak 1999). Hydraulic lift has been reported to occur in over 50 plant species worldwide (Caldwell et al. 1998, Dawson, unpublished data) and is conjectured to be a widespread feature as long as active roots are growing in soils with marked water potential gradients and the roots permit both uptake and loss of water. Several authors have suggested that hydraulic lift may have substantial community and/or ecosystem effects (Dawson 1996, Caldwell et al. 1998, Horton and Hart 1998, Jackson et al. 2000, Milikin and Bledsoe 2001, Meinzer et al. 2001). In addition, recent modeling efforts suggest that the influence of hydraulic lift on ecosystem water balance (Jackson et al. 2000, Dawson et al. in review) and on vegetation-climate interactions (Feddes et al. 2001) can be quite significant. Despite this, there have been very few empirical studies that have demonstrated the effects of hydraulic lift on community and/or ecosystem structure or function.

In savanna ecosystems where water availability can have a marked influence on all plants it is unclear how or if hydraulic lift might influence or alter tree-grass interactions. In such a system it seems important to know if competition or facilitation is occurring. If facilitation via hydraulic lift of understorey plants by savanna trees does exist, this could have important impacts on the productivity of savannas. Ecosystem productivity in turn has very clear impacts on the rest of the food web in African savannas which support tremendous amounts of animal biomass as well.

Previously, we have shown that hydraulic lift can occur in *Acacia tortilis* trees in an East African savanna. Mature *Acacia* trees can lift and exude between 75- 235 l of water each night to an area of more than 300 m^2 (chapter 4). At this same site, however, we also showed that the moisture content of the topsoil can be lower under trees compared to the open grassland. This suggested that water use by the trees and grasses together can be very high and therefore the potential for competition between them is also high (chapter 2,4). These observations stimulated us to ask the question whether hydraulic lift facilitates the growth of understorey grasses – or alternatively – whether water is so limited in this system that despite the fact that hydraulic lift does occur, competition for water between the grasses and the trees is most important.

This question was explicitly addressed in a field experiment in which we looked directly at the effects of hydraulic lift on grass growth by preventing tree-grass root interactions via root trenching. We hypothesized that: (a) if trees facilitate understorey grass production through hydraulic lift, root trenching will reduce grass production; (b) if trees and grasses compete for belowground resources root trenching will increase grass production; or (c) if there is niche separation of trees and grasses, as proposed by the two-layer hypothesis, root trenching will have no or very little effect on grass production. This is because, according to the two-layer hypothesis, grasses are the superior competitor for water in the topsoil while trees extract most of their water from deeper soil layers.

Materials and Methods

To test among the three alternative hypotheses stated above we measured above ground biomass, soil water content and plant nutrient concentration in control plots and plots around which all tree roots were trenched. In addition we measured the stable isotope composition of water in trees, grasses, soils, rain and ground water to determine whether root trenching changed the grass water source.

Site description and experimental design

The experimental trees were located in the northern part of Tarangire National Park (4° S, 37° E, 1200m ASL) in northern Tanzania. The soil at the site consisted of coarse sandy loams of lacustrine origin. The vegetation is wooded savanna with a tree cover of 10-20%. The dominant tree species is *Acacia tortilis,* the tree we used in our experiments and the herbaceous layer is dominated by C_4-grasses. Mean rainfall is 650 mm/year (s.d.=272 mm) and the wet season occurs from November until May. The first year of our study (1999) rainfall was slightly above average (750 mm) and stopped half way into May. The second year (2000) of the study was very dry with only 350 mm of rain that stopped early (by late April).

For the experiments we used 4 large isolated *Acacia tortilis* trees; they were all approximately 100 years old (Prins and Van der Jeugd 1993). The trees had an average dbh of 59 (s.d.=19) cm and a canopy diameter of 15 to 20 m. To test the effects of root trenching on grass production under each tree 4 plots of 3 by 3 m were laid out. Two plots were used as a control. Around the other two plots at the two sides closest to the target tree we dug trenches until we reached a hard pan layer at a depth of 60 to 80 cm. Because very few grass roots are able to penetrate a hard pan, we were confident that we prevented nearly all grass-tree root interactions in the trenching

treatment. Soil was removed from the trenches for the first time in April 1999; after which the trenches were refilled with the same soil that had been removed. This treatment was repeated in April 2000. There was little new root growth after the first year (1999) and within all eight plots only one large tree root had re-grown into one of the adjacent grass plots. To avoid possible edge effects we only used the inner 2 by 2 m of the plots; one half of each plot was used to determine plant biomass and the other half used to determine soil and plant water contents.

Soil water contents, aboveground biomass and plant nutrient concentrations

To test the effect of root trenching on soil water content, we took two soil samples in each plot. Samples were divided in two different depths from 0-10 cm and 20-30 cm. Soil water content in samples was determined gravimetrically by drying them at 100°C. In 1999, soil samples were collected on four different dates starting at June 3 and ending at August 13 and on 3 dates in 2000 between May 12 and July 17.

Around each sub-plot used for the aboveground biomass measurements, we constructed a chainlink exclosure to prevent grazing by large herbivores. Then within each of these sub-plots they were further sub-divided into three sampling-plots of 100 * 67 cm. On each sampling date, one of these sampling-plots was hand-clipped to ground level and plant material was sorted into live (green) and dead (non-green) grasses and herbs. Plants were dried in the sun for several days and then weighed. During the first harvest in 1999 plant material was only sorted by plant type (herbs and grasses). In both years aboveground biomass was determined 2, 8 and 14 weeks after the last rainfall event.

N/P ratio of plant tissues in this system have been shown to be good indicators of which nutrient limits the production of the vegetation (Koerselman and Meuleman 1996, Ludwig et al.2001, chapter 3). So, in order to test whether root trenching had affected potential nutrient limitations, a sub-sample of the biomass taken in 2000 was analyzed for total N and P concentration. N and P concentration was determined using a modified Kjeldahl procedure with selenium as a catalyst (Novozamsky et al. 1983).

Stable Isotope sampling

Variation in the oxygen and hydrogen stable isotope composition of source waters can be used to determine the zone of active water uptake by plant roots (Ehleringer and Dawson 1992). Therefore, in 2000, we collected grass, tree, soil, rain and ground water samples for oxygen stable isotope composition. Groundwater was obtained from two different bore (well) holes one about 500 m and one at 5 km from the experimental trees.

In each plot we collected one soil sample at a depth of 25 – 35 cm and at least one grass sample. From every tree we took root and stem samples to determine water sources of the trees following the methods outlined by Dawson and Ehleringer (1993). All samples were collected between 7 and 9 June 2000, 4 weeks into the dry season.

Water was extracted from soil and plant tissue using a cryogenic vacuum distillation apparatus (Ehleringer et al. 2000). 500 µl of the extracted water was injected into airtight vials flushed with 2000 or 3000 ppm CO_2 in He. After 48 hours CO_2 in the head space was analyzed for its oxygen isotope ratio with a Finnigan MAT
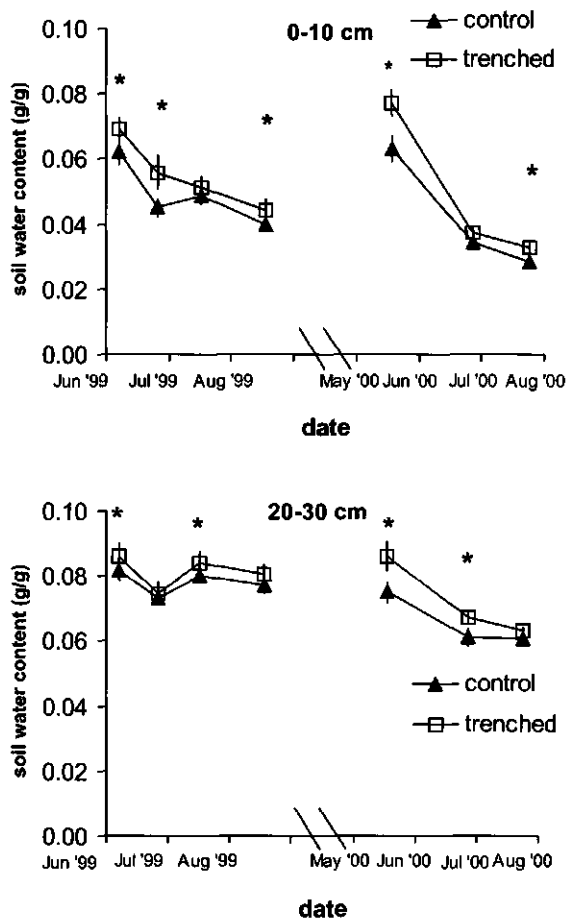
Figure 5.1. The effect of root trenching on soil water content under *Acacia tortilis* trees. Soil water content was determined in plots which were surrounded by root trenches and compared to control plots. Soil samples were taken from two different soil layers (0-10 and 20-30 cm) during the first 3 months of the dry season for two years. Data are averages ± s.e. and asterisks indicate a significant effect of root trenching on soil water content on that individual date

Delta[plus] XL isotope mass spectrometer (IRMS) interfaced with a GasBench II and PAL-80 autosampler following the method outlines by Tu et al. (2001). All $\delta^{18}O$ values are expressed in delta notation (‰) relative to an accepted international standard (V-SMOW) (see Ehleringer and Dawson 1992).

Statistical analysis

All data were statistically analyzed with SPSS 8.0 for Windows. $\delta^{18}O$ values in soil and grass water, soil water content, plant nutrient concentration, total aboveground biomass, herb biomass and life, dead and total grass biomass were analyzed with a general linear model with trenching treatment and sampling date (if more than one) as fixed factors and trees (blocks) as a random factor. In case of the soil water content, soil depth was taken as an additional fixed factor.
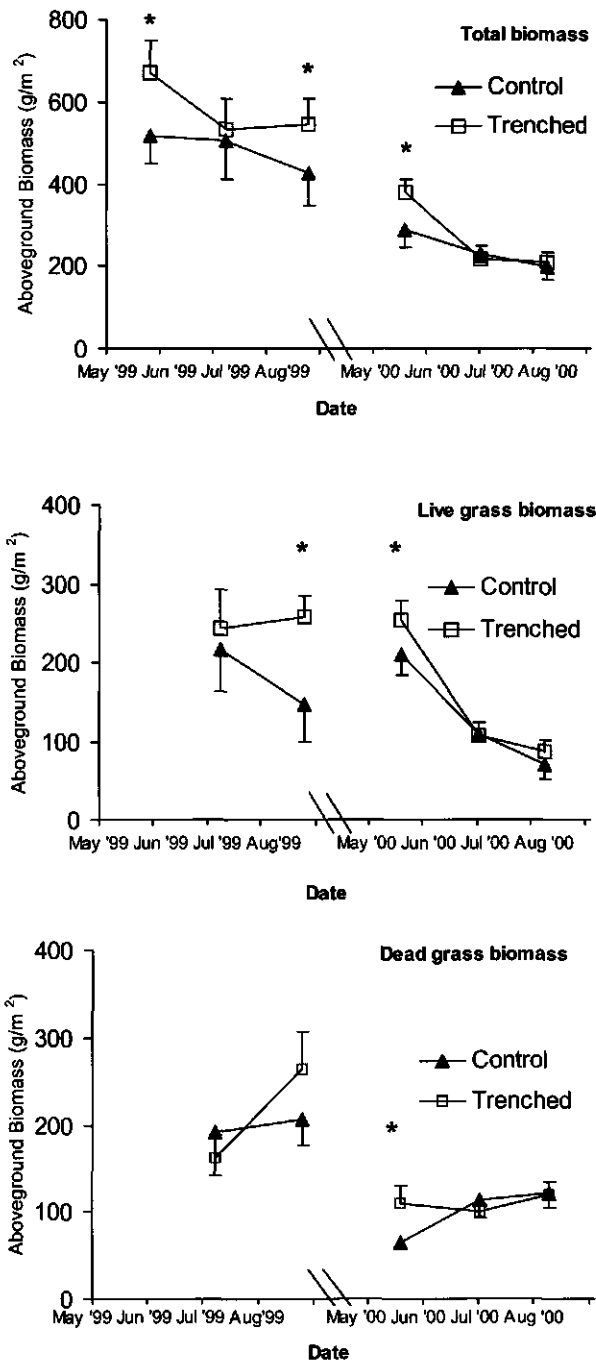
Figure 5.2. The effect of root trenching on total, and live and dead grass above ground biomass under *Acacia tortilis* trees. Biomass was measured in plots which were surrounded by root trenches and compared to control plots during the first 3 months of the dry season for two years. Data are averages ± s.e. and asterisks indicate a significant effect of root trenching on plant biomass on that individual date.

Results

Soil water content, aboveground biomass and plant nutrient concentration

Removing tree roots in the trenched plots resulted in a significantly higher soil water content compared to control plots (Figure 5.1; Table 5.1). Differences in soil water content between the control and trenched treatments were largest early in the dry season when trees were most actively conducting hydraulic lift (chapter 4). When the data from all sampling dates were pooled in the analysis, we found a significant effect of both trenching and sampling date (Table 5.1). The interaction between treatment and date was also significant indicating a stronger effect of trenching earlier in the dry season. The effects of trenching on soil water content were larger in the topsoil than in the deeper soil layer (20-30 cm) but at both depths soil water contents were lower in control than in trenched plots.

In trenched plots total above ground biomass was significantly higher than in control plots (Figure 5.2, Table 5.1). In 1999, biomass was higher in the trenched plots during the entire measurement period. In 2000, however, biomass was only higher at the end of the wet season; at 8 and 14 weeks into the dry season these differences were no longer detected. This was an extremely dry year and therefore plant growth was depressed and was relatively low compared with 1999 (Figure 5.2). Grass biomass followed the same trend as total biomass with a higher production in the trenched plots. In 1999 about 10-20% of the above ground biomass measured was from herbs but there was no effect of trenching on herb biomass (e.g., herbs did not respond as strongly to the trenching as did the grasses). In 2000, herb biomass was negligible. The amount of live grass was also significantly higher in the trenched plots while dead grass biomass was not affected by trenching (Figure 5.2, Table 5.1).

Nitrogen concentration of the vegetation was about 19 mg/g two weeks into the dry season in May 2000 and declined slightly to 15 mg/g in June and August. N concentration was not different between the control and trenched plots (Table 5.1). P

Table 5.1. Results of analyses of variance using a general linear model testing the effect of root trenching on soil water content, above ground biomass, plant nutrient concentration and $\delta^{18}O$ values in grass and soil water. Presented are F values and levels of significance. Aboveground biomass and soil water content was determined during both years of the experiment. However, plant nutrient concentrations and $\delta^{18}O$ values in plant and soil water were only determined during the second season of the experiment

	Soil water content		Aboveground biomass					Plant nutrient concentration			$\delta^{18}O$		
				Total	Total grass	Dead grass	Herbs	Life grass		N	P	N/P ratio		grasses soil	
	df	F	df	F	F	F	F	F	df	F	F	F	df	F	F
Trenching (Tr)	1	45.02***	1	16.12*	7.26*	4.527	0.50	46.25**	1	0.01	1.14	0.20	1	5.93*	1.09
Date (Da)	6	955.7***	5	7.88***	10.84***	11.97***	8.63***	14.84***	2	4.85*	11.47***	1.945			
Tree (block)	3	105.6***	3	16.98*	15.7*	57.80**	2.77	15.34***	3	1.16	6.65**	3.60*	3	0.38	0.95
Depth (De)	1	113.1***													
Tr * Da	5	2.208*	5	0.73	0.50	1.165	1.71	0.96	3	0.061	0.283	0.43			
Tr * De	1	1.327													
De * Da	6	17.23***													
Tr* De * Da	6	0.768													

* P<0.05, ** P<0.01, *** P<0.001

concentration of the vegetation was about 1.5 mg/g in May and again declined slightly to 1.2 mg/g by August. Also plant P concentrations were similar in trenched and control plots. N:P ratios of the vegetation were between 12 and 14 but trenching never had a significant effect on this ratio (Table 5.1).

Stable Isotopes

$\delta^{18}O$ values of precipitation were highly variable, with values between +1.5 ‰ and -3.9 ‰ (Figure 5.3). Most of the isotopic variation is explained by the type of rainfall event. Water collected during heavy (winter) rainfall events had more depleted and less variable $\delta^{18}O$ values (e.g., -3.7‰) while lighter rainfall events showed more variable and enriched (-0.9 to -2.2‰) values. The $\delta^{18}O$ of water collected from both bore holes (ground water) at the site showed nearly identical isotopic values (-3.9‰). Soil water $\delta^{18}O$ values were highly enriched which is probably due to evaporation. Mean $\delta^{18}O$ value in soil from control plots was +0.5‰ and this was slightly higher than in the trenched plots (-0.1‰) but these differences were not significantly different (Table 5.1, Figure 5.3). The isotopic value of water extracted from tree roots and stems was similar to that obtained from the ground water; this demonstrated that, one month into the dry season, trees used ground water exclusively and not water from the topsoil. Water extracted from the grasses growing in the control plots showed the same isotopic value as the tree roots while grasses from trenched plots had significantly higher values (more like light rainfall or shallow soil water) (Table 5.1; Figure 5.3). These data indicate that grasses switched to using a different water source as a result of tree root trenching.
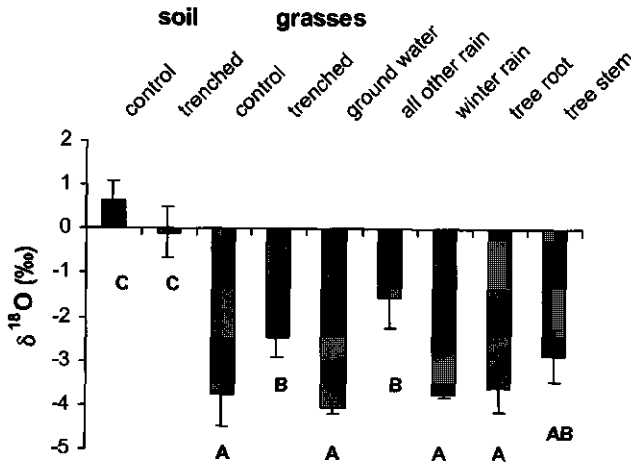
Figure 5.3. Mean $\delta^{18}O$ values (‰, with bars indicating ± s.e) of rain and groundwater and in tree twigs and roots of *Acacia tortilis* trees. These values were compared to water in soil and grasses in plots which were surrounded by root trenches and in control plots. Samples were collected one month into the dry season between 7 and 9 July 2000. Bars with the same letter are not significantly different (LSD-test, P>0.05).

Discussion

In a previous study we have shown that large, mature, *Acacia tortilis* trees in East African savannas conduct hydraulic lift and that significant amounts of water are redistributed to the topsoil each night (chapter 4). It has been suggested that this additional water can potentially affect the ecosystem water balance and tree-grass

interactions (Jackson et al. 2000, Meinzer et al. 2001) and this has been confirmed with both measurements (Dawson 1996, Dawson et al. *in review*) and modeling (Jackson et al. 2000, Feddes et al. 2001, Dawson et al. *in review*). We studied the effects of hydraulic lift on tree-grass interactions with a root trenching experiment to test whether hydraulic lift can facilitate the productivity of understorey grasses or not. Severing tree roots to remove the positive effects of hydraulic lift on soil moisture content had the opposite effect from what we expected; soil water content was higher in the trenched plots relative to the controls. This demonstrated that trees take up more water from the topsoil than they loose and in stead of facilitation, trees interfere with grasses and growth is depressed.

During both years of our experiments grass biomass was higher in trenched plots compared to control plots which showed that grasses benefited from reduced competition with trees. Also, the fact that there was more live biomass and a higher live/dead ratio in the trenched plots suggests that grasses had more water available and therefore grew more in trenched plots. While this belowground competition is most likely to be for water, we cannot eliminate the possibility that trenching may have also reduced competition for soil nutrients. However, foliar nutrient concentrations and the N:P ratio in the aboveground biomass of the herbaceous layer were hardly affected by root trenching which suggests that competition for soil nutrients between trees and grasses was minimal. So trees interfere with grass growth through belowground competition for water.

Our results show that trees extract significant amount of water from the topsoil. This indicates that there is no complete niche separation of rooting depth between trees and grasses and our results add to an increasing number of studies suggesting that the two-layer hypothesis cannot always explain competitive interactions in savannas (Le Roux et al. 1995, Mordelet et al. 1997, Higgins et al. 2000). Also the occurrence of hydraulic lift in savanna trees could complicate the two-layer hypothesis. From a cost-benefit perspective, it seems clear that trees which loose water from their roots to the topsoil would also take up this water again the next day, or this feature would be highly maladaptive (see Caldwell et al. 1998).

Our trenching results indicate that competition for water between trees and grasses in the upper soil layers is very important and very strong in this drought prone *Acacia* savanna. Although the effects of water competition prevail, it is still possible that the understorey vegetation receives some benefits from hydraulic lift. Our isotope data suggest that one month into the dry season neither grasses nor trees used water from the upper soil layers in control plots. Trees used ground water, as the isotope values indicate. The isotope values of grass water responded to root trenching; when trees were absent the grasses used a water source nearer to the surface. There are two possible explanations for this shift in grass water source: First, grasses from control plots used hydraulically lifted water provided by trees which explains the almost identical $\delta^{18}O$ values in grasses and tree roots. After trenching, grasses no longer have access to hydraulically lifted water and are more dependent on shallow water. A second explanation may be that due to competition with trees, grasses in control plots are forced to use a deeper water source directly and grow deep roots to access this water source, while after trenching grasses are released from strong competitive effects with trees, have access to a larger shallow water sources, and therefore use this resource more fully. Given the occurrence of hydraulic lift in this system and the fact that grasses are more shallow rooted species than trees and have a higher root density

in the top soil layers (Scholes and Archer 1997), the first explanation seems more likely than the second.

Hence, there are indications that grasses take up hydraulically lifted water but the beneficial effects of hydraulic lift for the understorey vegetation in this semi-arid savanna appear to be less important than competition for water between trees and grasses, at least in the two years of our experiment. Without hydraulic lift, however, competition between trees and grasses is very likely to be more severe. Several authors have suggested that hydraulic lift can have substantial ecosystem effects and that water lifting trees would facilitate understorey plants in a number of ways (Callaway 1995, Caldwell et al. 1998, Horton and Hart 1998), but so far there is little evidence from the field (but see Dawson *in review*). Actually, we are aware of only one study which showed that hydraulic lift causes a higher soil water content under trees compared to soil outside trees which was the case under *Acer saccharum* trees in the eastern United States (Dawson 1993, Emerman and Dawson 1996). Here, understorey grasses had a higher plant water potential and stomatal conductance if they took up more hydraulically lifted water (Dawson 1993). So, in certain situations facilitative effects of hydraulic lift can overwhelm competition for water but these positive effects of hydraulic lift were observed in an ecosystem which is much less limited by water than the semi-arid savanna we studied (Dawson 1993; Dawson et al. *in review*). Also, two other studies showed that hydraulic lift is more likely to occur in relatively wet than in dry years (Yoder and Nowak 1999, chapter 4). So, possibly in more mesic regions or wet years hydraulic lift might positively affect tree-understorey interactions but in arid regions or dry years the positive effects of hydraulic lift would usually be overwhelmed by water competition.

Acknowledgements

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Chapter 6

Consequences of large tree decline for herbivore forage quality in an East African savanna

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Abstract

The number of large savanna trees in East Africa has reduced sharply during the last 25 years. We studied how this affected the food availability and quality of large migratory herbivores of Northern Tanzania in Tarangire National Park.

Large *Acacia tortilis* trees had a positive effect on the overall forage-quality of grasses. This was indicated by a higher proportion of live leaves, a higher nutrient and protein concentration and a higher digestible organic matter (DOM) content in grasses from under tree canopies compared to grasses from open grassland. Grass growing 10 m outside tree canopies still had higher nutrient concentrations and DOM contents than grasses from open grassland.

With a linear model we predicted that wildebeest, the most abundant herbivore in the park, can meet all their energy, nutrient and protein requirements to maintain a stable body weight by selection forage from under or around tree canopies only. However wildebeest cannot cover their daily requirements by only selecting forage from open grassland. Although when forage from open grassland is combined with at least 10% of grass intake from under tree canopies wildebeest can obtain a diet which meets maintenance requirements. This shows that forage from under trees is essential for wildebeest but that only a relatively low tree cover is sufficient.

Previously collected tree transect data showed that between 1971 and 1996 the aerial cover of large *Acacia tortilis* trees reduced from 16 to 4%. We also calculated that in 1971, due to large trees, 20 % of the Acacia savanna was covered by a vegetation type associated with *Acacia trees* dominated by highly nutritious *Cynodon* species. As a result of the reduction in the number of large trees the cover of this nutritious vegetation declined to 5% in the 1996. The results of our linear model showed that a minimum 10% of the vegetation needs to be covered by this nutritious vegetation associated with trees to enable the wildebeest to use all grass available in the *Acacia* woodlands of Tarangire NP. In 1971 probably enough high quality forage was available for the herbivores but in 1996 the cover of the by *Cynodon* spp. dominated vegetation has dropped below the minimum needed by herbivores. So we conclude that a reduction in the number trees around Tarangire NP probably has reduced the dry season survival of migratory herbivores during the last 25 years.

Introduction

Semi arid savannas are characterized by a continuous grass layer and an open discontinuous layer of shrubs and trees. Especially in East-Africa, savannas are renowned for the high diversity and abundance of large herbivores (Prins and Olff 1998). During the last decades studies in savanna ecology have to a large extent focussed on two aspects. First of all, the interactions and co-existence of the two different plant life forms trees and grasses has recently received of lot of attention (Scholes and Archer 1997, Ludwig et al. 2001). Savanna trees have a large influence on grass productivity and the species composition of the herbaceous layer (Belsky 1994, Belsky et al. 1989). Others have studied the effect of soil water, nutrient and fire on tree – grass ratios and co-existence (Walker & Noy-Meir 1982, Higgins et al. 2000, Van Langevelde et al. *in review*). A second line of research in savannas has been on grazing by large mammals, especially studies on grass food supply and on how to explain a high diversity of different sized herbivores in savannas (Murray and Illius 1996, Prins and Olff 1998, Voeten and Prins 1999). These two different aspects of savanna ecology have never been really integrated. In this study we focused on how tree-grass interactions influence herbivore food availability and quality and how this is affected by a decline in large savanna trees.

Savanna trees can reduce grass growth by competing with grass for water and nutrients and decreasing light availability (Anderson et al. 2001, Le Roux et al. 1995). However, trees can also improve grass growth conditions by increasing soil moisture via hydraulic lift (chapter 4, Dawson 1993), reducing evapotranspiration (Amundson et al. 1995, Ludwig et al. 2001) and by increasing soil nutrient availability (Belsky et al. 1989, Kellman 1979, chapter 2). Both negative and positive effects of trees on grass production have been described. In East Africa, however, trees tend to increase grass production (Belsky et al. 1989, Belsky et al. 1993, Weltzin and Coughenour 1990). Although total plant production affects the total animal biomass, forage quality is of more importance to understand herbivore performance and food limitation (Prins 1996, Van Soest 1994) and the interplay between forage quality and quantity determines to a large extent the composition of the herbivore assemblage (Prins and Olff 1998, Fritz and Duncan 1994).

Under trees, the soil is often more fertile than in open grassland (Kellman 1979, Scholes and Archer 1997, chapter 2). If these extra nutrients are taken up by the grasses, then under equal biomass, the nutritional quality of the vegetation will increase (Lowry and Wilson 1999). Also shade and a lower water availability can increase grass nutrient concentrations because nutrients are less diluted due to a lower biomass. In previous studies, forage quality was usually determined in large homogeneous open grassland patches (Voeten and Prins 1999, Prins 1987). However by not including savanna grasses growing under trees food quality and availability could be underestimated.

In a previous study in Tarangire National Park in Northern Tanzania, Van de Vijver et al. (1999) showed that the number of large trees has declined dramatically over the last 25 years. In 1971, large trees had an average cover of 20 percent in the *Acacia* woodlands but in 1996 this was reduced to only 5%. The reason for this reduction is still unclear; it might be caused by an increased natural mortality or due to elephants or increased browsing pressure (Prins and Van der Jeugd 1993). In certain areas outside the park the situation is even more dramatic, here all large trees have been removed for charcoal production by local people and the border of the park

can literally be observed by the absence of large trees (pers. obs.). If trees indeed increase food quality and/or availability, a reduction in the number of trees will seriously affect the large herbivore populations in East African savannas.

In Tarangire NP, we studied the effect of savanna trees, in this case *Acacia tortilis,* on grass nutrient concentrations and digestibility. By using a linear programming model we determined whether herbivores can satisfy all their nutritional and energy requirement by selecting forage from open grassland, from under trees and/or a combination of both. We also analyzed the relation between tree size and the size of the herbaceous vegetation affected by the tree. Combining this relationship with tree transect data collected by Van de Vijver et al. (1999) we were able to analyze the effect of tree decline on forage availability and quality over the last 25 years.

Material and Methods

Site description

Data were collected in Tarangire National Park (4° S, 37° E, 1200m above sea level) which is located at the eastern side of the Great Rift Valley in northern Tanzania and encompasses an area of about 2600 km². Mean rainfall over the last 20 years is 650 mm/yr (Van de Vijver 1999). The wet season is from November until May with most of the rain typically falling during March and April. The Tarangire river runs through park and in the dry season this river is the main permanent fresh water supply within the entire 35 000 km² Masai ecosystem (Prins 1987).

Northern Tarangire NP is the dry season range of large migratory herds of Burchell's zebra (*Equus burchelli*) and wildebeest (*Connochaetes taurinus*) and to a lesser extent Cape buffalo (*Syncerus caffer*). The park is famous for its large herds of elephants (*Loxodonta africana*) which primarily reside in the park during the dry season and sometimes disperse to surrounding areas in the wet season. Other less abundant herbivores are impala (*Aepyceros melampus*), Coke's Hartebeest *(Alcelaphus buselaphus cokii)* and giraffe *(Giraffa camelopardalis).*

Two wooded savanna types dominate the park: *Acacia* savanna which can be found in the riverine area with lacustrine soils in which *Acacia tortilis* is the dominant tree species and the deciduous savanna, which is concentrated on the ridges and upper slopes on pre-cambrium well drained red loamy soils (see Van de Vijver et al. 1999). Here, the dominating trees are *Combretum* and *Commiphora* species. Most of the herbivores concentrate in the *Acacia* savanna (TCP 1997, Voeten 1999), probably because of the higher forage quality, so we focused our work on this savanna type. As *Acacia tortilis* accounts for 90% of the large trees in this savanna type (Van de Vijver et al. 1999) we focused our study on grass vegetation growing under and around this trees species.

Three different vegetation zones could be determined within the *Acacia* savanna. A zone under trees, one around the trees and in open patches more than 50 m from any tree. Previous studies showed that concentrations of all major nutrients are higher in the belowcrown soil than in open grassland and are intermediate in the area around tree canopies (Table 6.1). Soil water contents and soil water potentials were lower under than outside tree canopies (Chapters 2 & 4) and aboveground biomass of

the herbaceous layer was almost equal in the three different zones (Table 6.1) (Ludwig et al. 2001, chapter 3).

Table 6.1 Differences in abiotic and biotic environment under and outside canopies of large *Acacia tortilis* trees and in open grassland patches. Soil organic matter (s.o.m.), total N and P, available N ($NO_3^- + NH_4^+$) concentration and maximum yearly biomass were determined at the three different zones. Data from chapters 2 & 3

| | Soil properties | | | | Understorey Vegetation | | Light |
	s.o.m.	total N (mg/g)	total P (mg/g)	available N(mg/kg)	biomass 1998 (g/m^2)	biomass 1999 (g/m^2)	Relative light availability
Under tree canopy	44%	1.64	0.27	12.36	674	552	50%
Outside tree canopy	38%	1.16	0.22	6.39	680	508	92%
open grassland	37%	1.04	0.20	2.29	n/d	540	100%

Herbaceous layer vegetation

Species composition of the herbaceous vegetation was recorded at peak biomass in June 2000 in 2*2 m plots in each of the three different zones. Therefore we selected four large *Acacia tortilis* trees with an average canopy cover of 330 m^2 (s.d.= 125) and four open grassland patches at least 100m from any tree. Under tree canopies plots were located halfway the canopy and the stem. Outside the canopy plots were situated at a standerized distance from the stem which was twice the canopy radius. Plots under and outside trees were replicated in the four cardinal compass directions (N,S,E, and W). In each plot the aerial cover of all plant species was visually estimated. On each of the four different open grassland patches we estimated species composition in 2 different plots.

Grass sample collection and chemical analyses

To analyze grass nutrient concentration, grass samples were collected at maximum standing biomass in the early dry season, in June 2000. This is also the time that the migratory herds return back to Tarangire NP and start grazing at the study site. At each of the three different zones we collected samples of the most dominating grass species. Three *Cynodon* species, *C.dactylon, C.nlemfluensis and C.plectostachius*, were treated as one group because they are very similar, rarely flower and it is impossible to distinguish between the species without uprooting them and/or when the are not flowering (see Clayton and Renvoize 1982).

Grass samples were collected following the 'hand plucking method' (Wallis de Vries 1995). We plucked samples between the thumb and the backward-bent fore finger to simulate large herbivore grazing as close as possible. We collected one sample of every species around each of the four *Acacia* trees selected for the vegetation analysis. One sample consisted of between 15 and 25 pickings collected in small mono-specific stands at different spots within the same zone. To determine live/dead and leaf/stem ratios, the collected samples were sorted in: live stem, live leaves, dead stem and dead leaves. After sorting, samples were dried in the sun and weighed.

Different species were sampled in the three zones because of differences in species compositions. Under the tree we collected samples of *Cynodon spp., Panicum maximum,* and *Cenchrus ciliaris.* Outside canopies the vegetation was more species rich so we collected samples of *Cynodon spp., Cenchrus ciliaris, Digitaria macroblephera, Chloris virgata, Urochloa mosambicensis* and *Heteropogon contortis.* In open grassland the vegetation was dominated by only two different species so we only collected samples of *Heteropogon contortis* and *Sehima nervosum.*

Live leaves and stems were analysed for total N, P, K, Ca, Mg and Na using a modified Kjeldahl procedure with Selenium as a catalyst (Novozamski et al. 1983). After digestion, N and P concentrations were measured colorimetrically with a continuous flow analyser (Skalar SA-4000) and K, Ca, Mg and Na was analysed with an atomic absorption spectrophotometer (Varian Spectra AA-600). Neutral detergent fibre (NDF) was determined according to Goering and Soest (1970) and digestibility of organic matter (DOM) according to Tilley and Terry (1963). Crude protein content was calculated as 6.25 * total N concentration. DOM, NDF and Nutrient concentration of the vegetation per zone was calculated by multiplying the nutrient concentration in a specific species by its relative abundance within the vegetation.

Linear Model

A problem of having to comply with several different requirements can be analyzed with a linear programming model (Belovsky 1978, Voeten and Prins 1999). This is an optimization model whereby one goal is maximized or minimized subject to different constraints. Here, we used it to study whether herbivores can meet all their nutritional and energy requirements at the same time by selecting food from under or outside trees or from open grassland or a combination of food sources. As a basis we used the model described by Voeten (1999). We took the wildebeest as model species because it is the most abundant herbivore in Tarangire NP (TCP 1997) and nutrients and energy constraints of this species have previously been described by Murray (Murray 1993, Murray 1995). Each constraint was formulated as a general linear equation have the following form:

$$C \geq or \leq \sum C_i * I_i \tag{1}$$

Where C is a constraint value which stands for either nutrient, energy or fiber intake. We formulated minimum requirements for nutrient, protein and energy intake and a maximum value for fiber intake. I_i is the amount of food consumed of class i; in this study grass from under or around trees canopies or open grassland. The parameter C_i converts I into the same unit as C and is based on the nutrient, energy and fiber content measured in the grasses of the different zones.

Murray (1995) calculated, from a feeding trial in the Serengeti, northern Tanzania, that wildebeest need an energy intake of 22.32 MJ/day for maintenance. This was based on an average bodymass of 143 kg. The metabolic energy of grasses equals the digestible energy multiplied by 0.82 (Van Soest 1994). The digestible energy can be calculated from the digestibility of organic matter (DOM) multiplied by the gross energy of grass. The energy content of tropical grasses averages 19 MJ/kg (Crampton and Harris 1969). Thus the constraint equation for energy intake is:

$$22.32(MJ / day) \leq 19(MJ / kgDW) * DOM(\%) * 0.82 \tag{2}$$

Where DOM is the digestibility of organic matter as determined in vegetation. I is the intake rate (kg DW/day) and i stands for the foraging zone.

Digestible protein (DP) requirements at maintenance for ruminants can be calculated as:

$$DP(g / day) = 3.150 * W^{0.75} \qquad (3)$$

Where W stands for bodyweight. We used an average weight of wildebeest of 143 kg (Murray 1993) which means they need 130 g DP per day for maintenance. DP for tropical grasses can be calculated from crude protein using the following formula (Prins 1987):

$$DP(mg / g) = 0.91 * CP(mg / g) - 32.2 \qquad (4)$$

So the second constraint equation used in the model is:

$$130(g)DP / day \leq \sum DP * I_i \qquad (5).$$

For ruminants the daily intake rates are often constrained by rate of digestion and passage through the rumen (Voeten and Prins 1999). The digestibility rate of food is often correlated with the cell wall content, measured in the vegetation as neutral detergent fiber (NDF). Reid et al. (1988) calculated from a feeding trial of cattle on a C_4-grass diet that maximum daily NDF intake can be calculated as:

$$NDF(g) = 66.7g / kgW^{0.75} \qquad (6)$$

For wildebeest of 143 kg, the maximum intake is thus 2.76 kg NDF so the third constraint equation is:

$$2.76(kg)NDF / day \geq \sum NDF_i * I_i \qquad (7)$$

In addition, we defined two equation based on requirements of the two most important nutrients of wildebeest as determined by Murray (Murray 1995). The constraint equation for maintenance levels of calcium and phosphorus are:

$$5.75(g)P / day \leq \sum P_i * I_i \qquad (8)$$

$$3.59(g)Ca / day \leq \sum Ca_i * I_i \qquad (9)$$

Where P and Ca are the concentration measured in the vegetation.

Na is not considered in this model because wildebeest can cover their daily requirements through drinking water from the Tarangire river (Voeten 1999). Different constraint were used to calculate whether wildebeest can meet all nutritional and energy requirement for maintenance (to maintain a stable body weight) by selection forage from under or outside tree canopies, open grassland or a combination of these.

Relation between tree size and stargrass vegetation

As described previously, the herbaceous vegetation can be distinguished in three zones. The edge between the first (under canopy) and the second zone (outside canopy) is very sharp. The vegetation under tree canopies is dominated by mainly by *Cynodon* spp. and to a lesser extent by *Panicum maximum*, we called this 'stargrass' vegetation after the English name for *Cynodon*. Because these species produce a high quality forage for herbivores we determined what part of the vegetation within the *Acacia* savanna is covered by these species due to trees.

Because the edge is so sharp and can easily be observed in the field we could measure the size of the stargrass vegetation zone in relation to canopy size. So at three different sites within the *Acacia* savanna we selected 20 different sized isolated *Acacia tortilis* trees. Around each tree we measured diameter at breast height (DBH) and at the base. In addition we measured in the four cardinal compass direction (N,S,E and W) the distance between the canopy edge and the stem and the distance between the stem and the vegetation dominated by *Cynodon spp.* and *Panicum maximum.*

To calculate what part of the *Acacia* savanna of Tarangire NP is covered by the stargrass vegetation we used the tree transect data of Van de Vijver et al. (1999). They collected data of tree density and sizes in 1996 of all tree species along transects using the point–centered quarter method and compared this with data collected by Vesey-FitzGerald (1973) (for details see Van de Vijver et al. 1999). By combining the relationship between tree canopy size and stargrass vegetation size with the data on tree size and density we calculated the cover of the stargrass vegetation in 1996 and in 1971.

Statistical analysis

All data were statistically analysed with SPSS 8.0 for Windows. Data on live/dead ratio and leaf/stem ratio, nutrients concentration, NDF and DOM of grass samples were analysed with a General Linear Model (GLM) with distance, grass species and vegetation zone (under and outside tree canopies and open grassland) as a fixed factor and trees as a random factor. Relationship between tree canopy size and size of stargrass vegetation was analysed using a GLM in which research site was used as a fixed factor and size of tree canopy as a covariate.

Table 6.2. Average vegetation cover, leaf:stem ratio and live:dead ratio of grass species growing under and just outside canopies of large *Acacia tortilis* trees and in open grassland patches. Variance of data was analysed with a GLM with grass species and location (open grassland and under and outside canopies) as fixed factors. Species with the same letter are not significantly different (Tukey HSD, P>0.05)

Location	species	cover of vegetation at specific zone	live leaf	live stem	dead leaf	dead stem	leaf:stem ratio
Data							
Under tree canopy	*Panicum maximum*	9%	51% [a]	33%	11% [ab]	4%	1.806 [a]
	Cynodon spp.	62%	42% [a]	47%	6% [a]	4%	0.953 [ab]
	Cenchrus ciliaris	9%	28% [b]	41%	24% [ab]	7%	1.215 [ab]
Outside tree canopy	*Cynodon spp.*	7%	25% [b]	50%	19% [ab]	5%	0.801 [ab]
	Cenchrus ciliaris	6%	27% [b]	41%	16% [ab]	15%	0.825 [ab]
	Digitaria macroblephera	14%	27% [b]	44%	13% [ab]	16%	0.700 [ab]
	Chloris virgata	9%	25% [b]	39%	28% [b]	8%	1.135 [ab]
	Urochloa mosambicencis	21%	31% [b]	44%	17% [ab]	9%	0.912 [ab]
	Heteropogon contortis	17%	35% [b]	52%	8% [a]	5%	0.773 [ab]
Open grassland	*Heteropogon contortis*	38%	33% [b]	48%	10% [ab]	8%	0.768 [ab]
	Sehima nervosum	36%	29% [b]	50%	9% [a]	12%	0.621 [b]
Statistics							
Species		F	2.203*	1.33	2.54*	1.35	2.57*
Location		F	2.270	0.20	0.289	1.22	0.84
Species * Location		F	3.387*	0.88	6.358*	1.91	1.36

* P<0.05, *** P <0.001

Results

Species composition of the herbaceous layer

The *Cynodon* species covered 62% of the vegetation under tree canopies (Table 6.2). The other two abundant species under trees were *Panicum maximum* and *Cenchrus ciliaris*. The remaining 20% was covered mainly by herb species. Outside tree canopies the vegetation was more species rich with six more or less abundant grass species (see Table 6.2). In open grassland the vegetation consisted almost exclusively of the grass species *Heteropogon contortis* and *Sehima nervosum.* Nutritional properties of herbaceous layer vegetation

The proportion of live leaves in the grass samples was highest in species growing under trees canopies and was lowest in species from open grassland (Table 6.2). Interestingly, *Cynodon* grasses sampled from under canopies had a much higher percentage of live leaves than those sampled outside tree canopies. *Chloris virgata*, an annual species mainly growing outside trees, had a relatively high percentage of dead leaves. There was no significant difference between different grass species in percentage of dead or live stem but leaf/stem ratios of grasses were higher in species growing under canopies and lowest in open grassland species.

Digestibility of green leaf organic matter (DOM) was highest in *Cynodon* grasses growing under the canopy where 70% of green leaves was digestible (Table 6.3). DOM was lowest in *H. contortis* growing in open grassland. For NDF we observed a reversed pattern with the lowest values for *Cynodon* and highest for *H. contortis* and *S. nervosum*.

Table 6.3 Digestibility of organic matter (DOM), neutral detergent fiber (NDF) and nutrient concentrations of grass species growing under and just outside canopies of large *Acacia tortilis* trees and in open grassland patches. Variance of data was analyzed with a GLM with grass species and location (open grassland and under and outside canopies) as fixed factors. Species with the same letter are not significantly different (Tukey HSD, P>0.05)

| Location Data	species	DOM (%)	NDF (%)	protein mg/g	P mg/g	K mg/g	Ca mg/g	Mg mg/g	Na mg/g
Under	*Panicum maximum*	65.65[ab]	70.60[ab]	141.4[b]	1.77[ab]	40.62[a]	4.12[c]	3.25[b]	0.10[a]
tree	*Cynodon spp.*	70.33[a]	61.45[a]	165.1[a]	1.80[ab]	38.41[a]	6.91[a]	2.44[bcd]	0.12[a]
canopy	*Cenchrus ciliaris*	59.78[ab]	70.12[ab]	136.8[b]	1.74[ab]	44.83[a]	4.34[c]	1.95[def]	0.21[a]
Outside	*Cynodon spp.*	65.07[ab]	66.49[ab]	126.8[bc]	2.38[bc]	36.07[a]	6.70[ab]	2.58[bcd]	0.17[a]
tree	*Cenchrus ciliaris*	57.96[ab]	71.45[ab]	105.5[cd]	2.43[bc]	41.89[a]	3.30	1.87[def]	0.14[a]
canopy	*Digitaria macroblephera*	62.64[ab]	72.91[ab]	74.5[e]	2.85[cd]	38.35[a]	3.75	2.26[cde]	0.20[a]
	Chloris virgata	66.80[ab]	70.40[ab]	104.6[cd]	2.59[cd]	37.56[a]	4.91[bc]	3.03[be]	0.87[b]
	Urochloa mosambicencis	69.13[a]	64.77[ab]	104.0[cd]	3.59[e]	44.28[a]	5.28[ab]	4.00[a]	0.13[a]
	Heteropogon contortis	56.97[ab]	70.15[ab]	81.5[es]	1.46[a]	17.17[b]	3.30[c]	1.64[def]	0.14[a]
open	*Heteropogon contortis*	51.68[b]	74.00[b]	67.6[e]	1.65[ab]	15.08[b]	3.31[c]	1.22[f]	0.13[a]
grassland	*Sehima nervosum*	54.66[ab]	74.65[b]	60.8[e]	1.46[a]	12.02[b]	4.67[c]	1.47[ef]	0.14[a]
Statistics									
Species	F	2.25*	2.42*	14.09***	5.45**	8.79***	7.75***	13.51***	18.43***
Location	F	1.19	1.53	6.91***	9.07***	0.571	0.72	0.91	0.02
Species * Location	F	0.26	0.60	0.29	0.09	0.01	0.66	0.27	1.15

* P<0.05, *** P <0.001
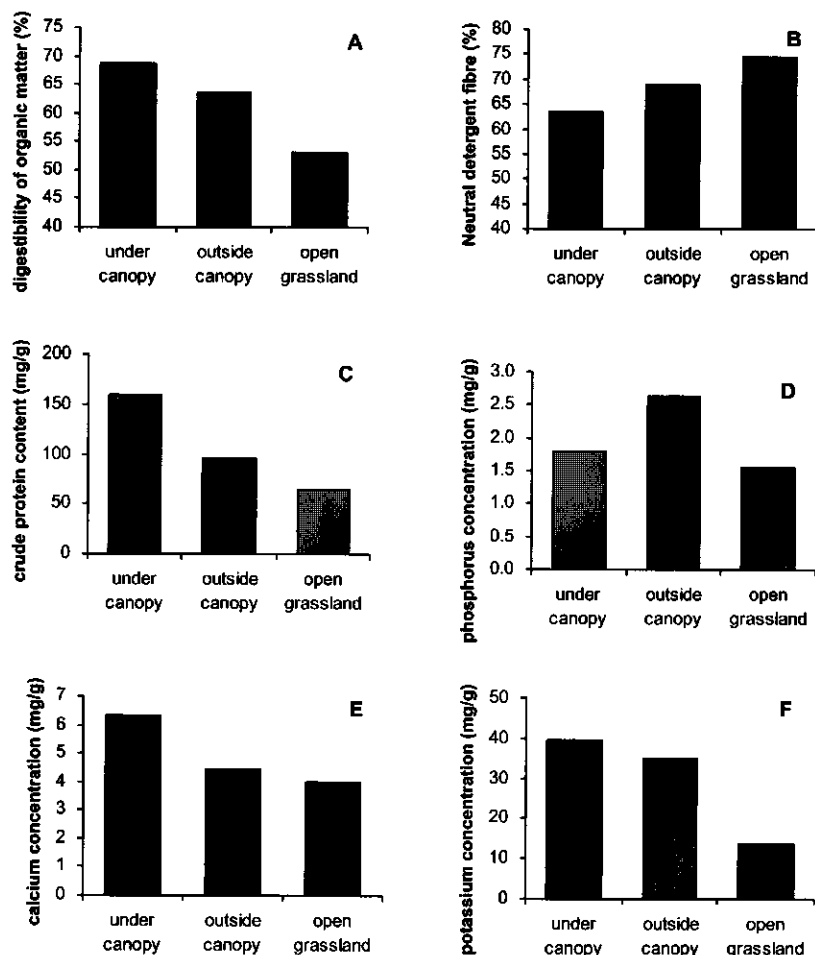
Figure 6.1 Digestibility of organic matter (A), Neutral detergent fiber (B), Protein,(C) Phoshprus (D), Calcium (E) and Potassium (F) concentration in green leaves in the vegetation under and outside the canopies of large *Acacia tortilis* trees and in open grassland patches.

Protein contents of grasses were highest under tree canopies. This was not only a species effect because *Cynodon spp.* and *C. ciliairis* showed a higher protein content under than outside tree canopies. However, *Cynodon* grasses growing outside canopies still had a higher protein content than other species growing in same zone. K, Ca, Mg and Na showed similar patterns with the highest concentrations in grasses from under tree canopies and lowest in grasses from open grassland. For P we observed a different pattern, concentrations were highest in grass growing outside canopies and lower concentrations in grasses from under canopies and in open grassland.
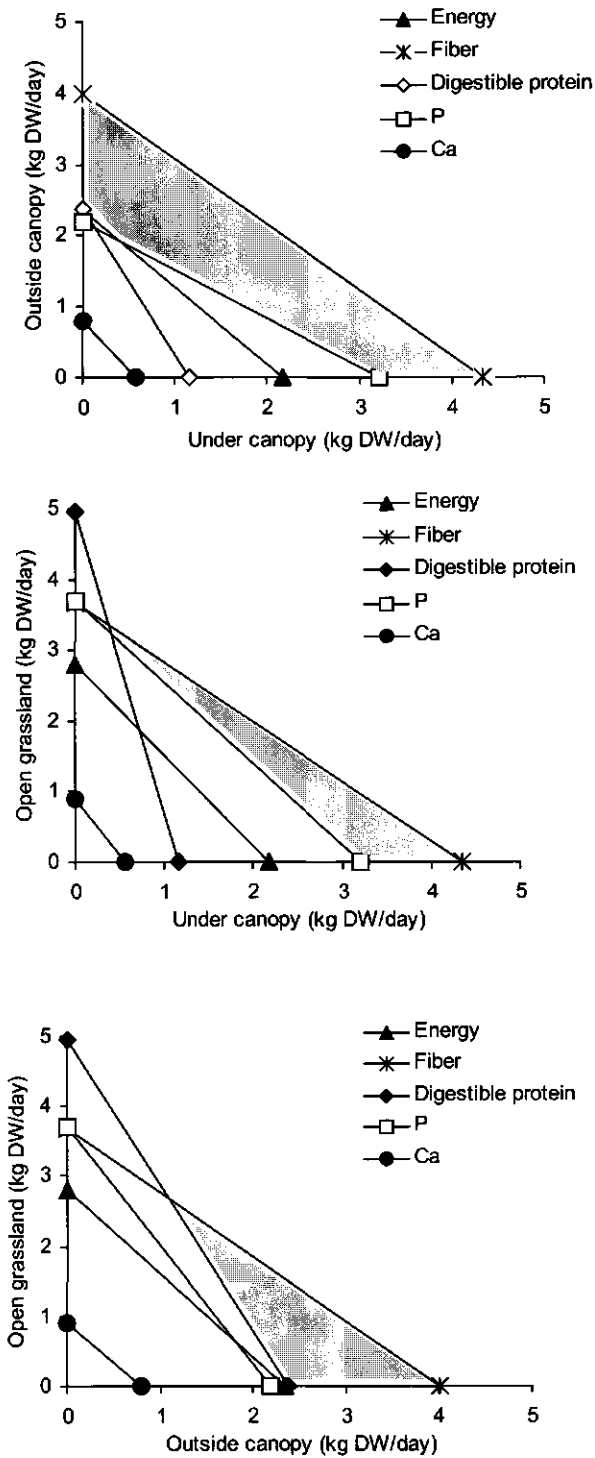
Figure 6.2 Results of linear programming model, predicting whether wildebeest can meet their daily requirements for energy, nutrients and protein by selecting forage from under or outside tree canopies or in open grassland patches. Each line indicates the minimum food intake required to meet nutrient, energy or protein requirement, for fiber the maximum intake is shown. The shaded part indicates all possible combinations of food sources which meet all nutrient, energy and protein requirements.

When expressed per vegetation zone the picture is even clearer; all nutrient concentrations except for P were higher in grass leaves from under the canopy than in grasses from open grassland and outside canopies (Figure 6.1). Only P concentrations were higher in the vegetation outside the canopy with lower values under canopies and in open grassland. There was also a considerable difference in percentage DOM and NDF with higher DOM and lower NDF values in the herbaceous vegetation under the canopy.

Linear model

The results of the linear model show that wildebeest can meet all their energy, nutrient and protein requirements by selecting forage from under tree canopies only (Figure 6.2). If wildebeest would maximize their energy or protein intake they would select forage from under tree canopies only. Also by only selecting grass from around tree canopies herbivores can satisfy all their nutritional and energy requirements. However, the linear model shows that herbivore can not satisfy all their energy and nutrient requirements by only selecting food from open grassland (Figure 6.2). Due to the high fiber content and low nutrient and protein concentrations in these grasses, maximum fiber intake is reached before nutrient requirements are satisfied. However the results of the model show that all requirements can be satisfied by combining forage from open grassland with either a minimum of 360 g grass per day from under the canopy or a minimum of 1100 g/day from outside canopies. When wildebeest select 360 gram of forage from under canopies this has to be combined with 3350 gram from open grassland. So according to the model at least 10% of forage has to be selected from under canopies to maintain a stable body weight.

Tree density and cover of stargrass vegetation.

The cover of by *Cynodon* species dominated 'stargrass' vegetation increased with an increasing cover of the *Acacia* tree canopy (Figure 6.3). The linear relationship between the tree canopy cover and the cover of the stargrass vegetation is described in equation 10. The stargrass vegetation started to develop once the tree canopy size extended above about 35 m^2, under smaller trees the stargrass vegetation is smaller than the tree canopy but once the tree canopy covers more than 100 m^2 the stargrass vegetation extents beyond the canopy edge. There was no difference in this relationship between the three different sites studied.

cover of stargrass vegetation (m^2) = 1.48*canopy cover (m^2) − 35 m^2 (10)

From the data set on tree density collected by Van de Vijver et al (1999) we calculated that in 1971 about 16% of the Acacia savanna in Tarangire NP was covered by large *Acacia tortilis* trees. Over 25 years the number of large trees decreased dramatically and in 1996 only 4% of the vegetation was covered by large trees (Figure 6.3). From the transect data of Van de Vijver et al. (1999) we used all the *Acacia* trees with a canopy cover of more that 35m^2. We assumed that under smaller trees the stargrass vegetation had not developed yet. From all the larger trees we calculated using equation (10) what percentage of the herbaceous layer was covered by the

strargrass vegetation in 1971 and 1996. These results showed that the cover of the strargrass vegetation declined from more than 20% in 1971 to 5% in 1996 (Figure 6.3).
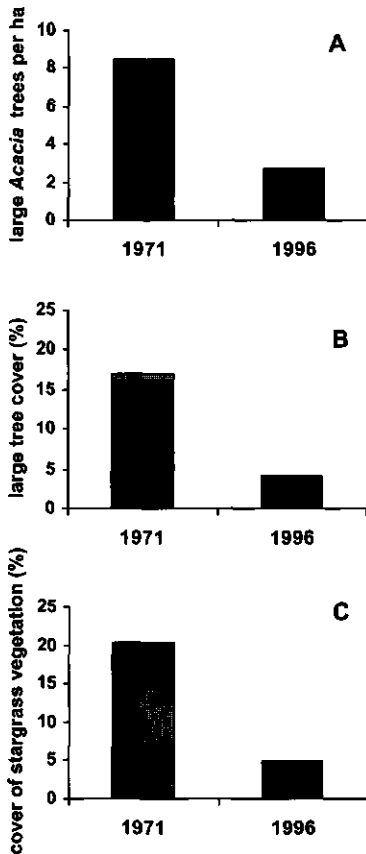

Figure 6.3 Number (A) and cover (B) of large *Acacia tortilis* trees in the *Acacia* savanna of Tarangire NP in 1971 and 1996. Figure C shows the calculated cover of the *Cynodon spp* dominated, nutritious stargrass vegetation around large *Acacia* trees in 1971 and 1996.

Discussion

Effects of trees on forage quality

Large savanna trees clearly increased the forage quality of the herbaceous vegetation. Grasses growing under tree canopies contained a lower fiber content and the highest concentrations of protein and several other nutrients. P concentrations showed a different trend with the highest concentration in grasses growing outside tree canopies. The reason for the relatively low P concentration in grasses growing under tree canopies is that grass production under trees is limited by P availability while outside trees the limiting nutrient is N (Ludwig et al. 2001, chapter 3). Increased forage quality under trees is partly caused by the different species which dominate the vegetation under large trees. However, *Cynodon spp.* growing under trees also had higher protein concentrations and DOM contents than the same species growing outside large trees. This shows that a higher belowcrown forage quality it is not only a species effect but also due to a different environment under trees. Interestingly, the

positive effect of trees on forage quality did not stop at the canopy edge. Grasses growing about 10 m outside tree canopies still had higher nutrient concentrations and live/stem ratios and a higher DOM than the two species dominating open grassland. So one mature *Acacia* tree with a canopy radius of 7 m can potentially increase forage quality over an area of more than 600 m^2.

Patterns of increased forage quality under savanna trees is probably not only limited to Tarangire NP but a more general phenomenon. Other studies also showed that both *Cynodon spp.* and *P. maximum* have a relatively high nutritional value compared to other East African grasses (Georgiadis and McNaughton 1990, Ben-shahar 1993, Belsky 1992). This in combination with other reports of *Cynodon* spp. and *P.maximum* dominating the understorey vegetation of savanna trees (Belsky et al. 1989, 1993) shows that a higher forage quality under savanna trees probably is a widespread phenomenon.

Increased forage quality under savanna trees can be caused by a range of different effects because savanna trees influence the availability of all the major resources needed by grasses. Trees reduce light availability through shade; often increase soil nutrient concentrations and compete with grasses for below ground resources, especially water (Belsky 1994, Scholes and Archer 1997, Anderson et al. 2001). Shade alone can already increase forage quality (Cruz et al. 1999). For example, two independent studies showed that N concentrations were increased in *Panicum maximum* growing under artificial shade (Deinum et al. 1996, Durr and Rangel 2000). However, most important probably is the increased soil nutrient availability under savanna trees. In a previous study under the same *Acacia* trees we found that concentrations of all major nutrients were much higher under trees compared to open grassland (see Table 2.6, chapter 2). At least part of these extra nutrients end up in the grasses which will increase forage quality. Under normal circumstances higher soil nutrient concentrations would lead to increased grass productivity which would then result again in reduced nutrient concentrations due to dilution. However grass productivity under these *Acacia* trees is mainly limited by water. In previous studies we found that soils under *Acacia* trees had lower soil moisture contents and soil water potentials than soils outside canopies (chapter 2 & 4). So, probably a higher forage quality under savanna trees is caused by a combination of reduced soil moisture and increased soil nutrient availability under canopies compared to open grassland.

Effect of trees on herbivore food selection

Migratory herds of herbivores often travel along rainfall gradients. During the wet season they concentrate in low rainfall areas and during the dry season they move to areas with a relatively high annual rainfall (McNaughton 1990). Both in the Masai and the Serengeti ecosystems of Tanzania, zebra and wildebeest follow such a migration pattern; in the wet season animals move to relatively arid open grasslands and in the dry season they stay in more mesic savanna woodlands (Murray 1995, Voeten and Prins 1999). These migration patterns are probably driven by grass mineral concentrations (McNaughton 1990, Voeten 1999). In both these ecosystems the wet season ranges are the driest with very seasonal rainfall but when there is grass available, the nutritional quality is relatively high. Due to the more abundant rainfall, the dry season ranges have a higher, more predictable, grass production but of a lower

quality (Voeten and Prins 1999, McNaughton 1988, 1990). In both these migratory ecosystems, these areas with relatively low quality grass are *Acacia* savannas. Within these savannas, islands of high quality forage created by large savanna trees are probably of great importance.

The results of the linear model showed that forage from open grassland in Tarangire NP, the wet season range for migratory ungulates in the Masai ecosysteem indeed has a relatively low nutritional quality. When wildebeest forage only in open grassland they cannot satisfy all their nutritional and energy requirements to maintain a stable bodyweight while grazing in the dry season in Taranigire NP. The grass species growing in open grassland have such a high fiber content that the intake of forage is limited and not enough to extract sufficient amounts of protein and P. Also the crude protein concentration is below 7-8% in grasses from open grassland. At these protein concentration the digestion rate is severely limited (Van Soest 1994) which is another indication that wildebeest cannot survive when foraging from open grassland only.

However both grass from under and around trees can satisfy all nutritional and energy requirements of wildebeest for maintainance while grazing in the dry season in Taranigire NP. The model also indicates that when forage from open grassland is combined with only 360 g/day grass from under tree canopies, wildebeest can obtain a diet which meets maintenance requirements. This shows that forage from under trees is essential for wildebeest but that a relatively low tree cover is sufficient. However, taking into account the low protein content of forage from open grassland which slows down digestion, the amount of grass needed from under trees might be underestimated by the linear model.

Effect of tree reduction on food availability

As forage from under trees is essential for herbivores in the *Acacia* savannas of Tarangire NP, the number of trees probably play an important role in regulating herbivore density. So the observed reduction in number of large trees in Tarangire NP over the last 25 years probably has severe consequences for large herbivores. What caused this reduction in large trees is still unclear. However, a study from Ruess and Halter (1990) shows that reductions in the number of large trees are not limited to Tarangire NP. They found that between 1972 and 1982 the number of mature *Acacia tortilis* trees reduced by 70% in the Seronera woodlands of the Serengeti. Also the tree cover in the *Acacia* savannas of the Mara Reserve in Southern Kenya reduced from 28% in 1950 to 1% in 1982 (Dublin 1995).

The decrease in the number of large *Acacia* trees in Tarangire NP probably caused a severe reduction in the cover of highly nutritious grass vegetation dominated by *Cynodon* grasses. While in 1971 probably about 20% of the *Acacia* savanna was covered with a 'stargrass' vegetation, in 1996 only 5% percent was left (see Figure 6.4). The results of the linear model suggests that wildebeest need to obtain 360 g/day forage from this 'stargrass' vegetation from under trees which is about 10% of their diet. Grass productivity under trees and in open grassland is almost equal (Ludwig et al. 2001, see Table 6.1). So 10% of the vegetation needs to be covered by the stargrass vegetation associated with trees to enable the wildebeest to use all grass available in the *Acacia* woodlands. In 1971 probably enough high quality forage was available for

the herbivores. However, in 1996, the cover of the stargrass vegetation has dropped below the minimum needed by herbivores.

Also, the areas surrounding Tarangire NP are still important grazing grounds for migratory herds of zebra and wildebeest and in these areas the situation concerning large trees is even more dramatic. *Acacia* trees can produce very good charcoal which is a relatively important source of income for the farming communities around Tarangire NP. This charcoal production has resulted in a disappearance of almost all large *Acacia* trees outside the park. This very likely resulted in a reduction of the forage quality of the grasslands around the park. As discussed before herbivores have to select at a least a part of their food from under trees. If trees are present, herbivores can satisfy the requirements by combining forage from open grassland with grasses from under or around trees. However when there are no trees at all it seems impossible for herbivores to meet all requirements for maintenance. So a reduction in the number trees both in and outside Tarangire NP probably has reduced the dry season survival of herbivores during the last 25 years due the a limited availability of forage of sufficient quality.

Acknowledgements

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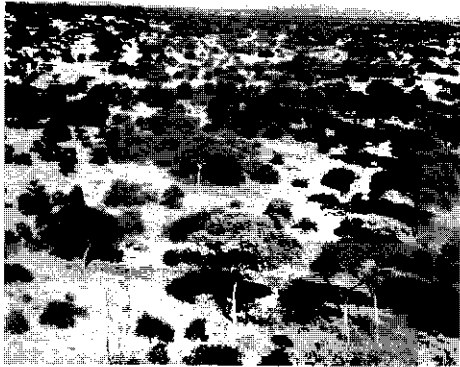
Inside Tarangire NP, although the number is declining, large *Acacia* trees still grow in the park.

Just outside the park (picture taken from the border), no large *Acacia* trees are left, only large Baobabs and bushes

Chapter 7

Synthesis

Fulco Ludwig

Introduction

Historically, changes in species composition and productivity of plant communities have been explained through competitive interactions. Over the last 50 years numerous experiments have shown that interference is one of the most important factors in structuring plant communities (Berendse 1983, Goldberg and Barton 1992, Fowler 1995). However, during the last decade, there is an increase in empirical evidence showing that positive interactions or facilitation also affect species distribution and plant productivity (Belsky 1994, Callaway et al. 1991, Callaway 1995, Weltzin and McPherson 1999). In the earlier work on facilitation people tried to show that either competition or facilitation was shaping plant-plant interactions (Callaway et al. 1991). A more likely explanation, however, is that both processes take place at the same time (Olff et al. 1999, Holmgren et al. 1997, Holzapfel and Mahall 1999, Callaway and Walter 1997).

Savannas are a good example of an ecosystem were both facilitation and competition take place. Interactions between the two different life forms in savannas, trees and grasses are an excellent system to study the contrasting effects of facilitation and competition because: (a) Trees can have both positive and negative effects on resource availability of grasses, (b) The functioning of the grass layer can be studied both under influence of trees, under canopies, and without trees in open grassland patches and (c) Both reduced and increased productivity under trees compared to open field have been described in the past which suggests that both facilitation and competition can dominate tree-grass interactions (Mordelet and Menaut 1995).

I studied this balance between facilitation and competition in a semi-arid savanna in East Africa through a set of different observations and experiments. (chapter 2 until 5). The main results showed that trees facilitate the understorey through increased nutrient availability but compete with grasses for soil water. The results of this thesis can be used to formulate a conceptual model which can easily explain the variety of positive and negative effects which savanna trees can have on grass production. This model is based on a balance between facilitation of the tree understorey through increased nutrient availability and interference by competition for soil water.

Of the two processes dominating tree-grass interactions, the effect of trees on soil nutrient concentrations is well described in the savanna literature (Belsky 1994, Scholes and Archer 1997) but water has been neglected in studies on tree-grass interactions. Nevertheless, modeling studies have stressed the importance of water in explaining tree-grass co-occurrence in savannas (Walker and Noy-Meir 1982, Van Langevelde et al. *in review*). While the balance of positive and negative effects of trees on grass nutrient availability changes over a period of decades (chapter 2), the effect of water can already change between different seasons and even over a number of days (chapter 4). The importance of water relations in explaining interactions between trees and grasses is discussed in relation to hydraulic lift in the second part of this chapter. In the last part of this chapter, the importance of interactions between trees and grasses for savanna herbivores is discussed and especially what the long term effects of large tree removal on grass production and forage quality are considered.

Tree-grass interactions in savannas: a balance between nutrient facilitation and water competition

Savanna trees have a multitude of positive and negative effects on the production of the understorey vegetation (Figure 7.1). Trees may facilitate grass growth through increased nutrient availability and hydraulic lift but trees also compete with grasses for belowground resources, both nutrients and water. Also shade supplied by the tree can increase productivity due to lower temperatures and decreased evapotranspiration but reduced light intensities can also limit grass growth. The balance between these facilitative and interfering effects of tree on the understorey vegetation determines whether productivity is higher or lower under tree canopies.

In this thesis several of these facilitative and competitive effects of trees on grasses are discussed (chapter 2 – 5). The results of my first, observational study presented in chapter 2 suggested that trees positively affected the nutrient availability of grasses but large trees reduce the amount of water available in the topsoil. Based on the high productivity around dead trees (see Figure 2.5), I hypothesized at the end of
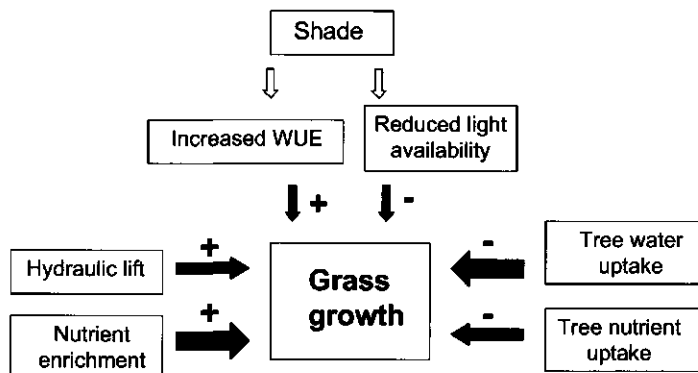
Figure 7.1 Model showing the positive (+) and negative (-) effects of trees on understorey grass growth. Trees can potentially increase grass productivity through hydraulic lift and nutrient enrichment but trees reduce grass growth through water and nutrient uptake. Shade can promote grass growth through increased water use efficiency (WUE) due to lower temperatures and shade reduces grass growth through reduced light availability. The size of the arrow indicates the hypothesized importance of the process.

chapter 2 that trees increase grass productivity due to increased soil fertility but reduce grass production due to belowground competition for water. With a nutrient experiment, (chapter 3) I showed that trees supply such an extra amount of nitrogen to the understorey grasses that they become limited by phosphorus in stead of nitrogen (Figure 3.2). Also nutrient addition increased productivity more in open grassland than under trees showing that grasses outside trees are more limited by nutrients than grasses from under the canopy.

A tree root trenching experiment showed that a higher nutrient availability under tree canopies did not result in an increased productivity because of belowground competition for water (chapter 5). So the two most important processes

regulating grass productivity under trees are soil nutrient enrichment and belowground competition for water. Comparing these results with observations and experiments described in several other studies it becomes clear that this is a general pattern. Trees will always facilitate understorey plant growth through increased nutrient availability and trees will always compete with the understorey vegetation for soil water. The balance between these two processes determine the net effect of trees on grass productivity. When there is only a slight increase in nutrient availability but severe water competition, trees will reduce grass productivity. If there is a substantial increase in nutrient availability and only limited water competition, through for example hydraulic lift, trees will increase plant production. These ideas were tested by reviewing the literature first on the effect of trees on soil nutrient and water availability. Thereafter in detail three other studies are discussed which compared productivity under trees and in open field in combination with measurements on both soil moisture content and soil nutrient concentrations.

Basically, in all situations soil nutrient concentrations are higher under savanna trees than in open sites. I reviewed more than 30 different publications which compared soil nutrient concentrations under and outside tree canopies in savannas and all of them showed increased nutrient concentrations under savanna trees (Breman and Kessler 1995, Callaway et al. 1991, Bernhard-Reversat 1982, Kellman 1979, King and Campbell 1994, Belsky et al. 1989, Weltzin and Coughenour 1990, Belsky et al. 1993, Anderson et al. 2001). Not all studies measure the same nutrients and often different methods are used so it is hard to compare different studies. However, the relative increase under trees compared to open field differs considerably between different savannas. In an oak savanna in the southern USA there was only a 10% increase whereas under Acacia trees in East Africa available nutrient concentrations can be twice as high under trees compared to open grassland (Belsky et al. 1989, 1993, chapter 2).

The situation concerning water is more complicated because it changes more during the season and is much harder to study than nutrient availability. There are fewer published studies on the effect of savanna trees on soil water availability and due to a high variability differences are often unclear. However, the general pattern is a lower water content under savanna trees compared to open sites (Callaway et al. 1991, Mordelet et al. 1993, Amundson et al. 1995, Anderson et al. 2001). (Chapter 2& 4) Often these differences are only clear in the dry season while in the wet season soil water content is too variable to distinguish any effect of trees. Increased soil water content under savanna trees compared to open field is, to my knowledge, only shown once in an oak savanna in southern Spain (Joffre and Rambal 1988).

Beside the study described in this thesis there are three other studies which compared productivity under trees and in open field in combination with measurements on both soil moisture content and soil nutrient concentrations. One of these studies described a positive effect of trees on grass production (Belsky et al. 1989, 1993, Belsky 1994), one described a negative effect (Anderson et al. 2001), one described both (Callaway et al. 1991) while the results described in this thesis show hardly any effect of trees on grass productivity (chapter 2 & 3). The contrasting results described in these studies can all be explained by a change in the balance between nutrient facilitation and water competition.

Belsky and co-workers found a large increase in grass productivity under savanna trees compared to open grassland in southern Kenya (Belsky et al. 1989,

1993). Here there was a large increase in soil nutrient concentration and there was hardly any effect of the tree on soil water content although some measurements indicated a lower soil moisture content under trees compared to open field (Belsky et al. 1989, Amundson et al. 1995). Tree root trenching hardly affected understorey plant production, suggesting limited water competition between trees and grasses (Belsky 1994). So, in this East African savanna increased productivity was caused by a large increase in soil nutrient concentrations while water competition did not appear to be important.

In an oak savanna in the southern USA, plant production under trees was much lower than in open field (Anderson et al. 2001). Here the key factor behind the reduced understorey productivity was water competition between trees and understorey plants. Soil N, Mg and K concentrations were higher under trees than in open sites. However, the increase in soil nutrient concentration was less than 10% which was not enough to compensate for the reduced water availability due to competition so the overall effect of the tree showed a reduced productivity of plants growing under trees compared to open field.

Callaway et al. (1991) studied oak trees which increased (positive trees) and a different group of trees but within the same savanna, which decreased understorey plant production (negative trees). Soil nutrient concentrations were higher under negative trees than in open grassland but nutrient concentrations were the highest under positive trees. Removing belowground competition with root exclosures increased the productivity of the understorey of the negative trees but not under the positive trees. Furthermore, tree water potential measurements showed that only positive trees had access to ground water and negative trees did not. Also in the dry season the highest soil water contents were observed in open grassland and the lowest under negative trees with intermediate values for positive trees. So under both groups of trees the same processes take place: both increase soil nutrient concentration and decrease soil water content but the balance between the two processes determined whether trees increased or reduced understorey productivity.

So, under a wide range of circumstances the balance between facilitation through increased nutrient availability and competition for water explains whether savanna trees increase or decrease grass productivity compared to open field (Figure 7.2). The model also explains some other controversies common in savanna ecology. For examples if trees have positive effects on grass production why does tree removal always increase grass productivity (Scholes & Archer 1997; Harington & Johns 1990; chapter 2)? This can be explained by the fact that after trees die the positive effect of increased nutrient availability remains but belowground competition for water is eliminated. From these tree removal experiments it was often concluded that trees negatively affect grass productivity. However, these conclusions might be wrong; only the positive effects remain longer than the negative effects but in the long term, tree removal can still decrease plant production once the higher nutrient concentrations have disappeared.

Although, it is now identified which processes determine whether trees increase or reduce grass growth, this is not enough to be able to predict whether trees increase or decrease belowcrown grass production. Therefore it is also essential to know what circumstances regulate tree – grass water competition and the accumulation of nutrients under tree canopies. Scholes and Archer (1997) proposed that a higher soil fertility under trees can be caused by three different processes (a)

trees attract mammals and birds which deposit feaces under the canopy, (b) trees act as an atmospheric trap for dust or (c) trees act as a nutrient pump taking up nutrients from deeper soil layers or from soil outside the canopy and depositing them under their canopy through litter fall or leaching (see also chapter 2). If animals play a significant role in increasing belowcrown soil nutrient concentrations then an increasing animal density and grazing pressure will result in a higher belowcrown nutrient concentration. This might explain the relatively high concentrations of nutrients found under trees in areas with high animal densities in East-Africa (Belsky et al. 1989, 1993, Georgiadis 1989, Chapter 2). A lower tree density will attract relatively more animals to one tree which will result in a more increased soil fertility. However soil nutrient concentration are also higher under trees in savannas without large herbivores (Breman and Kessler 1995, Kellman 1979). This, combined with the
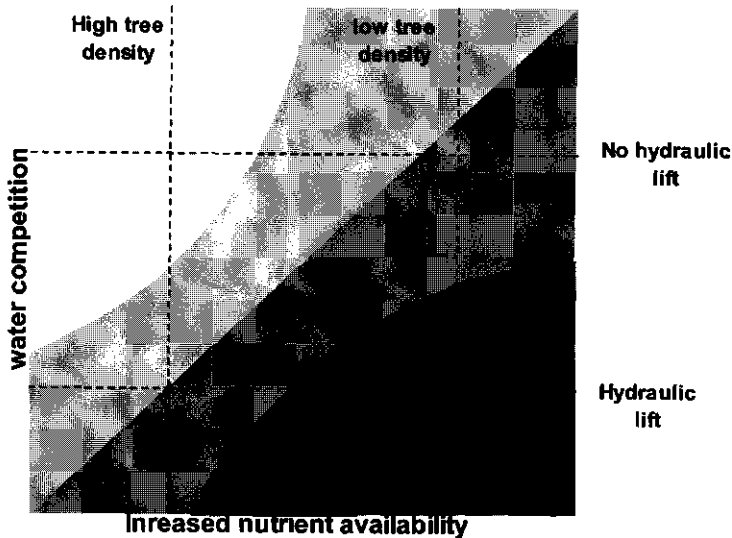
Figure 7.2. The effect of the extent of increased nutrient availability under trees and the severity of water competition between trees and grasses and grass productivity. Dark areas indicate increased grass productivity under savanna trees while lighter areas indicate reduced grass productivity. Dashed lines show the effect of tree density and Hydraulic lift as shown in Figure in 7.3

fact that I also found an increased soil nutrient availability under small bushes, suggests that it is unlikely that large herbivores play a major role in enriching belowcrown soils. Also the amount of data suggesting that trapping dust causes increased nutrient availability under trees is minimal (Scholes and Archer 1997)

The main reason for an increased soil nutrient availability under savanna trees is probably the tree itself acting as a nutrient pump (Kellman 1979; Chapter 2). Here the size of the tree root system determines the potential to concentrate nutrients under canopies. The more extensive the tree root system is, both horizontally and vertically, the more nutrients will be concentrated in the topsoil under the canopy (Figure 7.3 A & 7.4). Also important in determining the extent of nutrient accumulation is the ratio between the lateral extension of the roots and the size of the canopy. This is especially the case if nutrient accumulation is mainly caused by nutrient uptake from outside
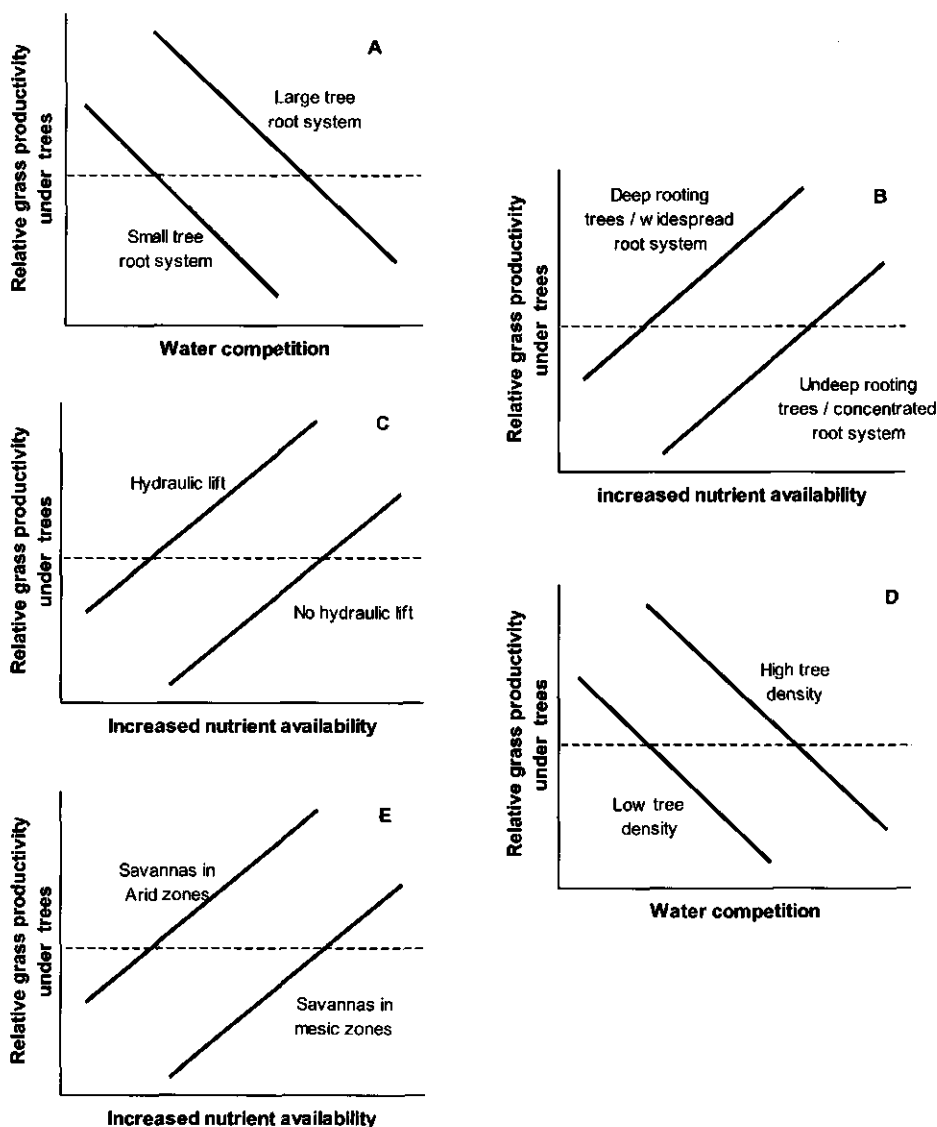
Figure 7.3 Hypothetical relations showing the effect of the severity of water competition between trees and grasses on relative grass productivity under trees (A and D) or the effect of the extent of increased nutrient availability under savanna trees on grass productivity (B, C and E). The dashed line indicates equal grass production under trees compared to open grassland. Values above this line indicate increased productivity and below the line indicate reduced productivity. Shown is how size of the tree root system (A), tree rooting depth (B), hydraulic lift (C), tree density (D) and climatic zone (E) affect relative grass productivity.

canopy which later end up under the tree crown through litterfall. This would theoretically also result in an impoverished zone around the tree canopies (Kellman 1979, Scholes and Archer 1997). However the results presented in this thesis show that also the zone around the canopy is more fertile the open grassland patches (chapter 2).
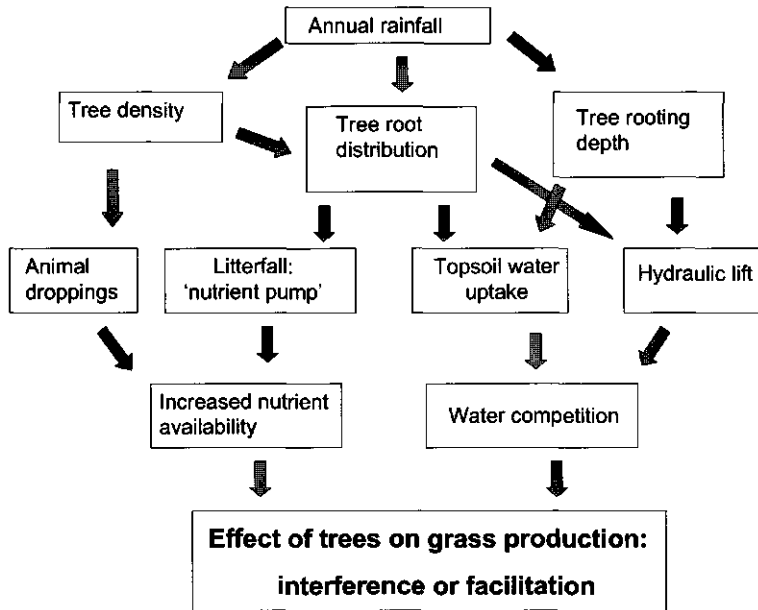
Figure 7.4 Conceptual model showing what determines whether trees facilitate or interfere grass growth under canopies. Trees basically always increase nutrient availability to some extent and trees and grasses almost always compete for water. Severity of water competition is determined by tree water uptake from the topsoil and exudation of water through hydraulic lift. The extent of the increase in belowcrown soil nutrient concentration is determined by the amount and nutrient content of tree litterfall and concentration of animal droppings under tree canopies. These four effects depend on tree root distribution, rooting depth and tree density, which are in turn affected by amount and pattern of annual rainfall

    Another conclusion is that trees and grasses compete for water in the topsoil in basically all savannas. The severity of this competition, however, can change between different savannas and tree sizes. Again the size of the tree root system is probably important in influencing the harshness of the competition. Deep rooting trees with access to groundwater will take up less water from the topsoil and thus compete less with grasses than trees which have their roots mainly in the topsoil. Also a more widespread root system which covers a large area of soil can reduce tree water uptake per square meter (Figure 7.3 B & 7.4). Another process which can potentially reduce tree – grass water competition is the redistribution of groundwater to the topsoil through hydraulic lift (Figure 7.3 C & 7.4) (chapter 4 & 5). Also for hydraulic lift the size of the root system is important. A tree with a deeper root system is more likely to reach groundwater and the more deep roots a trees has the more water it can lift.

So, both for the increase in belowcrown nutrient concentration as for the severity of water competition, the size of the root system seems to be important as well. A tree with an extensive lateral root system and a tap root is more likely to have a positive effect on understorey productivity than trees with all their roots concentrated under the tree canopy. In dryer savannas trees tend to have a more extensive root system than in humid savannas because trees need a larger area of soil to meet their water demands. This could indicate that in dry savannas trees might be more likely to increase understorey grass growth than in more humid savannas.

A study in southern Kenya showed that grass production was almost 100% higher under trees compared to open grassland in an arid savanna but in a more mesic savanna trees only increased production by 40% (Belsky et al. 1993). Also in oak savannas in North America, trees in areas with less than 500 mm yearly rainfall enhanced grass production but trees in wetter areas reduced understorey grass growth compared to open grassland (McClaren and Bartolome 1989). These results support the idea that trees are more likely to facilitate grass growth in arid savannas (Figure. 7.3 E & 7.4). Based on research, mainly in arctic regions, several authors have suggested that facilitation increases over a gradient of environmental stress (Brooker and Callaghan 1998, Mulder et al. 2001). Facilitation would most likely occur in stressful environments because in these areas plants can reduce abiotic stress for each other. Also in savannas facilitation seems to occur more often in dryer, more stressful environments. However in savannas this is caused by a reduction in competition in dryer regions and not by an increase in positive plant-plant interactions. A lower tree density and productivity in dry savannas reduces competition between trees and grasses and as result the positive effect of increased nutrient availability can dominate tree – grass interactions (Figure. 7.3 D & 7.4).

Ecosystem effects of hydraulic lift

Plant production in semi-arid savannas is limited by water for at least part of the year. In the previous paragraph it was discussed that the severity of water competition partly determines whether trees increase or decrease below crown productivity compared to open grassland. The size of tree root systems is an import factor affecting competition and a wide tree root system will probably reduce competition on a square meter basis. Another process which can affect competition between trees and grasses is hydraulic lift.

None of the previous studies on tree – grass interaction has taken hydraulic lift into account so whether it plays an important role is still unclear. Hydraulic lift has now been shown in more than 60 species and it probably is a widespread phenomenon (Caldwell et al. 1998; see chapter 1). However, the significance of hydraulic lift for ecosystem level water fluxes remains unknown (Jackson et al. 2000, Meinzer et al. 2001). Some studies have shown that hydraulically lifted water can be taken up by neighboring species but whether this actually increased production of neighboring species is still unclear. I found clear evidence for hydraulic lift in *Acacia tortilis* trees (chapter 4) and data on stable isotopes in soil and plant water indicated that understorey grasses take up hydraulically lifted water (chapter 4 & 5). However, a trenching experiment failed to show that understorey grass production is increased by hydraulic lift. The results of the trenching experiment clearly showed that *Acacia* trees reduce grass production as a result of competition for water. However the

Table 7.1. The effect of root trenching on relative plant water content of grasses growing under *Acacia tortilis* trees. Relative plant water content was determined between 8.00 and 9.00 AM (morning) and between 1.00 and 3.00 PM (afternoon) in plots which were surrounded by root trenches and compared to control plots. Data were analyzed statistically with an analysis of variance using a general linear model for relative plant water content of grass leaves. Apart from trenching, other fixed factors are grass species (*Cynodon dactylon* or *Cenchrus ciliaris*, time of day (morning or afternoon) tree (block factor) and Date. Data were first analyzed for all sampling dates, because of interactions with time, data were also analyzed for every sampling date separately.

Data		All dates 1999	May 1999	June 1999	August 1999	June 2000
Morning	Trenched		99.1 %	97.2 %	92.0 %	51.8 %
	Control		98.5 %	98.2 %	90.2 %	53.3 %
Afternoon	Trenched		94.8 %	94.3%	83.2%	45.6 %
	Control		94.1%	93.4%	83.6 %	45.3 %
Statistics	df	F	F	F	F	F
Trenching (Tr)	1	0.215	1.812	0.289	0.739	0.511
Time of day (Ti)	1	46.06^{***}	81.202^{***}	14.13^{***}	24.60^{***}	3.075^{+}
Species (S)	1	75.12^{***}	7.155^{*}	28.32^{***}	77.75^{***}	4.113^{*}
Date (D)	3	84.75^{***}				
Tree (block)	3	12.65^{***}	0.284	0.339	20.64^{***}	2.762^{+}
Tr*Ti	1	1.977^{+}	0.005	3.721^{+}	0.391	0.037
Tr*S	1	0.029	0.246	0.843	0.342	0.433
Tr*D	3	3.627^{*}				
Ti*S	1	3.738^{+}	0.508	0.063	4.948^{*}	0.487
Ti*D	3	4.106^{***}				
S*D	3	25.23^{***}				
Tr*Ti*S	1	3.056^{+}	0.885	4.219^{*}	1.999	0.047
Tr*Ti*D	3	0.382				
Tr*S*D	3	0.423				
Ti*S*D	3	3.662^{*}				
Tr*Ti*S*D	3	0.819				

+ $P<0.10$ * $P<0.05$, ** $P<0.01$, *** $P<0.001$,

severity of the competition could still be reduced by hydraulic lift. In other words, without hydraulic lift grass production would have been even more limited by water competition and thus hydraulic lift could still be an important factor in regulating understorey productivity. This is confirmed by measurements on relative grass water contents in plots surrounded by root trenches and control plots influenced by tree roots. These measurements were part of a root trenching experiment described in chapter 5.

In the morning during the early dry season, in June 1999, grass water contents were higher in control plots influenced by hydraulic lift than in plots surrounded by root trenches (table 7.1). In the afternoon, a reverse pattern was observed with higher plant water contents in trenched than in control plots. Later in the dry season (August) in 1999 the effect of trenching on plant water content could no longer be detected. In June 2000, I found the same trends as in June 1999 with higher plant water contents in control than in trenched plots in the morning and a reverse trend in the afternoon but these differences were not statistically significant.

Higher morning plant water contents in control plots in the early dry season may have been caused by uptake of hydraulically lifted water that becomes available

during the night. However, at mid-day, grasses from control plots always had lower relative water contents. This was probably caused by the fact that during the day grasses from control plots have to compete for water with trees while grasses in trenched plots have all soil water for themselves. Later in the dry season these differences disappear because the amount of hydraulically lifted water decreases when soil water potential declines and tree roots loose soil contact as shown by the hydraulic lift study (see chapter 4). So, there are indications that grasses take up hydraulically lifted water and that hydraulic lift can improve grass water status during the night. This indicates that without hydraulic lift, competition between trees and grasses is more severe. While our data indicate that in these savanna ecosystems there can be positive, facilitative effects of hydraulic lift on grass growth, these effects are not as strong as the negative impacts of competition with trees for water. An extensive study by Dawson and co-workers (Dawson 1993, Emerman and Dawson 1996, Dawson *in review*) on hydraulic lift in sugar maple trees shows a completely different picture. They showed that understorey plant growth, survivorship and seed production is increased as a result of water input through hydraulic lift of maple trees. This study is from a relatively wet and cold area in the north-eastern USA. The work described in this thesis and other work on HL was performed in more arid zones. This indicates, in contrast to earlier expectations, that hydraulic lift could be more important in more mesic than in arid zones. This is confirmed by the results presented in chapter 4 where I found clear evidence of HL in a relatively wet but not in a very dry year. Also Yoder and Nowak (1999) observed HL in relatively more species in a wet than in a dry year in plants from the Mojave desert in the eastern USA.

To fully understand if and when hydraulic lift affects the ecosystem water balance and productivity, it is important to know under what circumstances hydraulic lift takes place. For hydraulic lift to occur a difference in soil water potential between different parts of the root system is needed. So, hydraulic lift will not occur in very wet climates but there also seem to be features which limit or stop hydraulic lift in very dry soil. In areas with climates which are not too arid to limit hydraulic lift but where periods occur with plant water limitation, hydraulic lift will probably be most important. This also accounts for within a single area but with a large variation in rainfall. For example, in semi-arid regions during wet years hydraulic lift could be more important than during a dry year (see chapter 4; Yoder and Nowak 1999). Perhaps, hydraulic lift only increases plant production during short periods without rainfall in the wet season but not during the prolonged dry season. Also, in normal or above-average rainfall years, hydraulic lift may have positive effects and favor co-existence between grasses and trees. In drought years, however, these beneficial effects would be overwhelmed by the negative effects of interspecific competition. The dynamic oscillation between positive and negative interactions among species is therefore mediated by the interannual variability in the regional climate and rainfall patterns in particular. In the previous paragraph on tree-grass interaction I suggested that positive interactions are more likely to take place in more arid savannas. Concerning hydraulic lift, however, facilitation is more likely to take place in mesic than in arid savannas. So probably facilitation between trees and grasses is most likely to take place at intermediate rainfall. Breman and Kessler (1995) confirm this in their review on tree – understorey interactions in West Africa. Higher productivity under trees compared to open field occurs most often at intermediate rainfall in the southern Sahel and northern Sudan regions. On the other hand, in the more arid northern Sahel and the more mesic southern Sudan region, a reduced productivity under trees is more

common. Also Tielbörger and Kadmon (2000) showed in a very arid desert (mean rainfall = 100 mm/yr) in the middle east that during relatively wet years shrubs facilitate reproduction of annual plants but during dry years shrubs reduce the reproduction of understorey plants. As discussed previously, in an East African savanna, *Acacia* trees had a larger positive effect in a dryer savanna (450 mm/yr) than in a more mesic savanna (750 mm/yr).

Several of the hypotheses postulated above could be tested by studying the effect of hydraulic lift on tree – grass interactions over a rainfall gradient, during different times of the year. Experiments and measurements presented in this thesis focussed on the effect of hydraulic lift during the early dry season. During wet years or in humid savannas this might indeed be the time of year when hydraulic lift is most important. However, during dry years or in more arid regions, short dry periods within the wet season can already cause water stress and maybe then hydraulic lift is important in reducing water limitation for both trees and understorey grasses.

Also some of the hypotheses on regulating the balance between tree-grass water competition and nutrient facilitation can be tested over a rainfall gradient. Two important aspects which influence tree-grass interactions are different in arid and humid savannas. First of all tree density increases with rainfall and secondly the tree root system is relatively smaller in humid than in arid savannas (Breman and Kessler 1995). As stated above, tree density affects to what extent nutrients are concentrated under the tree crown and might also influence the horizontal extent of the tree root system. To prevent overlap of root systems, roots extend less outside canopies in areas with a higher tree density. Also in arid savanna trees are more limited by water than in more humid savannas. This probably results in larger area covered by tree root systems in arid than in humid savannas (Breman and Kessler 1995, Belsky et al. 1989, Mordelet et al. 1997). A smaller rooting area will reduce the capability of the tree to concentrate nutrients under the crown. In more humid savannas also the average rooting depth is smaller and more roots are concentrated in the topsoil (Le Roux et al. 1995). This increases the potential for competition between trees and grasses because also grasses have most of their roots in the topsoil. A lower rooting depth will also limit the potential for hydraulic lift.

The extent of the tree root system is thus really important and future research should focus on what environmental factors regulate both horizontal and vertical root extension. Although there are some good data sets available now on the maximum rooting depth of plants (Canadell et al. 1996), quantitative data sets on the size of tree root systems are still very rare (Jackson et al. 1997, 2000). Research in savannas should thus focus on the size of tree root systems and how this is affected by environmental factors. This should be related to plant water use, especially concentrating on what determines tree-grass competition and if and when hydraulic lift can ameliorate this process.

Long term effect of tree removal on grass production and forage quality: Costs of charcoal production are paid by pastoral communities

African savannas are famous for their herbivore populations, both the size of the populations and diversity are unique in the world (Prins and Olff 1998). The savannas outside protected areas are also used for livestock grazing and form an important source for income for large African communities. As grasses are the main food source of herbivores, both wild and domestic, effects of trees on grass functioning will also affect herbivores. As discussed in the previous paragraphs two processes, tree soil nutrient enrichment and tree – grass water competition are the main factors influencing the effects of savanna trees on understorey grass growth. Interestingly, both these processes have a positive effect on the forage quality of grasses for herbivores. Increased soil fertility usually results in higher grass nutrient concentrations and especially a higher nitrogen content has a positive effect on the feeding value of the grasses. Also a lower water availability can have a positive effect on forage quality of grasses. Reduced soil moisture availability will reduce grass growth and with equal soil nutrient concentrations this will result in higher grass nutrient concentrations (chapter 6; Breman & De Wit 1983).

If trees have such a positive effect on forage quality why is bush encroachment such a problem, especially on commercial rangelands (Scholes and Archer 1997)? Probably, two aspects cause these problems. First of all, a high tree density is more likely to suppress grass production than a few isolated trees and if production becomes too low, increased forage quality cannot compensate anymore for reduced grass productivity. Secondly, bush encroachment is often caused by a large and rapid increase in small trees. Small trees have few effects on increased nutrient availability and thus grass nutrient concentrations. Also under bushes grasses are replaced by herbs, probably due too shade. In chapter 2, I showed that small *Acacia* only slightly increase grass nitrogen concentration and that herbs cover a much larger part of the vegetation under bushes than in open grassland and under large trees. Small trees, especially those with spines and thorns can also cause a physical barrier preventing grazing. This explains why especially an increase of small trees or bushes, which is the case with bush encroachment, reduces food availability for herbivores.

These negative effects of bush encroachment should not be confused with the positive effects that large trees can have on food availability and quality (chapter 6). The removal of large trees can definitely reduce forage quality. The problem however is that this effect only becomes clear after at least 10 years (Figure. 7.5). Initially after trees die, grass production is increased. The results from chapter 2 showed that grass production is higher around dead trees than in open grassland and under large trees. Grass nutrient concentration and digestibility of organic matter are only slightly lower under dead than under large trees (unpublished data; Table 2.4) but the forage quality is still much higher than in open grassland. However after about 10 years *Cynodon* species favored by herbivores disappear around dead trees and the vegetation becomes as it is in open grassland with species as *Heteropogon contortis* and *Sehima nevervosum*. These species have a low leaf/stem ratio and low nutrient concentrations, indicating a low forage quality.

In general, *Acacia tortilis* seeds do not germinate under tree canopies (Loth 1999) so after trees have died or been removed many new seeds can germinate and a new generation of young *Acacia* bushes can establish. These small *Acacia tortilis* trees first repress grass growth. At the end of the growing season grass biomass under

bushes was only 330 g/m^2 compared to more than 500 g/m^2 under large trees and in open grassland (Figure 2.5). Compared to open grassland, bushes already increase protein concentrations of grasses but this increase in forage quality might not be enough to compensate for the reduced grass availability. Under small trees of about 25 years age the grass biomass at the end of the wet season is already about 400 g/m^2. Also once the tree crowns covers at least 50 m^2, *Cynodon* grasses invade the vegetation and these grass species have a relatively high forage quality (see chapter 6). However it will probably take more than 50 years before an *Acacia tortilis* tree reaches its maximum positive effect on the grass vegetation.

The main problem, however, is not that it takes more than 50 years before *Acacia* trees reach their maximum positive potential but that before trees have a positive effect on forage quality at a younger stage they reduce grass growth! Two observations in the first period after tree removal suggest that trees negatively affect grass production. First, grass biomass increases after trees are removed. Secondly, after about 10 years when the 'positive' effect of dead trees has disappeared, bushes start to repress grass productivity. This gives the impression that trees only repress grass productivity and a common reaction to this is bush clearing. However by removing all young trees, a situation in which trees can have a substantial positive effect will never be reached.

In Africa, trees are usually chopped down for charcoal production. Due to a sharply increasing human population, the demand for firewood and charcoal is rising especially around the larger cities. Charcoal is produced largely for use in urban areas but the cost of tree removal, reduced livestock food availability and quality, is paid by pastoral communities. Most of the areas where trees are chopped down are communal lands and controlling tree harvesting in these areas is extremely difficult. There are short term personal benefits but the long term cost is paid by the whole (pastoral) community.

Until now the positive effects that trees can have on forage quality have been largely neglected. If only the effect of trees on grass biomass production is analyzed, potential positive effects of trees could be missed. Even if trees reduce grass production, a change in understorey species composition or increase in plant nutrient concentration can positively affect wildlife and livestock populations. For example fast growing grasses in open grassland patches could be favorable for grazers in the early wet season but in the dry season when overall grass quality reduces (Prins 1996, Voeten and Prins 1999) food of relatively high quality but low productivity from under trees could be favored by herbivores. Also perennial grasses prefer habitats under trees while open grassland tends to be more dominated by annuals (Scholes and Archer 1997). A more species diverse grassland will increase the sustainability in semi-arid areas where rainfall is very variable. In a similar way trees can contribute to the herbivore species diversity. Larger herbivores prefer larger patches of a higher productivity, while small animals can select for smaller patches and need food of a higher quality. Savannas are creating these small patches with a superior food quality. For example impalas can be seen selecting food from under trees even if the remaining biomass is very small, while elephants will consume almost all the available grass (pers. obs.).

So a new line of future research should be the integration of studies on plant-animal with those on tree-grass interactions. Because trees have a multitude of positive and negative effects on grass productivity they also affect food availability

for herbivores. However the effect of savanna trees on herbivores is even more complicated because trees also affect the forage quality, either by changing the species composition or increasing the nutrient concentration of the same grass species (see Table 6.3). These effects of trees should be studied under trees of different age classes, under different climatic conditions and under different tree densities. These results can be used to formulate an optimal tree density. As argued above a very high tree density will probably suppress grass production while a low density can positively affect grass productivity and forage quality. So tree thinning might be useful under high tree density while under low tree density a stimulation a tree growth might be the best option!
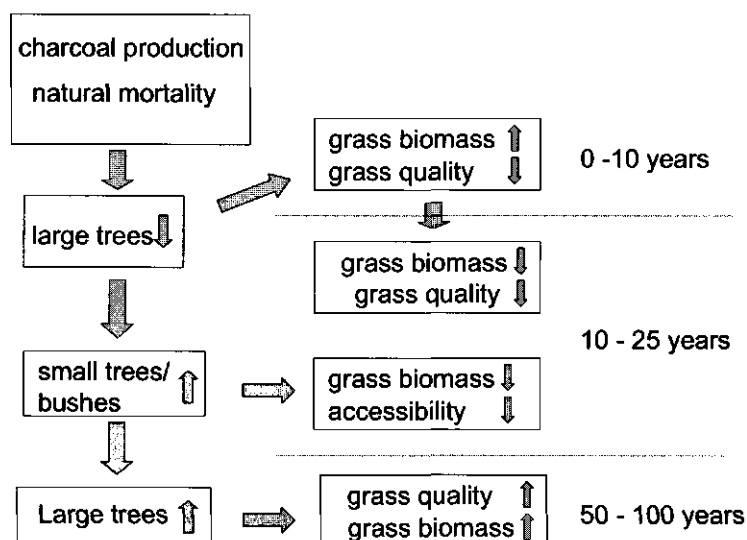
Figure 7.5. Conceptual model showing the long term effects of tree removal or mortality on grass biomass production and quality. When large density is reduced due to natural mortality or charcoal production first the amount of grass biomass increases and forage quality slightly decreases. In the next 10 years grass biomass reduces again and forage quality becomes even lower. After large trees have disappeared new tree seedling will establish. These small trees initially suppress grass growth and accessibility. When these small trees become larger grass biomass and forage quality will increase again.

Conclusions

The main goal of the research presented is this thesis was to study what determines whether trees interfere or facilitate understorey grass productivity and how hydraulic lift affects tree-grass interactions. The main conclusions are that there is not a single process determining the interaction between trees and grasses but that it is a balance between positive and negative effects. Trees facilitate understorey grass production through increased nutrient availability but at the same time interfere with grass productivity through belowground competition for water. The increased nutrient availability under trees changes the nutrient limitation of the herbaceous layer from nitrogen limited in open grassland to phosphorus limitation under the tree canopy. Exuding large amounts of water into the topsoil by large trees through hydraulic lift could not compensate for water competition between trees and grasses. However grasses probably have access to hydraulically lifted water which indicates that hydraulic lift reduces the severity of water competition between trees and grasses.

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Chapter 8

Samenvatting

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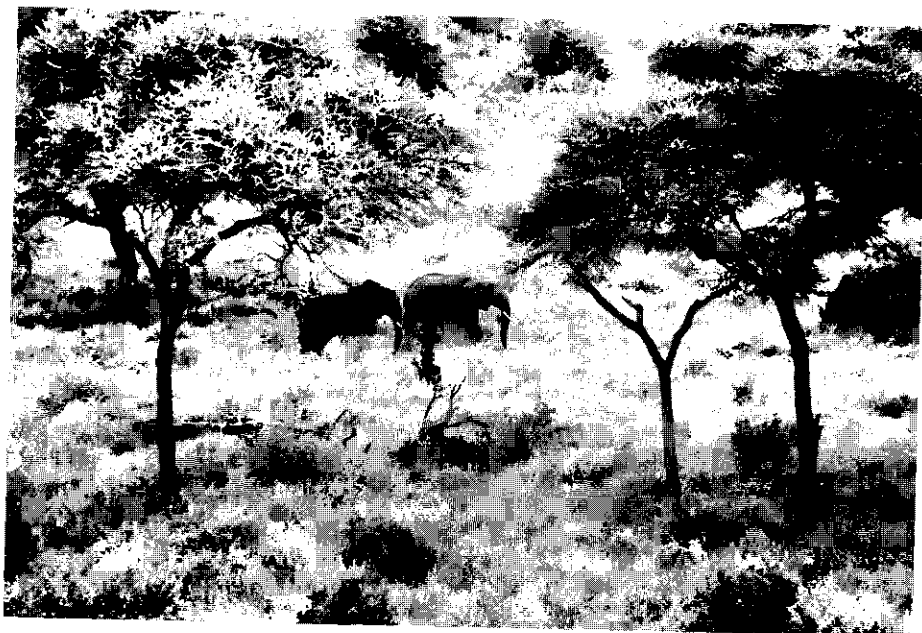
Boom-gras interacties op een Oost Afrikaanse savanne: het effect van concurrentie, facilitatie en hydraulic lift.

Inleiding

Op savannes komen voornamelijk twee verschillende type planten voor: kort levende grassen en relatief lang levende bomen. Meestal is de gehele onderlaag van de vegetatie in savannes bedekt met grassen met daar tussen in weidverspreid de bomen. Savannes in Afrika zijn beroemd om de grote kuddes zebra's, gnoe's en buffels die er voorkomen. Deze herbivoren eten voornamelijk gras. Bomen hebben echter een grote invloed op zowel de productie als de voedselkwaliteit van deze grassen. Bomen kunnen de groei van het gras remmen door concurrentie om water, licht en nutriënten, maar ze kunnen de productie van grassen ook bevorderen door bv. een verhoogde bodemvruchtbaarheid en schaduw. Ook kunnen bomen de beschikbaarheid van water voor de grassen verhogen door middel van hydraulic lift.

Hydraulic lift is het proces waarbij door boomwortels water wordt getransporteerd van natte naar droge bodemlagen (Figuur 1.1). Dit watertransport d.m.v. hydraulic lift vindt vooral 's nachts plaats als de huidmondjes dicht zijn en de bladeren van de boom geen water verdampen. 's Nachts gaat de boom door met het opnemen van water met zijn diepe wortels. Dit water wordt getransporteerd naar de ondiepe wortels in de droge bovenste bodemlagen en deze wortels stoten het water uit in de bodem. Het water wat 's nachts opgeslagen wordt in de bovenste bodemlagen kan de volgende dag weer worden opgenomen door de boom en eventueel ook door de grassen die onder de boom groeien.

Het onderzoek voor dit proefschrift is uitgevoerd in de savannes van Tarangire Nationaal Park in Noord Tanzania (Figuur 1.2). Tarangire NP maakt deel uit van het Masaai ecosysteem en de Tarangire rivier die midden door het park stroomt is de enige permanente waterbron in een gebied dat ongeveer even groot is als Nederland. In het Masaai ecosysteem leven grote kuddes migrerende zebra's, gnoe's en buffels. In het regenseizoen grazen de dieren buiten het park, vnl. op de Masaai steppe en in de droge tijd trekken de dieren terug het park in om te drinken uit de Tarangire rivier. Naast grote kuddes zebra's en gnoe's is Tarangire ook beroemd om de grote groepen olifanten die er leven.

Op de savannes van Tarangire NP in Tanzania heb ik onderzocht hoe bomen de groei van het gras en soortensamenstelling van de graslaag beïnvloeden en welke processen bepalen of bomen een positief of negatief effect hebben op de grasproductie. Daarnaast is bestudeerd of en hoe de bomen de voedselkwaliteit van het gras voor herbivoren beïnvloeden. Er is onderzocht of dieren beter gras van onder de boom kunnen eten dan uit het open veld. Als modelboom voor deze studie is gekozen voor de *Acacia tortilis,* de paraplu doornboom. Dit is de meest voorkomende boomsoort in Tarangire NP en vele andere savannes van Oost Afrika. Ik heb bestudeerd hoe deze Acacia's de beschikbaarheid van licht, water en nutriënten voor grassen beïnvloeden. Verder is onderzocht of en wanneer hydraulic lift plaatsvindt in Acacia's en of het water dat door de bomen omhoog gepompt wordt ook door grassen kan worden opgenomen. Met verschillende experimenten is verder bestudeerd hoe schaduw, nutriëntenbeschikbaarheid en ondergrondse concurrentie om water tussen grassen en bomen de productie van grassen beïnvloedt.

Het effect van bomen op nutriënten-, licht- en waterbeschikbaarheid

Uit chemische analyses van bodemmonsters blijkt dat onder bomen meer nutriënten beschikbaar zijn voor grassen dan in het open grasland. De hoeveelheid nutriënten in de bodem neemt toe naarmate de boom ouder wordt en concentraties zijn het hoogst in de bodem vlak bij bomen die net dood zijn gegaan (Figuur 2.3). Ook ongeveer 10m buiten de kroon van Acacia's zijn de concentraties aan nutriënten in de bodem hoger dan in het open veld. De belangrijkste nutriënten die een plant nodig heeft zijn stikstof en fosfor. Deze twee nutriënten werden experimenteel toegevoegd aan grassen die onder en buiten bomen groeien. Een deel van de plots kreeg alleen stikstof en een ander deel alleen fosfor toegediend en een derde groep plots kreeg beide nutriënten toegediend. Onder de boom was er een hogere grasproductie als er fosfor werd toegediend en buiten de boom als er stikstof werd toegevoegd (Figuur 3.2). Buiten de boom is stikstof dus het nutriënt dat beperkend is voor de grasproductie. De Acacia's voegen echter zoveel extra stikstof toe aan de bodem dat groei van het gras onder de boom niet meer door stikstof, maar door fosfor gelimiteerd wordt (Figuur 3.2).

Grote Acacia's houden ongeveer 50% van het licht tegen (Figuur 2.4). Schaduw kan de grasgroei remmen doordat de grassen minder licht krijgen, maar de lagere temperatuur in de schaduw kan er ook voor zorgen dat de grassen minder water gebruiken. Dit verminderde waterverbruik zou een positief effect kunnen hebben op de productie van grassen. Een experiment met kunstmatig schaduw, d.m.v. doeken, toont aan dat in het regen seizoen 55% schaduw de grasproductie vermindert, maar in de droge tijd heeft schaduw een positief effect op de grasgroei (Figuur 3.1). De totale jaarlijkse grasproductie is echter bijna gelijk in de schaduw als in vol zonlicht.

In droge gebieden zoals de savannes in Afrika is water vaak de beperkende factor voor de groei van planten. Door het gehalte aan water in de bodem te meten is aangetoond dat bomen een negatief effect hadden op de hoeveelheid water die beschikbaar is voor grassen. Het watergehalte in de bodem was namelijk lager onder dan buiten de boom (Figuur 2.1). Grassen die onder bomen groeien hebben dus minder water, maar meer nutriënten tot hun beschikking. Deze verschillende groeiomstandigheden hebben tot gevolg dat onder bomen andere soorten grassen en kruiden groeien dan in het open grasland. Ook de grootte van de bomen heeft invloed op de soortensamenstelling (tabel 2.6). Onder struiken komen bijvoorbeeld veel meer kruiden voor dan onder grote bomen. Verschillen in de soortensamenstelling van de graslaag onder de bomen en in het open veld leidde niet tot een verschil in de totale grasproductie. Biomassa van het gras was zowel gedurende het droge als het natte seizoen ongeveer gelijk onder de boom als in het open veld (Figuur 3.1). Onder de dode bomen was de biomassa van het gras echter 60% hoger dan onder levende bomen of in het open veld (Figuur 2.5). De grasproductie was hoger onder dode bomen omdat daar meer nutriënten in de bodem aanwezig zijn. Ook onder levende bomen zijn veel nutriënten beschikbaar, maar daar wordt de grasgroei geremd door concurrentie om water. Als de boom dood gaat verdwijnt de concurrentie en kunnen de grassen optimaal profiteren van een verhoogde nutriëntenbeschikbaarheid.

Hydraulic lift in Acacia's

Hydraulic lift in Acacia's werd bestudeerd d.m.v. continue bodem-waterpotentiaal metingen. De bodemwaterpotentiaal is een goede indicatie voor de

hoeveelheid water die in de bodem beschikbaar is voor planten. Deze metingen werden gecombineerd met bepalingen van stabiele isotopen in regen-, plant- en bodem-water. In het droge seizoen van 1998, na een relatief nat regenseizoen waren er duidelijke aanwijzingen voor hydraulic lift in Acacia's. 's Nachts nam het vochtgehalte toe in de bodem onder de boom waarna het de volgende dag weer afnam (Figuur 4.1 & 4.2). Deze dagelijkse fluctuaties werden waargenomen tot 10m vanaf de stam. Eén grote Acacia stoot dus water uit over een oppervlakte van meer dan 300 m^2. En met behulp van de grootte van de fluctuaties is uitgerekend dat één boom per nacht 70 tot 235 liter water per nacht omhoog kan pompen. Twee jaar later in 2000 tijdens het droge seizoen na een regentijd met heel weinig neerslag vonden we bijna geen hydraulic lift in de Acacia's (Figuur 4.5). Dit toont aan dat hydraulic lift tijdens zeer droge perioden niet voorkomt.

Door metingen aan stabiele zuurstofisotopen kon onderscheid gemaakt worden tussen regen en grondwater. Uit deze bepalingen van stabiele isotopen blijkt dat grassen die onder de boom groeien grondwater op kunnen nemen dat door de boom omhoog gepompt wordt, terwijl grassen die buiten de boom groeien vooral water uit de bovenste bodemlaag opnemen (Figuur 4.7).

Door middel van een trenching experiment hebben we getest of grassen sneller groeien omdat bomen water omhoog pompen d.m.v. hydraulic lift. Rond plots werden geulen gegraven (trenches) en alle boomwortels werden doorgehakt zodat de wortels geen invloed meer hebben op de grasgroei. In tegenstelling tot wat verwacht werd was het watergehalte in de bodem van getrenchte plots hoger dan in controle plots (Figuur 5.1). Acacia's nemen dus meer water op uit de bovenste bodemlaag dan ze uitstoten d.m.v. hydraulic lift. De grasproductie was ook hoger in getrenchte plots (Figuur 5.2) wat aantoont dat concurrentie om water tussen grassen en bomen belangrijker is dan facilitatie d.m.v. hydraulic lift. Hydraulic lift vermindert echter wel de concurrentie om water tussen bomen en grassen. Zonder hydraulic lift zou er nog meer concurrentie om water zijn en zouden de grassen waarschijnlijk nog langzamer groeien.

Interacties tussen bomen en grassen worden dus voornamelijk gestuurd door twee processen, concurrentie om water en een verhoogde nutriëntenbeschikbaarheid (Figuur 7.1 & 7.2). De hogere concentraties aan nutriënten in de bodem onder de boom zorgen ervoor dat de grasgroei door bomen gestimuleerd wordt, terwijl de concurrentie om water de grasgroei remt. De balans tussen groeistimulerende en remmende processen zorgt ervoor dat de grasproductie onder bomen en in het open veld ongeveer gelijk is.

Boomkap vormt een bedreiging voor de voedselvoorziening van het wild

Acacia's hebben dus geen positief effect op de grasproductie, maar de voedselkwaliteit van het gras is wel veel hoger onder de boom dan er buiten. Grassen die onder bomen groeien hebben relatief meer groen blad, een hoger eiwitgehalte en zijn beter verteerbaar in vergelijking met grassen die in het open veld groeien (Figuur 6.1). Grassen die net buiten de kroon van grote Acacia's groeien zijn van een slechtere kwaliteit dan grassen die onder bomen groeien, maar zijn beter dan grassen uit het open veld. Om aan hun dagelijkse voedselbehoefte te voldoen hoeven herbivoren dus minder gras te eten van onder bomen dan wanneer ze alleen maar gras zouden eten uit het open veld. De belangrijkste herbivoor in Tarangire is de gnoe, een

herkauwer. De hoeveelheid voedsel die herkauwers per dag kunnen eten wordt beperkt door de snelheid waarmee ze hun voedsel verteren. Hoe hoger het vezelgehalte van de grassen, hoe langzamer de vertering, des te minder de gnoe's kunnen eten. Het vezelgehalte van grassen uit het open veld is zo hoog dat gnoe's van dit gras maar 3800 gram kunnen eten. Het eiwitgehalte van deze grassen is echter zo laag dat 3800 gram niet genoeg is om aan de dagelijkse behoefte aan eiwitten te voldoen. Gnoe's kunnen dus niet overleven door alleen maar te grazen in het open veld. Het gras van onder de bomen is daarentegen van zo'n hoge kwaliteit dat gnoe's maar 10% van hun voedsel hoeven te halen uit grassen van onder bomen om te kunnen overleven (Figuur 6.3). Grote bomen zijn dus essentieel voor de herbivoren om te overleven, maar een relatief klein aantal bomen (10% bedekking) is al genoeg om ervoor te zorgen dat herbivoren al het gras optimaal kunnen benutten.

In de afgelopen 25 jaar is het aantal grote Acacia's in Tarangire NP drastisch afgenomen. In 1973 bedekte grote bomen nog ongeveer 16% van de savannes in het park, in 1996 was dit nog maar 4% (Figuur 6.2). De gevolgen hiervan zijn dat er veel minder hoog-kwalitatief voedsel beschikbaar is voor herbivoren. Herbivoren worden hierdoor gedwongen een grote hoeveelheid laag-kwalitatief gras te eten wat tot een verslechterde conditie van het wild kan leiden. De afname in het aantal grote bomen heeft dan ook waarschijnlijk geleid tot een afname in het aantal dieren dat in Tarangire NP kan leven. Buiten het park is de situatie nog zorgelijker want daar zijn bijna alle grote Acacia's omgehakt voor de productie van houtskool en is de hoeveelheid aan hoog-kwalitatief gras dus nog lager. Dit heeft tot gevolg dat op de savanne buiten het park minder vee kan grazen, wat kan leiden tot een grotere armoede onder de lokale bevolking.

Grote bomen zijn dus essentieel voor het functioneren van savanne-ecosystemen omdat grote bomen een positief effect hebben op de kwaliteit van de grassen. Deze hogere voedselkwaliteit leidt tot een betere conditie van zowel het wild als het vee. Na het wegkappen van de bomen verdwijnen de positieve effecten op de graskwaliteit echter niet meteen. Over een periode van 10 jaar gaat de kwaliteit van de grassen langzaam achteruit. De desastreuze effecten van de boomkap worden dus niet meteen opgemerkt. In eerste instantie heeft het weghalen van bomen zelfs een positief effect op de hoeveelheid gras. Rond dode bomen groeit namelijk meer gras dan onder levende bomen. De eerste indruk na het kappen van de boom is dus dat het weghalen van bomen voordelig is voor begrazing omdat er meer gras komt. Een ander probleem is dat jonge boompjes een negatief effect hebben op de hoeveelheid aanwezig gras. Onder jonge bomen groeien namelijk relatief meer kruiden en minder grassen. Deze jonge boompjes worden dan ook vaak verwijderd om de grasgroei te bevorderen. Dit heeft tijdelijk een positief effect, maar als alle jonge bomen weggehaald worden zullen er nooit volwassen grote bomen komen die de voedselkwaliteit van het gras verhogen. Op korte termijn lijkt het er voor de lokale bevolking op dat bomen een negatief effect hebben op de beschikbare hoeveelheid gras. Maar op lange termijn hebben grote bomen een positieve invloed op de voedselkwaliteit van grassen. Het behoud van deze bomen is dan ook essentieel in het beheer van Afrikaanse savannes.

Summary

The Earth's savanna ecosystems are associated with seasonally dry or semi-arid climatic zones and are characterised by broadly spaced trees and shrubs within a continuous grass layer. Savanna trees have a wide range of positive and negative effects on the growth of understorey grasses. Trees reduce grass growth through belowground competition for water and nutrients. However trees can also increase grass production through increased nutrient availability and hydraulic lift. Shade can potentially increase grass growth through reduced temperatures which can increase water use efficiency of the understorey plants but reduced radiation due to shade can also limit grass productivity. As a result of these facilitative and interfering effects of trees on the understorey vegetation, grass production can both be higher and lower under savanna trees.

In an East African savanna in Tarangire National Park I studied what determines whether trees facilitate or interfere with grass growth and how interactions between trees and grasses affect forage availability and quality for large herbivores. Therefore, the effect of savanna trees on soil nutrient, water and light availability was studied and how changes in resource availability affect understorey species composition and plant production. I especially focussed on the effect of hydraulic lift in *Acacia tortilis* trees on tree - grass interactions. Hydraulic lift is the process of water movement from relatively wet to dry soil layers through plant roots. This transport takes place most commonly during the night when the leaf stomata are closed and the major water potential gradient is between the deep (wet) roots and the drier surface roots in the top soil. With different experiments I studied the effect of shade, nutrient addition, hydraulic lift and belowground competition on grass productivity under and outside canopies of *Acacia tortilis* trees.

Availability and concentrations of all major nutrient were higher under *Acacia tortilis* trees than in open grassland. Soil nutrient concentrations increased with tree age and size and were highest around dead trees. Also just outside tree canopies nutrient availability was still higher than in open grassland patches. A nutrient addition experiment showed that large *Acacia* trees supply such an extra amount of nitrogen that understorey grass production becomes limited by phosphorus. Outside trees grass production is limited by nitrogen. Large *Acacia tortilis* trees reduced light availability of understorey by about 50% and an experiment with artificial shade cloth showed that a 55% reduction of light reduces grass productivity during the wet season. However, during the dry season grass productivity is increased due to shade. As a result, three months into the dry season aboveground grass biomass is equal under shade and in full sunlight.

Soil water content and soil water potential were both lower under than outside canopies of *Acacia tortilis* trees, indicating that grasses growing under trees had less water available than grass growing in open grassland. These differences in resource availability resulted in a different species composition of the herbaceous layer under *Acacia* trees compared to open grassland. Also the vegetation under bushes of *Acacia tortilis* was different from both open grassland and the understorey of large trees. The main factor causing differences in species composition is probably nutrient availability because species compositions were similar under situations of equal soil nutrient concentrations even when light and water availability were different. Changes in species composition did not result in differences in above ground biomass, which was remarkably similar under different sized trees and in open grassland. The only exception was around dead trees where herbaceous plant production was 60% higher than under living trees. This shows that trees facilitate grass

production through increased nutrient availability but reduce grass growth through competition for water.

Although grass production was not increased under trees, they had a very positive effect on the overall forage-quality of grasses. Grasses growing under trees had a higher proportion of live leaves, a higher nutrient and protein concentration and a higher digestible organic matter content compared to grasses from open grassland. With a linear model I predicted that wildebeest, the most abundant herbivore in the park, can meet all their energy, nutrient and protein requirements to maintain a stable body weight by selecting forage from under tree canopies only. However wildebeest cannot cover their daily requirements by only selecting grass from open grassland. When forage from open grassland is combined with at least 11% of grass intake from under tree canopies, wildebeest can obtain a diet which meets all maintenance requirements. This shows that forage from under trees is essential for wildebeest but that a relatively low tree cover is sufficient. A decrease in the number of trees in Tarangire NP during the last 25 years has caused a reduction in the availability of high quality forage has which has probably affected the dry season survival of large herbivores.

With a combination of soil water potential measurements and stable isotopes in soil, rain, plants and groundwater I tested if and when hydraulic lift occurs in large *Acacia tortilis* trees. In the dry season of 1998, after a relatively wet rainy season, I observed distinct diel fluctuation in soil water potential, with increasing values during the night and decreasing again the following day. These fluctuations in soil water potential indicating hydraulic lift were found up to 10 m from the tree. This indicated that mature *Acacia* trees can lift water over an area of more than 300 m^2 and it was estimated that each tree can lift between 70 and 235 litres of water each night. Two years later, in 2000, during a drought there was little evidence of hydraulic lift.

The contrasting findings I observed where hydraulic lift occurred in wetter years and did not in drier years was consistent with $\delta^{18}O$ values in soil, rain, and groundwater. The $\delta^{18}O$ of water extracted from the xylem showed that only grasses growing near trees they had values similar to the groundwater. This could be because grasses near trees use either water from deeper soil layers or hydraulically lifter water provided by the tree. Grasses growing outside of the tree canopies probably used water from the topsoil.

With a trenching experiment we tested whether the observed hydraulic lift under *Acacia* trees facilitates the growth of understorey grasses. However, severing tree roots to remove the positive effects of hydraulic lift on soil moisture content had the opposite effect from what we expected; soil water content was higher in the trenched plots relative to the controls. This demonstrated that trees take up more water from the topsoil than they loose. The higher soil moisture availability in trenched plots resulted in an increased grass biomass production relative to the un-trenched control plots indicating that trees and grasses were competing for water in the topsoil.

However, stable isotope analysis of plant and source waters in the un-trenched control plots showed that grasses which compete with trees use a greater proportion of deep water compared with grasses in trenched plots. This indicates that grasses probably use hydraulically lifted water provided by *Acacia* trees although it is also possible that grasses take up deep soil water directly by growing deeper roots when competition with trees occurs. This shows that positive effects of hydraulic lift for neighbouring species may be limited in this savanna system because they are overwhelmed by water competition.

The results of different experiments and observations show that the interactions between trees and grasses in this East African savanna are not controlled by a single

mechanism but that there is subtle balance between competitive and facilitative processes. Trees facilitate understorey grass growth through increased nutrient availability and trees interfere with grass growth through belowground competition for water. Although large *Acacia* trees exude large amount of water into the topsoil through hydraulic lift, competition for water is more important. However hydraulic lift probably reduces the severity of competition for water between trees and grasses.

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Ilja, you have always told what not to write to you in my acknowledgements but I will end with you anyway. Thank you very much for sharing all the good and bad times wherever we were in the world. Whether it is was drinking beer at the lodge at the end of a sunny day and seeing a giraffe being killed or being chased by elephants during your first day in the park. Whether it was a rainy cold day in Arusha or a sunny day at the beach in Zanzibar or sharing a small room in Utrecht or painting our new house it was always great to be with you. What I appreciate about you most is that although you have difficulties with taking small steps you were never afraid to the take the big steps in life with me. Thanks for everything.

Fulco Ludwig, November 2001

Curriculum Vitae

Fulco Ludwig was born on August 25, 1972. In 1990, he finished his Atheneum B degree (A-levels equivalent) at Fioretticollege in Lisse. Thereafter he moved to the USA to live in Dothan, AL for one year were he obtained his American High School diploma. In 1991 he started his Biology degree at Utrecht University and in 1996 he graduated with an M.Sc. in Environmental Biology.

He did his first M.Sc. did a project with Prof. Dr. Rien Aerts of the Landscape Ecology group at Utrecht University. He studied the effect of water table changes on the emission of greenhouse gases from Dutch wetlands. Thereafter, he went to South Africa to study the long term effects of global change on natural grasslands. Under the supervision of Prof. Dr. Willy Stock (Department of Botany, University of Cape Town) and Prof. Dr. Hans Lambers (Ecophysiology group, Utrecht University) he studied vegetation changes, nutrient cycling and photosynthesis around a natural CO_2 spring.

In 1997, he started to work as a researcher at the sub-department of Nature Conservation of Wageningen University to work on a Ph.D. project under supervision of Prof. Dr. Hans de Kroon, Prof. Dr. Herbert Prins, and Prof. Dr. Frank Berendse. From 1998 until 2000 he lived in Tanzania to do fieldwork in Tarangire National Park. Here he studied the interactions between trees and grasses in semi-arid savannas. He especially focused on the effects of hydraulic lift on the functioning of savanna ecosystems and the importance of trees for herbivore forage quality. At the end of 2000, he worked for two months as a visiting scientist at the lab of the Prof. Todd E. Dawson of the Department of Integrative Biology, University of California, Berkeley. Here, he analyzed samples collected in Tanzania at the Center of Stable Isotope Biogeochemistry.
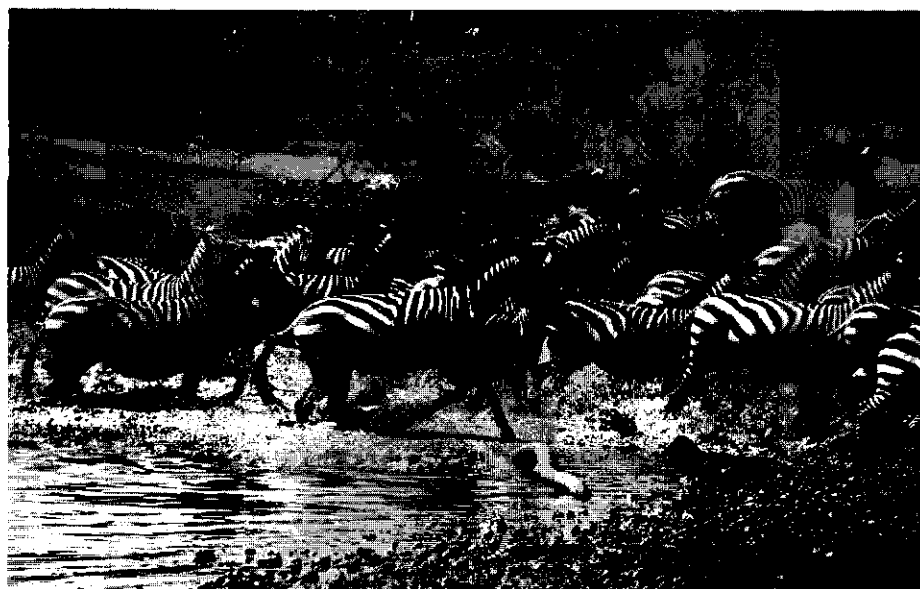
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