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PATTERNS AND DYNAMICS OF SECONDARY *ACACIA ZANZIBARICA* WOODLANDS AT MKWAJA RANCH, TANZANIA

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Summary

In recent decades African savannas have been increasingly used for large-scale private cattle ranching; the success of ranching enterprises has, however, often been limited by problems of bush encroachment. There are various reasons for woody encroachment in savanna rangelands. Livestock reduces the vigour of grasses while promoting seed germination, establishment and survival of woody species. Lower grass biomass diminishes the frequency and intensity of fires, which also favours the woody component. Finally, domestic livestock tend to be predominantly grazers but they displace a range of native browsers that control tree seedlings effectively or keep small trees in the fire flame zone. Various studies have documented the causes of bush encroachment under ranching in Africa and elsewhere; almost none, however, have investigated the changes in vegetation dynamics in secondary bushlands or woodlands after the abandonment of ranching. This study investigates aspects of bush encroachment on a former cattle ranch (Mkwaja Ranch) in a savanna ecosystem on the Tanzanian coast. The ranch was in operation for 46 years (until August 2000) and now forms part of the newly created Saadani National Park (gazetted in October 2003). The main focus of the work described here concerns the patterns, dynamics and changes of secondary *Acacia zanzibarica* woodlands after cattle grazing has ceased.

In a first study at landscape scale we described the main vegetation types of the area of Mkwaja Ranch and former Saadani Game Reserve and related their patterns of distribution to the former use of the ranch for cattle. Following field surveys in late 2001, 15 distinct types of grassland and bush vegetation were defined and a vegetation map was created using a Landsat TM satellite image of 1994. Two main spatial trends were detected in the vegetation. One was a large-scale decrease in the cover of bushland from the most intensively used parts of the ranch through more extensively used areas to the game reserve; this trend was attributed to differences in management history as well as to climatic and topographic factors. A second trend was a radial vegetation pattern associated

with the enclosures where cattle were herded at night (paddocks). High amounts of three bushland (respectively woodland) types [dominated by (i) *Acacia zanzibarica*, (ii) *Dichrostachys cinerea*, *Acacia nilotica* or *Acacia mellifera* and (iii) *Terminalia spinosa*] occurred in a zone between 300 and 2500 m from the paddocks, with a peak in bush density at about 900 m (mean value for 18 paddocks). There was also a radial trend in the grassland communities: close to the paddocks there was short grass vegetation containing many ruderals, while the tall grassland types occurred further away in the areas less affected by cattle.

Subsequent work focussed on the structure and dynamics of *Acacia zanzibarica* woodlands in an area intensively used by cattle until 2000. In two survey studies we described vegetation structure and biomass, ecological processes and tree demography along a gradient from open savanna to dense woodland at three different sampling dates. We established and surveyed 97 circular study plots on which we sampled or estimated various parameters of soil characteristics, grass biomass, *A. zanzibarica* tree stands and recruitment. By multiple regression techniques we analysed the trends and interrelationships between different parameters along the tree density gradient. In the third study we experimentally investigated how the creation of woodland gaps affects environmental conditions, vegetation development and tree regeneration. In each of four study areas, twelve plots were selected and assigned to three treatments: control plots (NN), plots where all trees were felled by chain saw (FN), and cut plots where tree stumps were poisoned (FP). At three sampling dates the same parameters were assessed as in the two other studies. Additionally, in June 2002 transpiration rates of acacia and grass leaves were measured in a cut plot and in a control plot. In February 2003, temperatures of fire were measured at two sites, and the effects of fire on acacia seeds were assessed.

The first survey study showed that tree density reflected an underlying soil texture gradient, with few trees on more sandy soils and closed woodland mostly on loamy-clayey soils. Levels of soil organic matter and phosphorus increased along this gradient, and nitrogen levels were highest in dense tree stands.

Spinescence of branches was highest on trees in open savanna, while the abundance of pseudogalls and ant nests only increased with increasing tree size. Ant nest counts and tree living wood ratio (~ tree vigour) best explained foliage flush during the two wet seasons. During the dry season, competition with the grass layer and other trees in dense stands had a higher influence on tree foliage. The grass layer was strongly influenced by fire; live biomass also decreased with increasing tree density. Although the leaf area index (LAI) of the tree layer was on average about half that of the grass layer, the overall transpiration rates were estimated to increase with increasing tree density.

The data on tree size distribution suggested that stands were not even-aged but that there had been several phases of tree establishment during the last 20 years. There was little evidence of self thinning due to competition, and the main cause of tree death during the study period was probably fire. Some trees, especially those of low vigour (as measured by the living wood ratio) were probably directly killed by fire. However, our results suggest that most tree mortality was caused only indirectly by the fire, and resulted mainly from water stress on clayey soils where water probably did not percolate beyond the grass rooting zone during the subsequent wet season with below-average rainfall. A hypothetical model of the impact of fire on tree stands is presented and explained.

Flowering and pod production were highly correlated with tree size. In contrast to flowering, pod production decreased in dense stands, indicating intra-specific competition for resources. Seed production of about 7.4 m^{-2} was very low compared to other woodlands with invasive leguminous trees. Seedling density was significantly related to soil and grass layer variables but not to seed rain. No seedlings survived until the late dry season, probably because of drought. Half of the trees 'killed' by fire (i.e. topkill) responded by producing coppice shoots from the stem base.

The experimental study showed that grass growth during the wet seasons was significantly higher in cut plots than in the control plots, but until the dry season there were no longer significant differences of grass biomass between treatments. Grazing by wild animals was minor, but significantly higher on cut plots than on controls. Soil water content measured 14 days after rainfall was higher on cut plots compared to controls. This difference was apparently due to maybe three times higher rates of transpiration by *A. zanzibarica* trees than by grasses, as indicated by the porometer study. Seedling establishment and persistence were significantly higher on cut plots than on controls. Seedling establishment was also influenced by fires; seeds were scarified by low intensity fires but killed in hot fires. The seedbank appeared to be transient. No seedlings were found in the late dry season, confirming other observations that there is presently no successful recruitment. There was also little evidence of successful vegetative propagation. On FN plots 68 % of stumps had coppice shoots three months after felling of which only 28 % were still alive at the end of the study. There was no increase in shoot lengths during the study period, suggesting that the shoots were unable to escape above the grass layer. The density of root suckers varied among sites, but was not affected by the cutting treatments or by fire.

We conclude that, although bush encroachment had a significant impact on grazing resources for cattle and native wildlife, soil factors and fire are more important determinants of the structure of savanna in the long term. Dieback of *A. zanzibarica* occurred even in the absence of large, destructive herbivores such as elephant; tree recruitment was not successful under the prevailing conditions, with very low mammalian herbivory and regular fires. Hence, the woodland will probably revert naturally to predominantly grassland vegetation within the next 10-20 years. However, savanna regeneration can also be promoted by wood cutting which does not disturb the soil and affect tree roots (probably leading to increased root suckering). *A. zanzibarica* woodlands may, therefore, be seen as a transitional state or as the extreme end of bush density in a still resilient humid savanna. However, if there are future changes in the numbers of large herbivores or the frequency of fires, the balance between grass and tree components could change again. With regard to former ranching practices, we conclude that the problem of bush encroachment does not inevitably make ranching impossible. We conclude that it should be possible to develop a long-term rotation system that is both profitable and sustainable.

Acacia zanzibarica is distinguished by its association with symbiotic ants from other African species of *Acacia* which are mainly chemically defended against herbivores. Some of the results obtained during this study indicated that this association may have some significant consequences for the trees' responses to impacts such as fire, and ultimately tree demography. A final chapter provides an overview of current knowledge about ant-acacia associations in Africa and makes some suggestions for further studies.

Zusammenfassung

Die wirtschaftliche Nutzung afrikanischer Savannen durch Viehbeweidung ist in den letzten Jahrzehnten vermehrt vorangetrieben worden, oft durch grosse Privatunternehmen; der Erfolg wurde jedoch häufig gedämpft durch unerwartete Probleme von Verbuschung auf den Weideflächen. Es gibt verschiedene Gründe für die Verbuschung von Savannen unter starker Beweidung. Der Weidedruck sowie der Huftritt der Kühe bewirken eine Schwächung der Grasnarbe, wogegen das Spriessen von Baumsamen sowie der Wuchs und das Ueberleben von Holzsprösslingen favorisiert werden. Weniger Grasbiomasse vermindert die Häufigkeit und Stärke von Buschfeuern in Weidegebieten, was ebenfalls die Verjüngung von Holzpflanzen begünstigt. Des Weiteren fressen Kühe in erster Linie Gras, aber grosse Viehherden verdrängen eine Vielzahl von einheimischen Wildtieren, welche Baumsprösslinge abäsen und kleinere Bäume am Wachsen hindern, wodurch diese durch Buschfeuer verwundbar bleiben. Viele Studien in Afrika und anderswo haben bisher die Ursachen von Verbuschung in Savannenweidegebieten untersucht; es gibt jedoch äusserst wenige Studien über die Veränderungen der Vegetationsdynamik in sekundären Buschwäldern, nachdem die Weidenutzung aufgegeben wurde. Die hier präsentierte Studie untersucht verschiedene Aspekte der Verbuschung auf einer ehemaligen Viehranch (Mkwaja Ranch) in einem Savannenökosystem in der tansanischen Küstenebene. Die Ranch war während 46 Jahren in Betrieb (bis August 2000) und wurde kürzlich Bestandteil des neu gegründeten Saadani Nationalparks (amtlich seit Oktober 2003). Der Schwerpunkt der hier beschriebenen Arbeit liegt auf der Untersuchung der räumlichen Muster, der Dynamik und der Veränderungen von sekundärem *Acacia zanzibarica*-Buschwald, nachdem die Nutzung durch Viehbeweidung aufgegeben wurde.

In einer ersten Studie auf Landschaftsebene haben wir die wichtigsten Vegetationstypen im Gebiet der Mkwaja Ranch und des ehemaligen Saadani Wildreservates beschrieben und wir haben deren Verbreitungsmuster in Bezug

gesetzt zu dem ehemaligen Beweidungsmuster auf der Ranch. Aufgrund von Feldaufnahmen gegen Ende 2001 wurden 15 verschiedene Typen von Grasland- und Buschlandvegetation definiert, und eine Vegetationskarte wurde erstellt mit Hilfe eines Landsat TM Satellitenbildes aus dem Jahre 1994. Die Analysen zeigten in erster Linie zwei räumliche Vegetationstendenzen. Eine erste Tendenz war eine grossräumige Abnahme der Verbreitung von Buschland von den am intensivsten genutzten Gebieten der Ranch über die eher extensiv genutzten Gebiete zum Wildreservat; dieser Trend wurde erklärt mit Unterschieden der Landnutzungsgeschichte sowie klimatischen und topographischen Faktoren. Eine zweite Tendenz war ein radiales Vegetationsmuster in Verbindung mit den eingezäunten Weideplätzen (Koppeln oder Bomas), wo die Viehherden unter Bewachung die Nacht verbrachten. Grosse Bestände von drei Typen von Buschland (bzw. Buschwald) [dominiert von (i) *Acacia zanzibarica*, (ii) *Dichrostachys cinerea*, *Acacia nilotica* oder *Acacia mellifera* und (iii) *Terminalia spinosa*] befanden sich in einer Zone von 300 bis 2500 m Distanz zu den Koppeln, mit der grössten Dichte bei ungefähr 900 m Distanz (Durchschnitt für 18 Koppeln). Es gab auch ein radiales Vegetationsmuster in den Grasland-Pflanzengesellschaften: In der Nähe der Koppeln gab es vorwiegend kurze Grasvegetation mit vielen Ruderalgräsern, wogegen die hochwüchsigen Graslandtypen in Gegenden zu finden waren, die weniger beeinträchtigt waren durch Viehbeweidung.

Die danach folgenden Arbeiten konzentrierten sich auf die Struktur und Dynamik der *Acacia zanzibarica*-Buschwälder in einem Gebiet, das intensiv beweidet wurde bis ins Jahr 2000. In zwei Feldstudien beschrieben wir die Struktur und Biomasse der Vegetation sowie ökologische Prozesse und demographische Aspekte der Bäume entlang eines Gradienten von offener Savanne zu dichten Baumbeständen zu drei verschiedenen Zeitpunkten. Auf 97 permanenten, runden Aufnahmeflächen wurden Messungen gemacht (durch Auswertung von Stichproben oder visuellen Schätzungen) von verschiedenen Parametern wie Bodentextur und Nährstoffe, Grasbiomasse, Baumbestände von

A. zanzibarica und deren Verjüngung. Mit multiplen Regressionsmethoden ermittelten wir dann die Tendenzen und Interrelationen zwischen den verschiedenen Parametern entlang des Baumdichte-Gradienten. In einer dritten Studie untersuchten wir experimentell, welchen Einfluss die Auslichtung von dichten Baumbeständen auf die Umweltbedingungen, Vegetationsentwicklung und Baumverjüngung hat. In jedem von vier Studiengebieten wurden zwölf Studienflächen ausgewählt und drei Behandlungen zugeordnet: Kontrollflächen (NN), Flächen, auf denen alle Bäume mit einer Motorsäge gefällt wurden (FN), und gefällte Flächen, auf denen die Baumstrünke zusätzlich vergiftet wurden (FP). Zu drei Zeitpunkten wurden dieselben Parameter gemessen wie in den oben erwähnten Studien. Zusätzlich wurden im Juni 2002 die Transpirationsraten von Akazien- und Grasblättern auf einer Kontrollfläche und einer abgeschnittenen Fläche gemessen. In zwei Studiengebieten wurden im Februar 2003 die Temperaturen von einem Buschfeuer gemessen, und die Einwirkung des Feuers auf Akaziensamen wurde untersucht.

Wie die erste Studie zeigte, widerspiegelte die Dichte der Baumbestände einen Gradienten in der Bodentextur; auf Sandboden hatte es wenig Bäume, wogegen dichte Baumbestände vorwiegend auf Böden mit einer feinen Textur (Ton-Schluff) zu finden waren. Auch der Gehalt von organischem Material und Phosphat stieg entlang dieses Bodentexturgradienten; Stickstoff war zudem besonders angereichert unter dichten Baumbeständen. Akaziendornen waren am dichtesten an den Aesten von Bäumen, die in der offenen Savanne standen, wogegen die Häufigkeit von Hohldornen (Pseudogallen) und Ameisennestern nur mit der Baumgrösse korrelierten. Die Anzahl von Ameisennestern und der Lebend-Holz-Anteil (~ Lebenskraft) eines Baumes waren die wichtigsten Faktoren, die während der Regenzeit mit dem Blattwuchs korrelierten. In der Trockenzeit hatte demgegenüber die Ressource-Konkurrenz mit der Grasschicht und anderen Bäumen offenbar einen grösseren Einfluss auf den Blattanteil der Baumkronen. Die Grasschicht wurde stark beeinflusst durch Buschfeuer; frische Grasbiomasse war zudem unter hoher Baumdichte reduziert. Obwohl der

Blattflächenindex (LAI) der Baumschicht nur etwa halb so gross war wie derjenige der Grasschicht, so ergaben die Schätzungen dennoch, dass die Gesamt-Transpirationsrate in zunehmend dichteren Baumbeständen ansteigt.

Die Daten über die Grössenverteilung der Bäume deuteten darauf hin, dass die Baumbestände nicht gleichaltrig waren, sondern dass es während der letzten 20 Jahre wohl mehrere Etablierungs-Episoden gegeben hatte. Es gab wenig Anzeichen von Selbst-Auslichtung durch Ressource-Konkurrenz in dichten Baumbeständen; die wichtigste Ursache für das Absterben von Bäumen im Zeitraum dieser Studie war wahrscheinlich Feuer. Einige Bäume, besonders jene mit einer niederen Lebenskraft (gemessen an dem Lebend-Holz-Anteil), wurden wahrscheinlich direkt getötet durch Feuereinfluss. Unsere Resultate deuteten jedoch darauf hin, dass der Hauptanteil des Baumsterbens nur indirekt durch Feuer verursacht wurde. Das Baumsterben erklärte sich in der Folge vorwiegend aus dem Wassermangel auf Böden mit hohem Tongehalt, wo Wasser oft nicht tiefer sickern kann als in die Graswurzelzone, besonders nach den leichten Regenfällen in der darauffolgenden frühen Regenzeit. Ein hypothetisches Modell für die Ursachen des Baumsterbens wird präsentiert und erklärt.

Die Produktion von Blüten und Hülsenfrüchten korrelierte stark mit der Baumgrösse. Im Gegensatz zur Blütenproduktion war die Früchteproduktion jedoch negativ beeinflusst in dichten Baumbeständen, was auf intraspezifische Ressource-Konkurrenz hindeutete. Die Samenproduktion von ca. 7.4 m^{-2} war sehr gering verglichen mit anderen Buschwäldern von invasiven, leguminösen Bäumen. Die Dichte der Sprösslinge war in erster Linie erklärbar aus Variablen der Boden- und Grasschicht, jedoch nicht aus der Samenproduktion der Bäume. Kein Sprössling überlebte bis in die späte Trockenzeit, wahrscheinlich aus Wassermangel. Die Hälfte der Bäume, die durch Feuer getötet wurden (d.h. Baumstammtod), spross wieder aus dem Wurzelstock.

Die experimentelle Studie zeigte, dass der Graswuchs während der Regenzeit erheblich höher war in abgeschnittenen Flächen verglichen zu Kontrollflächen, aber bis zur Trockenzeit gab es keine signifikanten Unterschiede mehr in der

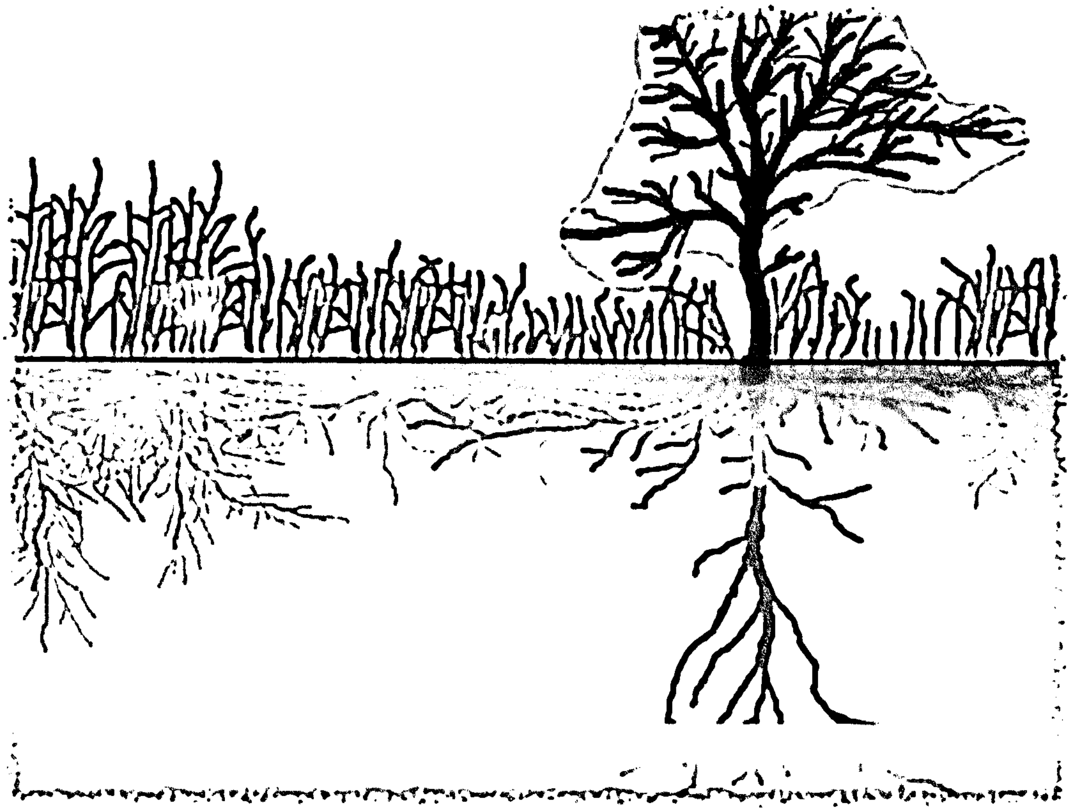
Grasbiomasse zwischen experimentellen Behandlungen. Das Abgrasen durch wilde Tiere war relativ unbeachtlich, aber dennoch deutlich höher auf Schnittflächen verglichen mit Kontrollflächen. Der Wassergehalt im Boden 14 Tage nach einem heftigen Regenfall war höher auf Schnitt- als auf Kontrollflächen. Dieser Unterschied war offenbar zu erklären durch eine schätzungsweise dreimal höhere Transpirationsrate bei *A. zanzibarica* Bäumen als bei Gräsern, wie die Porometerstudie indizierte. Die Etablierung und das Ueberleben von Sprösslingen waren erheblich höher auf Schitt- als auf Kontrollflächen. Die Etablierung war auch beeinflusst durch Buschfeuer; die Dormanz von Akaziensamen wurde gebrochen durch Feuer mit niedriger Intensität, wogegen viele Samen getötet wurden durch sehr heisse Feuer. Die Samenbank schien transient (vorübergehend) zu sein. Keine Sprösslinge wurden in der späten Trockensaison gefunden, was andere Beobachtungen bestätigte, dass gegenwärtig keine erfolgreiche Verjüngung stattfand. Auf den FN-Flächen fanden sich bei 68 % der Baumstrünke junge Triebe 3 Monate nach Baumschnitt, wovon aber nur 28 % (19 % Total) überlebten bis Ende der Studie. Im Allgemeinen wuchsen die Triebe nicht während des Studienzeitraumes, was andeutete, dass die Triebe nicht fähig waren über die Grasschicht hinauszuwachsen. Die Dichte von Wurzeltrieben variierte zwischen den Studiengebieten, wurde aber nicht beeinflusst durch Schnittbehandlungen und auch nicht durch Buschfeuer.

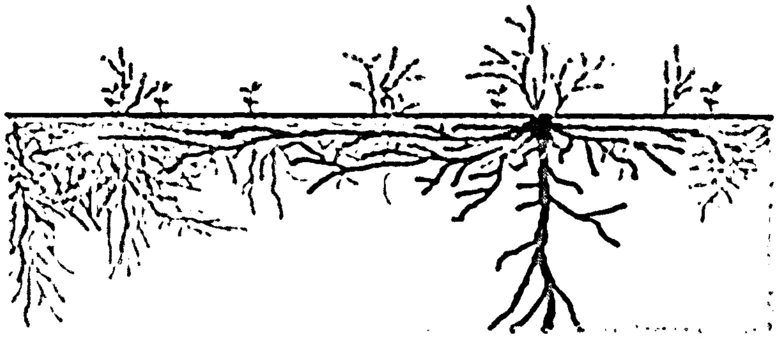
Wir schlussfolgern, dass, obgleich die Verbuschung einen erheblichen Einfluss auf die Weideressourcen von Vieh und von Wildtieren hatte, langfristig Bodenfaktoren und Feuer die Savannen-Struktur als massgebende Determinanten bestimmen. Auslichtung von *A. zanzibarica*-Beständen geschah auch ohne grosse, destruktive Herbivoren wie Elefanten; die Verjüngung war nicht erfolgreich unter den gegebenen Bedingungen mit sehr wenig Beweidung und regelmässigen Buschfeuern. Deshalb wird der Buschwald wohl wieder auf natürliche Weise einer offenen Savannenlandschaft stattgeben über die Zeit der nächsten 10-20 Jahre. Des Weiteren ist aber auch eine beschleunigte Oeffnung der Baumbestände möglich durch Abholzung, welche nicht den Boden und die Baumwurzeln beeinträchtigt (was möglicherweise das Ausschlagen von Wurzeltrieben fördert). *A. zanzibarica*-Buschwälder könnten deshalb als Uebergangsstadien betrachtet werden oder als ein Extremzustand von Buschdichte in einer elastischen, immer noch resistenten Feuchtsavanne. Gäbe es jedoch zukünftige Veränderungen in der Anzahl von grossen Herbivoren oder der Frequenz von Feuer, könnte sich das Gleichgewicht zwischen Gras- und Baumkomponenten erneut verändern. Bezüglich der ehemaligen Viehwirtschaft folgern wir, dass Verbuschung nicht unbedingt zum Misserfolg des Unternehmens führen muss; es sollte möglich sein auf lange Zeit ein Rotationsbetriebssystem zu entwickeln, welches beides, profitabel und nachhaltig ist.

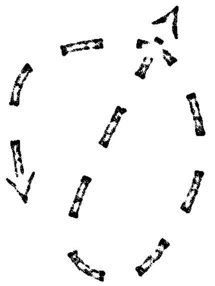
Acacia zanzibarica unterscheidet sich durch die Symbiose mit Ameisen von anderen afrikanischen Akazienarten, welche sich vorwiegend mit chemischen Blattstoffen gegen Herbivoren verteidigen. Einige der Resultate dieser Studie deuteten an, dass diese Symbiose möglicherweise erhebliche Konsequenzen hat auf die Art und Weise, wie der Baum auf solche dramatischen Einflüsse wie Buschfeuer reagiert, und schlussendlich auf die Demographie des Baumes. Ein letztes Kapitel gibt einen Ueberblick über das gegenwärtige Wissen über Ameisen-Akazien-Gemeinschaften in Afrika und macht einige Vorschläge für weitere Studien.

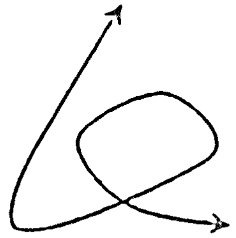
The dashing arrow is resting.

Zenon









General Introduction

This thesis examines the impact of intensive cattle grazing on an area of savanna vegetation on the Tanzanian coastline. It focuses particularly upon how dense bushland dominated by various native woody species invades areas heavily affected by cattle. The topic is one of considerable ecological interest, posing important questions about the impact of individual species upon ecosystem function and about the resilience of savanna ecosystems; however, it is also of economic importance because the problem of bush encroachment makes commercial cattle ranching difficult or impossible in many parts of Africa. In this thesis, I present our attempt to understand the reasons for bush encroachment in the study area, its impact upon the savanna ecosystem, and its long-term development after cattle are removed.

SAVANNAS: DEFINITION AND PROCESSES

Tropical savannas cover about 20 % of the landmass of the world, and 65 % of Africa; they occur in regions with highly seasonal rainfall and monthly mean temperatures higher than 10° C (Cole 1986, Scholes & Walker 1993). Savanna is structurally defined as a vegetation type where grasses and trees are spatially separate; trees are typically taller than 2 m, and canopy cover is higher than 5 % but less than 80 % (Scholes & Walker 1993). In a functional view, ecological processes, such as primary production, hydrology and nutrient cycling are, therefore, strongly influenced by both woody plants and grasses, and only weakly by plants of other growth forms (Walker 1987). Grasses and trees particularly differ in their ability to exploit water at different depths in the soil, and the two-layer soil-moisture competition model (Walker & Noy-Meir 1982) has frequently provided a theoretical basis to explain tree-grass ratios in savannas.

Other attempts to explain the balance between trees and grasses in savanna have centred on the dynamic nature of savanna landscapes, often emphasising the role of herbivory and fire as two major intrinsic modifying forces (van de Koppel & Prins 1998, van Langevelde *et al.* 2003, Higgins, Bond & Trollope 2000). In Africa, savanna vegetation evolved with a rich assemblage of grazing and browsing ungulates (du Toit & Cumming 1999), and in their morphology, physiology and life histories many plants reflect a long history of coevolution with herbivores. Several studies have observed that significant vegetation changes often coincide with changes in the herbivore communities (e.g. Prins & van der Jeugd 1993, Leuthold 1996, Lenzi-Grillini, Viskanic & Mapesa 1996, Ruess & Halter 1990). In other savannas, particularly in humid coastal areas, frequent fires (often caused by humans) may be a more important impact maintaining the unique tree-grass balance (Gillon 1983, Backéus 1992). Based on early succession theories, savannas have often been viewed as an intermediate, transitional vegetation state which would eventually change to another vegetation type (e.g. tropical forest), if it would be relieved from dynamic forces (Scholes and Walker 1993). However, such considerations remain largely theoretical, and today the view prevails that savannas are relatively stable states with a broad range of dynamic variation (Blösch 2002).

Spatial variation and dynamics is inherent in tropical savannas and occurs at different scales from small patches (e.g. the local influence of a termite mound) to regional landscape patterns (e.g. migrations of wildebeest in the famous Serengeti, or savanna-forest mosaics shifting due to the long-term influence of fire). Spatial patterns in plant species distribution mean that savannas are also spatially heterogeneous in terms of forage productivity and quality (Belsky 1992, Belsky 1994, Belsky and Amundson 1998, Veetas 1992). However, feedbacks are also important: selectivity of grazers is dependent on patch size of available fodder, thereby altering spatial patterning in the vegetation (Owen Smith 1982, Ben-Shahar & Coe 1992, Wallis de Vries, Laca & Demment 1999). Inherent site differences induced by the interaction of topography and rainfall regime are also significant, for example in forming cells of degradation, such as local soil erosion (Walker 1993, Rietkerk *et al.* 2000).

THE IMPACT OF CATTLE RANCHING: A CASE OF BUSH ENCROACHMENT

Savanna ecosystems are increasingly coming under pressure from domestic livestock. The profound environmental impacts of intense livestock grazing have been extensively documented in the literature (e.g. Walker 1993, Skarpe 1991, Snyman 1998, Behnke, Scoones & Kerven 1993, Dodd 1994, Burrows *et al.* 1990, Brown & Archer 1989, Reid & Ellis 1995, Schultka & Cornelius 1997, Turner 1998, Augustine 2003, Young, Patridge & Macrae 1995, Rietkerk 1998); important ecosystem changes which have been observed in savanna rangelands on all continents include replacement of palatable grass species with weeds, encroachment of woody species, nutrient transfer from pastures to herding places, and severe damage to soils.

While livestock managers are usually concerned with "rangeland degradation" from an economic perspective, ecologists are increasingly worried about the possible effects of permanent species loss in savannas (e.g. Solbrig, Medina & Silva 1996, Medina & Huber 1994), particularly in Africa, where in many areas the functional diversity of herbivores is replaced with a single, medium-sized grazer, the cow (du Toit and Cumming 1999). Even in those areas not used for agriculture wildlife populations may be affected by the changes in landuse in neighbouring areas. This is because conservation of individual species requires preservation of entire habitats of sufficient size (Walker 1992). Natural habitats inside protected areas may deteriorate if the integrity of the ecological system is disrupted on a larger scale (Sinclair *et al.* 1995). The long-term conservation outlook of some communities of large African wildlife is bleak. Isolation of small reserves within an anthropogenically modified landscape matrix has, for example, already resulted in local extinctions of some major wildlife populations which depended upon an extensive range of natural habitats (Newmark 1996, Mwangi 1997, du Toit 1995). In the light of accelerated degradation of natural habitat and associated biodiversity decline even within areas set aside for conservation, it has recently been suggested to adopt a new conservation strategy that considers the importance of habitat renewal in addition to habitat preservation (Sinclair *et al.* 1995). To that end, however, managers concerned with conservation need information about the potential rates of recovery of degraded areas.

Significant changes in the vegetation of savanna rangelands are often episodic, occurring in response to rare and extreme events or particular sequences of events, e.g. a very dry year followed by a very wet year (Walker 1993). The reason for this episodic behaviour is that both successful reproduction and mortality in plants depend on particular conditions. Therefore events of seedling recruitment of woody plants (e.g. Brown and Carter 1998, O'Connor 1995) as well as die-off of established tree stands (e.g. Young and Lindsay 1988, Fensham & Holman 1999) often coincide with extreme climatic episodes.

One form of vegetation change that has become a problem in rangelands of all savannas around the world is bush encroachment. In Australia and America bush encroachment on rangelands has frequently been by introduced, exotic species often of African origin (Humphries *et al.* 1991, Solbrig, Medina & Silva 1996); in contrast, until now, exotic species appear to be a relatively minor problem in African savannas (Solbrig, Medina & Silva 1996), with the exception of some parts of South African fynbos (a similar vegetation type to savanna; Holmes & Cowling 1997). This poses the question whether the trend towards bushland is reversible, so that open savanna can be restored when cattle grazing ceases. Although resilience has been considered in modelling studies of encroached savanna pastures in Australia (e.g. Ludwig *et al.* 2001), we do not know of any field study that has focused on post-impact vegetation changes within secondary bushlands established on intensively grazed savanna pastures in Africa.

THE ROLE OF MODELS IN UNDERSTANDING SAVANNA VEGETATION DYNAMICS

The way we interpret savanna dynamics today is to some extent a matter of cultural history, language and personal bias. The very term of "savanna" has, for example, been contested by researchers in the field (see Scholes & Walker 1993, Blösch 2002); especially for classification purposes alternative, structural terms have been suggested, such as "tropical wooded grassland" and "bushed grassland" (e.g. White 1983). Yet, the classical term is today firmly established, and most researchers accept that savannas are somewhat distinctly different from other grasslands (e.g. steppes and prairies) and open woodlands (e.g. miombo).

However, what are the distinctive features of savannas in terms of ecosystem function? Walker (1993) has listed four major areas of complexity characteristic of rangeland dynamics in savannas: spatial variation and dynamics, the significance of rare and extreme events, lag effects and thresholds, and multiple meta-stable states coupled with multiple trajectories of change. A lag effect has for example been observed where a high proportion of unpalatable species has been induced through high grazing pressure: in many cases, reduction in stocking rates does not lead to an increase in the proportion of palatable species. Threshold effects may be illustrated by the dynamics of the grass-woody plant ratio in savannas: grazing promotes the woody component by reducing grass competition for resources and by decreasing the fuel load for fires (Walker 1993). Yet, so-called "lag effects" and "thresholds" can be observed in virtually all ecosystems to varying degrees (c.f. Briske, Fuhlendorf & Smeins 2003). "States" and "trajectories" are abstract terms which are useful in conceptual models but do not allow for the fact that nature is neither static nor can any process outcome ever be projected with absolute mathematical certainty. Furthermore, individual processes are rarely independent from other system processes; they do only exist as clear vectors in our imagination and in computer models. The degree and nature of system complexity and its challenge to our views and paradigms as scientists may, therefore, itself be a defining point; researchers from temperate hemispheres are becoming increasingly aware, that ecosystem processes in savannas (as probably in most ecosystems) are difficult to describe and cannot be represented as a simple linear sequence.

To some extent these conceptual difficulties can be overcome using computer models. With the enormous increases in the capacity of computers since the 1970's, it has become possible for scientists to test complex hypotheses about savanna dynamics using simulations. Modelling approaches have profoundly influenced the academic debate during the last two decades, and modelling studies are amongst the most-cited papers dealing with tree-grass interactions in savannas (e.g. Walker & Noy-Meir 1982, Westoby, Walker & Noy-Meir 1989, Walker & Langridge 1996, van de Koppel & Prins 1998, Jeltsch *et al.* 1996, 1997, 1998, Higgins, Bond & Trollope 2000, Anderies, Janssen & Walker 2002, van Langevelde *et al.* 2003, Simioni, Gignoux & le Roux 2003; c.f. also review in Blösch 2002). Computer models provide an excellent tool for testing hypotheses under an assortment of potentially occurring conditions, and can provide a framework for theoretical debate; however, they are of limited value unless their predictions can be tested by actual observations in the field. Thus, field ecologists can gain important insights from models, while theoreticians depend upon the results of field studies in order to develop more realistic models. Today, ecologists are able to use ever greater amounts of data in their models and process them at scales unforeseen by researchers just 20 years ago. Indeed, one of the reasons why savanna ecologists are increasingly critical of earlier concepts such as Clementsian succession theory (c.f. Blösch 2002), is because they are now better placed to investigate the multivariate complexity of savanna ecosystems along the space-time grid.

THE STUDY SITE

Mkwaja Ranch occupies an area of 462 km^2 of humid, coastal savanna and forest directly to the North of the Saadani Game Reserve in the Pangani District of N.E.

Tanzania. The site was particularly suitable for a research project on the long-term impacts of cattle ranching for the following points:

1) Prior to the establishment of the ranch in 1954 by Amboni Ltd, a Swiss-based company, the region was an open savanna landscape that was barely touched by human settlements. According to documentary and oral descriptions, the area was relatively rich in wildlife, including large numbers of giraffes and antelopes. The conditions prior to the ranching impact could thus probably qualify as "natural". The savanna vegetation at Mkwaja probably replaced moist evergreen and dry evergreen coastal forests only in quaternary times (Klötzli 1980). The main types of savanna grassland on rather sandy soils (i.e. types 2 and 4 *sensu* Klötzli 1980) are dominated by mostly high-growing grasses such as *Andropogon gayanus*, *Diheteropogon amplectens* and *Hyperthelia dissoluta*; those types may be assigned to the moist dystrophic savanna type (c.f. Huntley 1982, East 1984). The grassland types on more clayey soils, richer in nutrients (i.e. types 3 and 5 *sensu* Klötzli 1980) are dominated by *Heteropogon contortus* and several black-cotton species. Presumably, the most important determinant of these savannas is fire, although herbivores probably contributed to the opening up of dense woodlands and hence facilitated fire penetration. Long-grass communities naturally experience more high-intensity fires than short-grass communities (Baruch 1996), which probably explains why doum palms, *Hyphaene compressa*, represent the dominant species in long-grass communities whereas acacias are prevalent in short-grass communties.

2) As one of the biggest private ranches in Tanzania, with over 13'000 head of cattle, the former Mkwaja Ranch could be viewed as representative of the kind of conventional large livestock enterprises that have been - and still are - actively supported by governments in many African countries (du Toit and Cumming 1999, Dahlberg 2000, Little 2003). It is also an illustrative example of a technology-based livestock enterprise that failed within the savanna environment. The ranch area supported a total of 16 grazing sectors centred on night paddocks (cattle bomas). Stocking rates differed between paddocks, and some paddocks

were abandoned in different years during the 1980'ies and 1990'ies, with the last paddock (Kichangani) being abandoned in August 2000. All major vegetation characteristics commonly associated with long-term overstocking or brushcutting activities in savanna rangelands are obvious on Mkwaja Ranch; these include high nutrient enrichment and very low species richness (almost exclusively *Cynodon dactylon*) on former bomas, ruderalisation and dense bush patches (including presence of a few exotic species) in the vicinity of bomas, and thick bush encroachment (mostly *Acacia zanzibarica* and *Terminalia spinosa*) at some distance from bomas.

3) Since the beginning in 1954 monthly and yearly reports have been prepared by Amboni Ltd. These represent a data set that is probably without comparison in Africa. The reports provide detailed information about various aspects of ranching activities including numbers of head of cattle in each paddock, data about calving rates and rates of cattle loss, monthly rainfall data, information about brushcutting activites in different grazing sectors, economic data, and other observations of qualitative value, such as statements about bush encroachment and other problems, and intended strategies. Furthermore, work conducted by Klötzli and co-workers (e.g. Klötzli 1979, Klötzli 1980, Klötzli *et al.* 1995, Kozák 1983, Lupi and Walther 1994) document vegetation changes from 1974 to 1995 and give information about the value of pastures for grazing.

4) Since October 2003 the area encompassing the former Mkwaja Ranch, Saadani Game Reserve and Zaraninge State Forest has been protected as the Saadani National Park, Tanzania's newest national park, and the first encompassing a part of the East African shoreline. The former small Saadani Game Reserve (209 km^2) adjacent to the South of the ranch was home to sizeable populations of herbivores such as giraffe, buffalo and hartebeest that were common in the savanna around Mkwaja until 1954. It is a useful area to compare with the highly modified savanna at Mkwaja Ranch. Furthermore, it will probably serve as a major pool for immigration of wildlife to Mkwaja North after

cattle have been withdrawn from the ranch and the whole area has been protected (c.f. Treydte 2004).

STUDY OUTSET AND OVERVIEW

Preliminary observations showed that the original savanna vegetation of Mkwaja Ranch had been substantially altered during 50 years of heavy grazing pressure from domestic livestock. These were mirrored by available older documentation such as the Amboni reports, scientific studies by Klötzli and coworkers, and aerial photographs. Four major ranching-related changes within the ecosystem at Mkwaja were identified:

1. A major decrease in wildlife numbers, due to cattle ranching and poaching by ranch employees.
2. Serious bush encroachment (mainly *Acacia zanzibarica* and *Terminalia spinosa*) under heavy livestock grazing (mentioned already in the 1958 year report).
3. Serious bush re-encroachment (mainly *A. zanzibarica* and *Hyphaene compressa*) after brushcutting activites.
4. Decrease of pasture quality, mainly as a result of bush encroachment and overgrazing around night paddocks.

We wanted to quantify and evaluate past changes. In a first step (section 1, chapter 1) I analysed vegetation patterns at a landscape level within the Mkwaja-Saadani ecosystem, including the former Mkwaja Ranch (462 km^2) and Saadani Game Reserve (209 km^2). I was particularly interested in how ranching activities led to an increase in the abundance of certain woody savanna species (mainly *Acacia zanzibarica* and *Terminalia spinosa*). In accordance with observations on the ground, I expected bushlands of *Acacia zanzibarica, Terminalia spinosa* and other woody plants to be most abundant in areas surrounding the paddocks. A vegetation map was produced from a LANDSAT TM picture of 1994, and several statistical analyses were performed on the data.

Principally, however, this thesis is concerned with the patterns and ecological processes at work in secondary *Acacia zanzibarica* woodlands following the giving up of cattle grazing (section 2, chapters 2-4). In theory, such processes could (1) maintain the present state („alternate stable state“ *sensu* Westoby, Walker & Noy-Meir 1989), or lead to further change (2) in the direction of a savanna ecosystem similar to that which existed before ranching (savanna resilience), or (3) in a different direction towards a new alternate state (succession).

Preliminary observations indicated that these woodlands had a more or less continuous grass layer. There was hardly any recruitment from seedlings within dense, even-aged stands of acacia woodland, and only acacias on the periphery of the woodlands and individuals in the open savanna actually flowered and set significant amounts of seeds. But would such observations really be confirmed by data? If so, were they really due to tree density, or were they due to other factors, such as stand age, soil conditions or competition with the grass layer? To what degree were tree stand structure and grass layer biomass influenced by the underlying soils and disturbances such as fire and herbivory? The first two studies (chapters 2 and 3) are based on multivariate analyses of soil and vegetation data from 97 permanent study plots along a woodland-savanna gradient. The aim was to provide a picture of trends in biomass and the ecological processes at work along the tree density gradient (spatial dimension) at three different dates during one year (time dimension).

Another observation which we made before the study in September 2000, was that some openings in the woodland where acacia trees have fallen were often covered by a carpet of nitrophilic grasses, such as *Panicum infestum* or *Brachiaria leucacrantha*, which appeared to inhibit acacia regeneration. On the other hand, we knew from ranch reports and the work of Klötzli and co-workers that *A. zanzibarica* was a vigorously resprouting tree, and that brush cutting was not successful in bush control but rather compounded the problem of woody encroachment. We were therefore interested in whether woody regeneration would also be successful after ranching had been abandoned. What were the main changes occurring in terms of grass biomass, transpiration and soil nutrients within manually created woodland gaps? Would cut trees of *A. zanzibarica* also be able to regenerate in the absence of heavy grazing? In the third study (chapter 4) we therefore cut 8 woodland plots at each of 4 study sites; on half of these plots tree stumps were poisoned. We then observed during one year the changes in the grass layer and tree regeneration. The aim was to test the impact of tree removal, be it by management of by natural forces such as elephant. Taken together, these various studies provide a picture of a highly dynamic ecosystem which responded very strongly to the impact of cattle grazing, and which is already showing responses to the abandonment of this form of landuse.

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Indeed, as I learned, there were on the planet where the little prince lived—as on all planets—good plants and bad plants. In consequence, there were good seeds from good plants, and bad seeds from bad plants. But seeds are invisible. They sleep deep in the heart of the earth's darkness, until some one among them is seized with the desire to awaken. Then this little seed will stretch itself and begin—timidly at first—to push a charming little sprig inoffensively upward toward the sun. If it is only a sprout of radish or the sprig of a rose-bush, one would let it grow wherever it might wish. But when it is a bad plant, one must destroy it as soon as possible, the very first instant that one recognizes it.

Antoine de Saint-Exupéry,
The Little Prince

The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania

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Summary

1. The success of large-scale cattle ranching in African savanna vegetation has often been limited by problems of bush encroachment and disease (in particular trypanosomiasis spread by tsetse flies). Mkwaja Ranch, occupying an area of 462 km^2 on the coast of Tanzania, is a recent example of a large ranching enterprise that failed within the savanna environment. It was closed in 2000 after 48 years of operation. In this paper we describe the main vegetation types of the area (excluding closed forest vegetation) and relate their patterns of distribution to the former use of the ranch for cattle.

2. The study area comprised the former ranch and parts of the adjacent Saadani Game Reserve, which had not been grazed by cattle for many years and had never been used for large-scale ranching. Following field surveys, 15 distinct types of grassland and bush vegetation were defined and a vegetation map was created using a Landsat TM satellite image. A multispectral classification using the maximum likelihood algorithm gave good results and enabled all 15 vegetation types to be distinguished on the map.

3. Two main spatial trends were detected in the vegetation. One was a large-scale decrease in the cover of bushland from the most intensively used parts of the ranch through more extensively used areas to the game reserve; this trend was attributed to differences in management history as well as to climatic and

topographic factors. A second trend was a radial vegetation pattern associated with the enclosures where cattle were herded at night. High amounts of three bushland types (dominated by 1. *Acacia zanzibarica*, 2. *Dichrostachys cinerea*, *Acacia nilotica* or *Acacia mellifera*, and 3. *Terminalia spinosa*) occurred in a zone between 300 and 2500 m from the paddocks, with a peak in bush density at about 900 m (mean value for 18 paddocks). In contrast, bushland dominated by *Hyphaene compressa* was scarce close to the paddocks and became more abundant with distance. There was also a radial trend in the grassland communities: close to the paddocks there was short grass vegetation containing many ruderals and invasive weedy species, while the tall grassland types with species such as *Hyperthelia dissoluta* and *Cymbopogon caesius* occurred further away in the areas less affected by cattle.

4. *Synthesis and Applications.* The intensive modern livestock ranching as practised on Mkwaja Ranch proved to be unsustainable both economically and ecologically. In the end, the biggest problem faced by the ranch managers was not controlling disease, as had originally been feared, but preventing the spread of bush on pasture land. The results of our study demonstrate just how severe the problem of bush encroachment was, especially in areas close to paddocks. An important lesson for management is that grazing patterns need to be taken into consideration when determining the sustainable stocking rate for an area. To reduce the risk of bush encroachment in grazing systems with focal points such as paddocks or watering points, stocking rates need to be lower than in systems with a more uniform grazing distribution.

Key-words: bush encroachment, East Africa, grazing patterns, Landsat TM, remote sensing, vegetation classification

Introduction

Savanna vegetation is dominated by varying proportions of mainly grasses and woody plants (Walker 1987). The characteristics of natural savannas are determined by a strongly seasonal climate, limited availability of moisture and nutrients, fire and herbivory (Scholes & Walker 1993). Grazing by domestic livestock can have a dramatic impact on savanna ecosystems and is often responsible for extensive bush encroachment (e.g., Brown & Archer 1989; Behnke, Scoones & Kerven 1993; Perkins & Thomas 1993a; Hudak 1999). There appear to be various reasons for this effect. One is that livestock reduce the vigour of grasses, while promoting seed germination, establishment and survival of woody species (Brown & Archer 1989; Van Staden, Kelly & Bell 1994; Brown & Carter 1998). Secondly, livestock may act as dispersal agents for seeds of woody species (Reid & Ellis 1995; Miller 1996; Brown & Carter 1998). Thirdly, intensive grazing may diminish the frequency and intensity of fires by reducing the grass biomass, which also favours the woody component of the vegetation (Scholes & Walker 1993; Roques, O'Connor & Watkinson 2001). Finally, domestic livestock tend to be predominantly grazers, but they displace a range of native browsers such as impala *Aepyceros melampus* (Liechtenstein, 1812) and kudu *Tragelaphus strepsiceros* Pallas, that control tree seedlings more effectively (Cole 1986; Du Toit & Cumming 1999).

During the past few decades, many African governments have supported the development of large livestock enterprises (Okigbo 1985; Du Toit & Cumming 1999; Hudak 1999; Dahlberg 2000). This is because modern ranching methods, which make use of fences, artificial water holes and a variety of measures to control pests and diseases, allow a much higher stocking rate. However, cattle tend to feed on a limited number of grass species which can soon be overexploited, particularly during severe drought years, while bush encroachment may reduce the area of available pasture (Skarpe 1991). Partly for these reasons, and also because of problems of disease, many intensive ranching enterprises in tropical Africa have failed after a few years (Okigbo 1985).

The changes that occur in savanna vegetation as a result of cattle ranching have been described in various field studies (e.g., Brown & Archer 1989; Skarpe 1990; Friedel 1997; Schultka & Cornelius 1997; Bossdorf, Schurr & Schumacher 2000). A common finding is that the impact of grazing declines with increasing distance from focal points such as night paddocks and permanent watering points (Perkins & Thomas 1993a; Young, Patridge & Macrae 1995; Turner 1998; Rietkerk *et al.* 2000). Among the few studies of bush encroachment at a landscape scale, Perkins & Thomas (1993b) described the spatial pattern of bush encroachment in relation to grazing gradients around waterholes in Botswana, and Jeltsch *et al.* (1997) developed a simulation model to describe this process in South African savannas. Both of these studies were conducted in semi-arid savannas and there are no comparable large-scale studies of bush encroachment in more humid savannas. The distinction is important because in more humid savannas the most important factors affecting the equilibrium between grasses and woody plants are often herbivores and fire, rather than water availability (Walker 1985; Frost & Robertson 1987; Hopkins 1992; Valone & Kelt 1999).

The study of vegetation patterns at a landscape scale requires appropriate methods for the large-scale capture and analysis of data. Satellite images from the Landsat Thematic Mapper (TM) have proved a valuable tool for mapping vegetation at such a scale (Goodchild 1994; Wyatt 2000). At 30 m, the resolution of the TM sensor is high enough to distinguish the small patches of woody vegetation that frequently occur in savannas, but coarse enough not to be influenced by individual trees. The reflectance of vegetation in the six spectral bands recorded by TM depends on the abundance of woody plants, canopy structure, grass biomass and on the presence of particular species (Fuller, Prince & Astle 1997). These are the same criteria that are used for classifying savanna vegetation in conventional field surveys (White 1983).

The aims of this study were to: (i) describe the vegetation types and their patterns of distribution on a large cattle ranch on the coast of Tanzania; (ii) show the distribution of bush around former paddocks; (iii) demonstrate the usefulness of remotely sensed data for investigating the influence of ranching on vegetation.

Study area

Mkwaja Ranch (5° 43' S, 38° 47' E), occupying an area of 462 km^2 on the Tanzanian coast (Fig. 1), provides a recent example of a technology-based, big ranching enterprise that failed within the savanna environment. Amboni Estates Limited acquired the land in 1953 and began to stock it with East African zebu cattle and boran bulls *Bos indicus* L. (Ford & Blaser 1971). In the following years Mkwaja Ranch developed into one of the largest private ranches in Tanzania, supporting over 13000 head of cattle during the 1970s. However, problems of disease control and bush encroachment meant that the ranch was never profitable. Aerial photographs from 1954 show that initially the savanna was much more open than it is today. During the 1970s and early 1980s, extensive use was made of brush-cutting but the practice was finally given up as it became clear that it was not only expensive but also exacerbated the problem of encroachment. After 1980, the number of animals was gradually reduced and parts of the ranch were abandoned; it was finally closed in August 2000 following years of financial deficits.

Mkwaja Ranch is divided into two parts, known as Mkwaja North (240 km^2) and Mkwaja South (222 km^2). The whole area was organised into 18 paddock systems (Fig. 2) and 40 dams were built to ensure an adequate water supply. Up to 1500 cows were herded into each paddock for the night. In the morning the cattle were divided into herds of 200-400 animals and led by a herdsman to pasture areas and later to a nearby dam. Initially, daily grazing routes were not fixed and tended to differ between seasons. In 1976, a rotational system was introduced to let the herds graze in different areas for a limited amount of time and so reduce the impact on any one area (Ford & Blaser 1971; Gates *et al.* 1983; Trail *et al.* 1985).

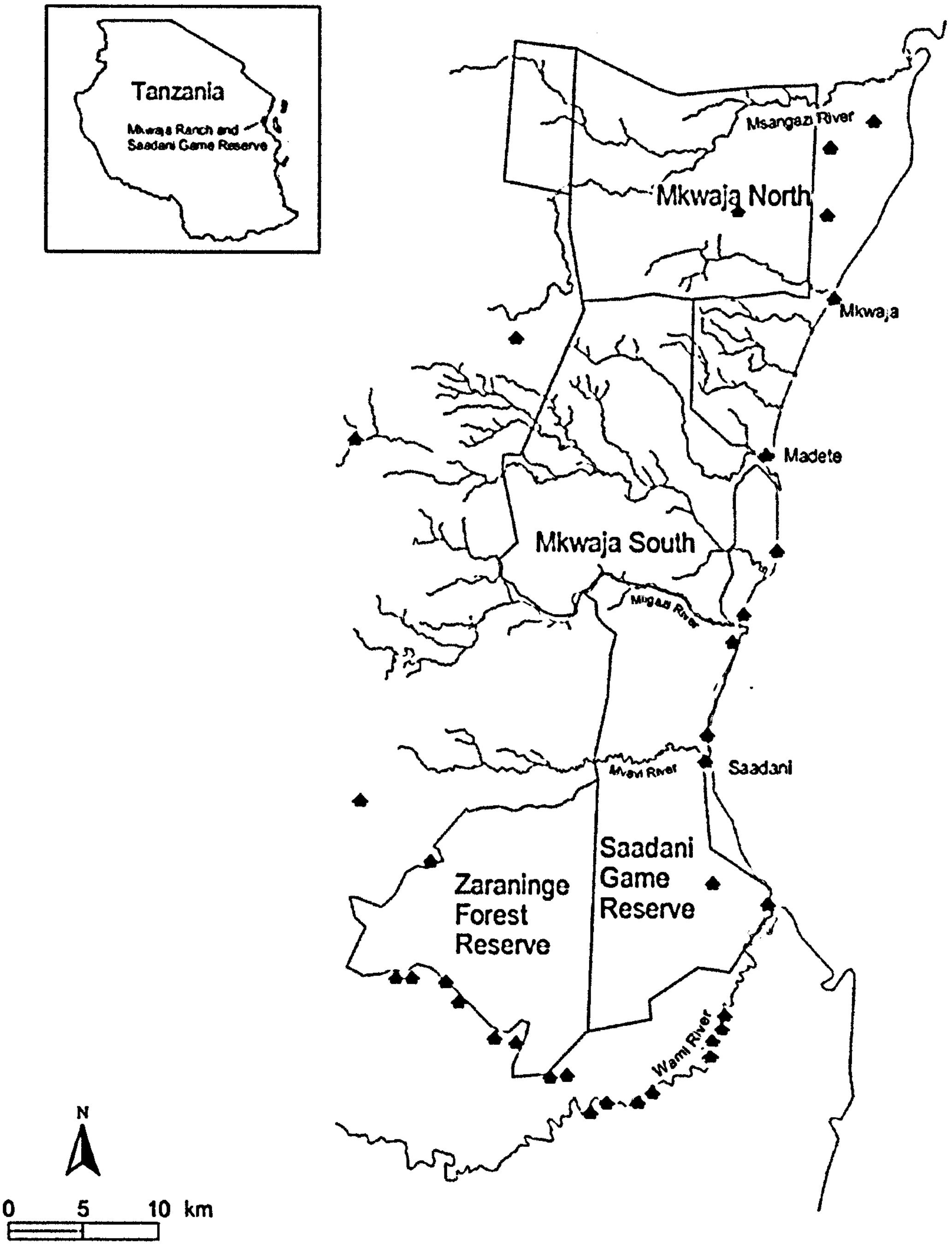

Fig. 1. Map showing the location of the study area on the coast of Tanzania.

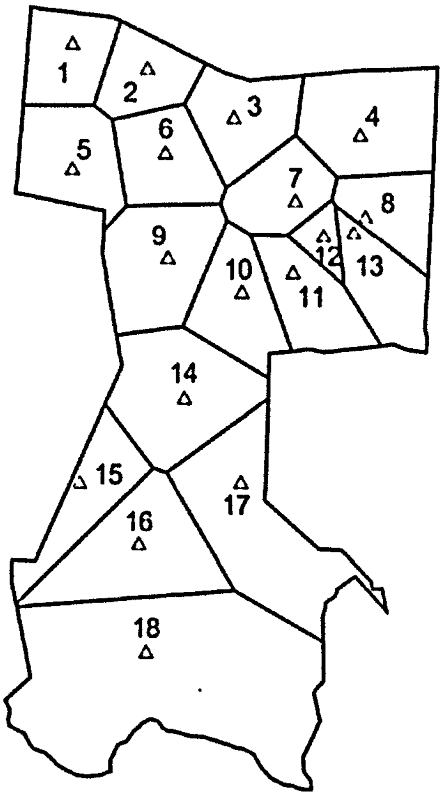

Fig. 2. The locations of the night paddocks (triangles) on Mkwaja Ranch. The Thiessen polygons define the land associated with each paddock system.

In addition to the livestock, Mkwaja Ranch supported mostly non-migratory populations of several species of herbivores, including warthog *Phacochoerus africanus* Gmelin, waterbuck *Kobus ellipsiprymnus* Orgilby, bush pig *Potamochoerus larvatus* F. Cuvier, reedbuck *Redunca redunca* Pallas, bushbuck *Tragelaphus scriptus* Pallas, buffalo *Syncerus caffer* Sparrman, duiker *Silvicapra grimmia* L., sable antelope *Hippotragus niger* Harris, hartebeest *Alcelaphus buselaphus* Pallas, giraffe *Giraffa camelopardis* L., hippopotamus *Hippopotamus amphibious* L., kudu and elephant *Loxodonta africanus* Blumenbach (Gates *et al.* 1983). Little information is available on population sizes of these native herbivores but Trail *et al.* (1985) estimate that the total biomass of wildlife was up to one quarter of that of livestock.

To the south of Mkwaja Ranch lies the Saadani Game Reserve (209 km^2, 6° 02' S, 38° 45' E), which was gazetted in 1974. The same species of wildlife are present as in Mkwaja, though mostly in much larger numbers (Robinson 1999). There has been no cattle grazing in the Saadani area since it became a game reserve, and only small areas around the villages are used for collecting firewood. The most important factors affecting the present vegetation are wild herbivores and frequent fires. It therefore provides a useful reference site when investigating the influence of cattle on Mkwaja Ranch. In 1996, Mkwaja South was incorporated as an extension to the Saadani Game Reserve. Now that ranching at Mkwaja has ceased, it is planned to establish a new national park comprising the Saadani Game Reserve, the adjacent Zaraninge Forest Reserve, and the whole of the former Mkwaja Ranch (Fig. 1).

While Saadani is mostly flat, Mkwaja has an undulating topography with several small hills of mesozoic limestone (Klötzli 1980). Alluvial floodplains with recent sedimentary deposits occur along the larger rivers and estuaries, and the zone immediately adjacent to the coast is composed of fairly recent marine sediments such as coral sand and clay (Milewski 1993). The relatively nutrient poor soils consist of greyish fine sand or loamy sand in the flats and reddish loamy sand over clay on slopes and hilltops (Klötzli 1980; Milewski 1993).

The mean annual temperature recorded at the ranch complex in Mkwaja North (1973-1998) is 25° C, with an annual range of 5° C and a daily range of 8° C. The annual rainfall has varied between 500 mm and 1700 mm during the last 50 years, with a mean of around 900 mm. There is a short rainy season from October to December during which monthly averages exceed 100 mm. January and February are usually rather dry. Rains start again in March and continue until the beginning of June, followed by four drier months. Due to its location on the coast, Mkwaja Ranch has very few months with no rain. However, August and September are often dry enough to allow extensive bush fires, many of which are started deliberately by local people.

Methods

FIELD DATA

The main goals of the field survey were to classify the different vegetation types and to collect training sites for a multispectral classification of the satellite image. The field survey was carried out between September and November 2000. The vegetation was first classified according to the major structural types as given by White (1983), i.e. forest, woodland, bushland, thicket, grassland and wooded grassland. A stratified sampling scheme was then established, with 70 sample plots representing all of the vegetation types except closed forest, which was not used by cattle. The percentage cover and height of the most abundant grass species were recorded in a 5 × 5-m subplot at each sampling site. Bush or tree density was measured using the point-centred quarter method (Mueller-Dombois & Ellenberg 1974). On the basis of this information, the classification of vegetation types was further subdivided. For woodlands and bushlands, the dominant woody species were the most important criterion. The grasslands and wooded grasslands were classified by the dominant grass species because these contribute most to the reflectance of these vegetation types. The range of vegetation types finally recognized was restricted by the requirement that each type must be distinguishable in a satellite image. The vegetation types were named by adding the dominant species or an adjective to the basic structural types as defined by White (1983) (e.g. *Acacia zanzibarica* bushland or deciduous woodland).

As a next step, training sites for a multispectral classification were selected in the field. For each vegetation type at least 15 sites in different parts of the study area were chosen. The location of all sites was determined using a handheld GPS receiver (Garmin 12XL, GARMIN International Inc., Kansas, U.S.A).

IMAGE DATA

No recent Landsat TM image was available in which the entire study area was cloud-free. The best image available was taken on 15 December 1994, when Mkwaja North was almost free of clouds but there was rather high cloud cover over Saadani and some areas of Mkwaja South. The fact that the image was taken towards the end of the short rain season when the vegetation was already regenerating made it suitable for vegetation mapping.

The image was registered and geo-referenced to Universal Transverse Mercator (UTM) coordinates using a topographic map as reference. After a preliminary inspection of the image, it was decided to keep six of the seven bands for further analyses (omitting band 6). As the field survey took place six years after the satellite image was recorded, we were concerned that possible changes in the vegetation would influence the classification. We therefore collected training data only in areas that, to judge from the present vegetation, were unlikely to have changed significantly during the last few years. As a further precaution, outliers were removed using a correspondence analysis of all the training sites with the spectral information for each of the six bands as variables.

The maximum-likelihood algorithm was used for classifying the image. Clouds, shadows and the ocean were classified first, expanded by two pixels and then used as a mask for the classification to avoid misclassification at the edge of a cloud or shadow. A total of 380 training points were used for the final classification of 15 vegetation types. Additional classes for water, sand, and bare soil were defined from the satellite image. Due to the small-scale heterogeneity of the landscape, single-pixel training was chosen to avoid using mixed pixels. This method also reduces effects of spatial autocorrelation and can therefore improve the classification (Gong & Howarth 1990).

No independent accuracy assessment was performed because a sample size of 30 to 60 samples per vegetation type, as suggested by Richards (1986), was beyond the scope of this study. Nevertheless, some idea of the accuracy can be gained by comparing the classification result for the training sites with the vegetation recorded at these sites.

DATA ANALYSIS

A Geographical Information System (ArcView 3.2; ESRI, Redlands, CA) was used to investigate the spatial distribution of the vegetation. Unless otherwise stated, the whole of Mkwaja Ranch excluding areas of closed forest (and excluding unclassified pixels) was used for the analyses. Cover of a vegetation type is defined here as the percentage of the total classified area occupied by that vegetation type; it does not refer to the cover of individual plants within vegetation types.

As it was impossible to determine the exact grazing pattern, it was assumed that any particular point was grazed by cattle from the nearest paddock. The area of each paddock system was therefore defined using Thiessen polygons (Fig. 2). To investigate the abundance of different vegetation types in relation to the distance from a paddock, the vegetation within a polygon was analysed in annuli of 100 m width centred on the paddock. At first, the grazing area within these annuli increases with distance from a paddock (Fig. 3); however, due to the proximity of neighbouring paddocks (mostly 4-8 km) the mean available area decreases beyond 2000 m. On average, 80% of the available area lies within 3500 m of the nearest paddock. Areas more than 4000 m away from any paddock are only found in some areas in Mkwaja South and were not included in the analyses.

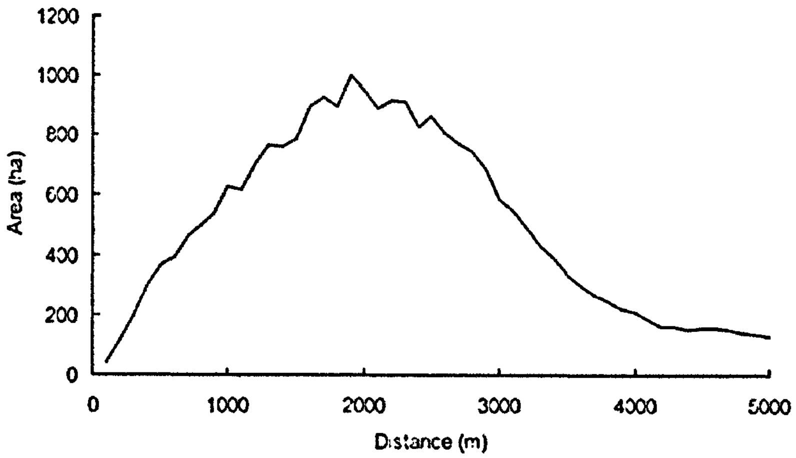

Fig. 3. Relationship between the available area and the distance from the nearest paddock calculated in annuli of 100m width.

The ratio of bushland to grassland (B/G ratio) was calculated as a means of quantifying bush encroachment. In calculating this ratio, 'grassland' was taken to include both grasslands and thicket-grassland mosaics. *Panicum* wooded grasslands were excluded because they occur on wetter sites and are not susceptible to encroachment by the main bushland species. Polynomial regression was used to find relationships between the distance to the paddocks and the intensity of bush encroachment.

To investigate the influence of grazing intensity on the spread of bushland, the B/G ratio was related to the stocking rate and area of grazing land in each paddock system. For this purpose, grazing land included all bushland and grassland within the Thiessen polygon. The average stocking rates in hectares per livestock unit (ha lsu^{-1}) between 1989 and 1994 were calculated for 11 paddock systems using information from the monthly reports (Table 1). Where two paddocks were very close together it is likely that areas were grazed by cattle from both paddocks. For this reason paddocks 8, 11, 12 and 13 were not included in the analyses. Paddocks 1, 17 and 18 were excluded because of a high cloud cover.

Table 1. Area, stocking rate and bushland/grassland (B/G) ratios within Thiessen polygons defining the various paddock systems at Mkwaja Ranch, Tanzania. The grazing area includes all grassland, thicket-grassland mosaic, wooded grassland and bushland vegetation types. Average number of cattle and stocking rate as ha per livestock unit (lsu) between 1989 and 1994 are also given. Grassland includes grasslands and thicket-grassland mosaics; wooded grassland was not included as these moist grasslands are less susceptible to bush encroachment.

Paddock system	Area (ha)	Grazing area (ha)	Number of cows	Stocking (ha lsu^{-1})	Bushland (%)	Grassland (%)	B/G ratio
2	1476	811	634	1.3	0.3	0.21	1.43
3	1996	1222	447	2.7	0.25	0.22	1.14
4	2985	1793	254	7.1	0.24	0.24	1.00
5	2180	901	464	1.9	0.22	0.14	1.57
6	1908	1051	674	1.6	0.25	0.17	1.47
7	1628	1033	407	2.5	0.32	0.2	1.60
9	2717	1432	595	2.4	0.32	0.12	2.67
10	1940	1415	466	3.0	0.41	0.31	1.32
14	3272	2280	672	3.4	0.29	0.29	1.00
15	1813	1151	360	3.2	0.37	0.37	1.00
16	3298	2252	524	4.3	0.3	0.44	0.68

Results

VEGETATION TYPES

The vegetation of Mkwaja Ranch and Saadani was classified into 15 different vegetation types. Names for grasses follow Ibrahim & Kabuye (1988), names for trees and shrubs follow Beentje, Adamson & Bhanderi (1994). A map showing the distribution of different vegetation types is shown in Fig. 4.

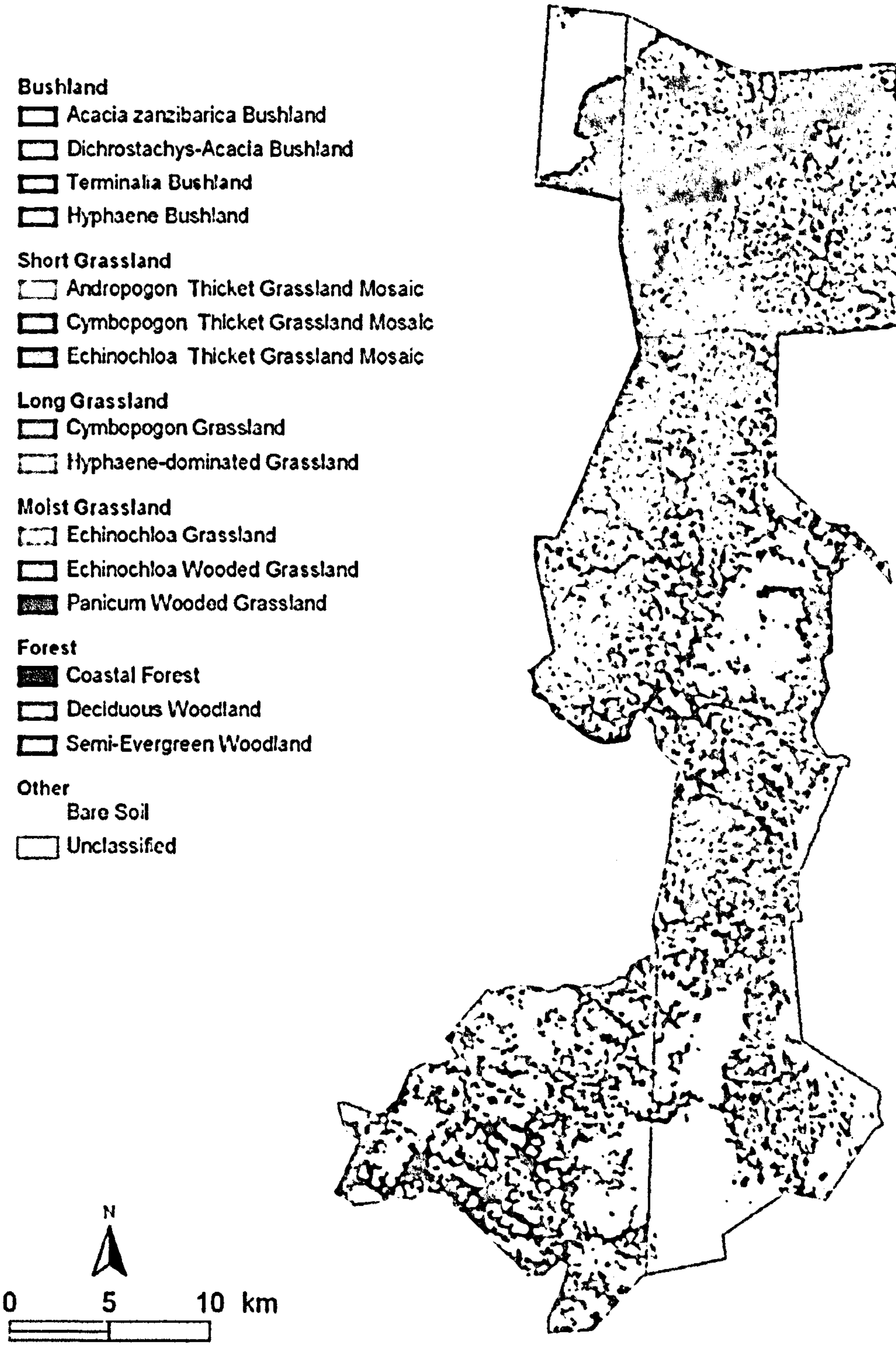

Fig. 4. Vegetation map of Mkwaja North, Mkwaja South, Saadani Game Reserve and Zaraninge Forest Reserve in Tanzania based on interpretation of a Landsat TM satellite image.

Bushlands

Four different types of bushland were identified. *Acacia zanzibarica* is the main tree species in *Acacia zanzibarica* bushland, where it could form dense, almost mono-specific stands with up to 1500 trees ha^{-1}. This bushland type is commonly found close to paddocks where the soil and grass layer had been severely disturbed by cattle grazing and brush cutting. In the Saadani Game Reserve dense stands of *Acacia zanzibarica* occurred mainly along the coast, but some recent bush development seemed to have occurred in heavily grazed areas within the reserve.

The *Dichrostachys-Acacia* bushland was defined mainly on structural grounds as a mixed bushland of various small (1.5-2.5 m in height) woody species. It commonly occurred in homogeneous patches of several hectares on well drained soils near paddocks. Abundant species included *Dichrostachys cinerea, Acacia nilotica* and *Acacia mellifera,* all of which are known to be encroaching species (Klötzli 1980; Fritz, Garine-Wichatitsky & Letessier 1996; Skowno *et al.* 1999). Other commonly found tree species in this vegetation type were *Catunaregam nilotica, Piliostigma thonningii, Harrisonia abyssinica, Balanites aegyptiaca, Commiphora africana, Terminalia spinosa, Annona senegalensis* and *Acacia nigrescens.* Tree densities are between 400 and 900 ha^{-1}.

Terminalia spinosa, a common tree in many savanna vegetation types, was the dominant species in *Terminalia* bushland, which was frequent on well drained soils in disturbed areas such as close to paddocks. In this bushland type *Terminalia spinosa* could form very dense, homogeneous stands of < 1000 trees ha^{-1}. In the shade of older *Terminalia* trees, young evergreen species were found, suggesting that *Terminalia* bushland represents a successional stage from open savanna to forest.

Hyphaene bushland had a high abundance of the palm *Hyphaene compressa* and several woody species also found in *Dichrostachys-Acacia* bushland. On Mkwaja Ranch it occured chiefly in parts of the fly belt (a strip of land which was regularly cleared of woody plants to prevent the spread of tsetse flies) and in some areas where *Hyphaene*-dominated grassland is the main surrounding vegetation type. *Hyphaene compressa* is known to form dense stands in response to brush cutting (Klötzli 1980).

Grasslands

Tall grasses such as *Hyperthelia dissoluta* and *Cymbopogon caesius* dominated the grass layer of the two 'long grassland' vegetation types. *Hyphaene*-dominated grassland may be dominated by either of these grasses; the woody stratum in this vegetation type is mainly represented by *Hyphaene compressa* with a density of 20-80 individuals ha^{-1}. Towards the south of the study area, *Hyphaene*-dominated grassland graded into *Cymbopogon* grassland. This grassland type was dominated by *Cymbopogon caesius* and palms were mostly replaced by scattered trees (< 30 ha^{-1}), mainly *Terminalia spinosa* and *Acacia zanzibarica*. Fire seemed to be an important determinant of these vegetation types.

The thicket-grassland mosaic was a common vegetation type composed of small clumps of dense, semi-evergreen trees and bushes dispersed in an open grassland of short to medium height. There was a high diversity of woody plants including a mix of savanna and forest species. Tree and bush density is between 20 and 100 ha^{-1}. The species composition of the grass layer varied. In Saadani, *Cymbopogon caesius* was the dominant species, but was replaced by *Echinochloa haploclada* on moister soils. *Andropogon gayanus*, which often occurred interspersed with *Cymbopogon caesius*, became dominant and replaced *Cymbopogon caesius* in the north. Although these two grasses are tall, they occurred intermixed with short grass species such as *Heteropogon contortus*, *Panicum infestum*, *Digitaria milanjiana* and *Eragrostis superba*. For this reason, the thicket-grassland mosaic vegetation types are summarised under 'short grasslands'.

The grasses *Echinochloa haploclada* and *Panicum maximum* are typical representatives of 'moist grassland'. *Panicum maximum* forms homogeneous and almost impenetrable stands in *Panicum* wooded grassland on floodplains and along riverine forests. The bush *Hibiscus tiliaceus*[1] was the main component of the woody stratum with a density between 30 and 100 trees ha^{-1}. In drier areas *Panicum maximum* was gradually replaced by tall-growing *Echinochloa haploclada* (*Echinochloa* wooded grassland). This was also the dominant grass in the almost treeless *Echinochloa* grassland, a vegetation type occurring mainly on pure black cotton soils in the south. Other typical grasses in this type were *Setaria incrassata*, *Sporobolus* spp. and *Bothriochloa insculpta.*

Forests and Woodlands

The evergreen or largely evergreen coastal forests were divided by Klötzli (1980) in two subclasses: hilltop forests and riverine forests. Forest species lists can be found in Burgess *et al.* (1992), Sheil (1992), Burgess, Dickinson & Payne (1993), Burgess, Clark & Rodgers (1998) and Mwasumbi, Burgess & Clarke (1994). Deciduous woodland or miombo was a common vegetation type in the western part of Mkwaja and outside the ranch area. It was an open woodland dominated by deciduous trees and a continuous grass layer. It occurred mainly on sandy soils. A listing of common species of this vegetation type can be found in Knapp (1973). Semi-evergreen woodland was characterized by a fairly homogeneous tree layer of semi-evergreen, medium-sized (3-4 m) species such as *Piliostigma thonningii*, *Commiphora africana* and *Annona senegalensis*. *Pancium maximum*, which is known to be shade tolerant (Boonman 1993; Scholes & Walker 1993), was the main grass in the undergrowth.

The overall classification accuracy for the training sites was 77% (kappa coefficient 0.75). Producer accuracy for the individual vegetation types ranged

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[1] wrongly stated as *Cordia ovalis* in the publication

from 50% to 100%, and user accuracy from 57.7% to 100%. It was lowest for deciduous woodland, which was confused with semi-evergreen woodland, *Dichrostachys-Acacia* bushland, confused with other bushland types, and for *Echinochloa* thicket grassland mosaic, which was confused with *Dichrostachys-Acacia* bushland.

SPATIAL DISTRIBUTION OF VEGETATION TYPES

Table 2 summarizes the differences in the distribution of the main structural types of vegetation. Grassland cover increased by a factor of four from Mkwaja North to Saadani. Thicket-grassland mosaic also increased while bushland and woodland decreased towards the south. As a result the ratio of bushland to grassland (B/G ratio) decreased by a factor of three from Mkwaja to Saadani. The B/G ratio also varied considerably between different parts of the ranch, from 0.68 for paddock system 16 to 2.67 for paddock system 9 (Table 1).

Table 2. Cover of the main structural vegetation types in Mkwaja North, Mkwaja South and the Saadani Game Reserve, Tanzania. The B/G ratio for each area is also shown (for this purpose grassland includes thicket-grassland mosaics).

	Cover (% of classified)		
Vegetation type	Mkwaja North	Mkwaja South	Saadani
Grassland	6.3	15.1	23.9
Thicket-grassland mosaic	19.3	29.4	29.8
Wooded grassland	12.1	9.2	10.7
Bushland	29.7	28.4	21.7
Woodland	20.3	9.5	3.4
Forest	9.7	6.3	6.8
Bare soil	2.6	1.9	3.6
B/G ratio	1.2	0.6	0.4

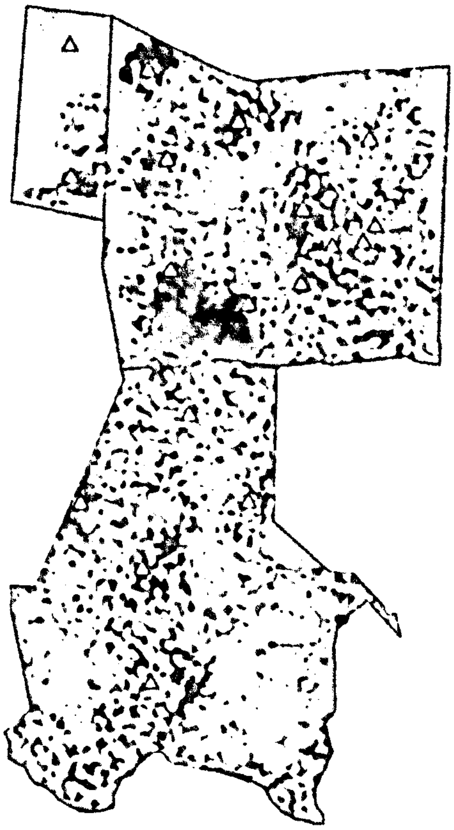

Fig. 5. Bush encroachment on Mkwaja Ranch as indicated by the percentage of bushland. The map was created applying a 10 × 10 mean filter to the vegetation map (Fig. 4); bush pixels were assigned a value of 1 and all the other pixels 0. Darker areas have a higher bush cover. Triangles show the location of the paddocks; white areas are unclassified.

Bush vegetation was most strongly developed around paddocks (Fig. 5). Figs 6 and 7 depict the changes in mean cover of the main vegetation types in relation to distance from the paddocks. In the first few hundred metres, bush cover increased to reach a peak at 500-1000 m. For some paddocks cover then gradually decreased (e.g. 3, 4 and 6), whereas for others it declined to a more or less constant minimum level (e.g. 7 and 16). Polynomial regression using the data for all paddocks showed that grassland increased linearly with distance from the paddock (F=242.78, df=39, P<0.001, R^2=0.865). Bushland showed a different pattern, increasing first and then decreasing (Fig. 6). In the first few hundred metres the impact of cattle (mainly trampling) was so high that there was bare soil. Beyond about 900 m the cover of bushland decreased. The relationship between the B/G ratio and distance from the paddock after 900 m is best described by a quadratic equation (F=2690, df=31, P<0.001, R^2=0.995; Fig. 8). There is a significant negative correlation between the B/G ratio and the available grazing area within a paddock system (F=15.80, df=9, P= 0.004, R^2=0.662; Fig. 9). There is also a statistically significant (α=0.05) correlation between stocking rate and the B/G ratio (F=6.13, df=9, P= 0.038, R^2=0.434).

There are interesting differences in the spatial patterns of the different types of bushland (Figs. 6b, 7). *Dichrostachys-Acacia* bushland had a marked peak at around 250 m from the paddock. In contrast, amounts of *Acacia zanzibarica* and *Terminalia* bushland at first increased rapidly with distance and peaked between 800 and 1100 m from the paddock. *Dichrostachys-Acacia* bushland and *Terminalia* bushland then decreased steadily, while *Acacia zanzibarica* bushland decreased up to 2000 m and then remained constant at around 10%. *Hyphaene* bushland exhibited a completely different pattern, being scarce close to the paddocks and becoming more abundant with distance (Fig. 6b); this pattern is similar to that for long grassland (Fig. 6a). *Acacia zanzibarica* bushland was widespread and was only missing from moister areas occupied by wooded grasslands or from areas where forests or woodlands predominate. In these areas, *Terminalia* bushland was more common. *Terminalia* bushland could also be found mixed in with forest and woodland vegetation. *Dichrostachys-Acacia* bushland showed a pattern similar to that of *Acacia zanzibarica* bushland but with a greater concentration around paddocks.

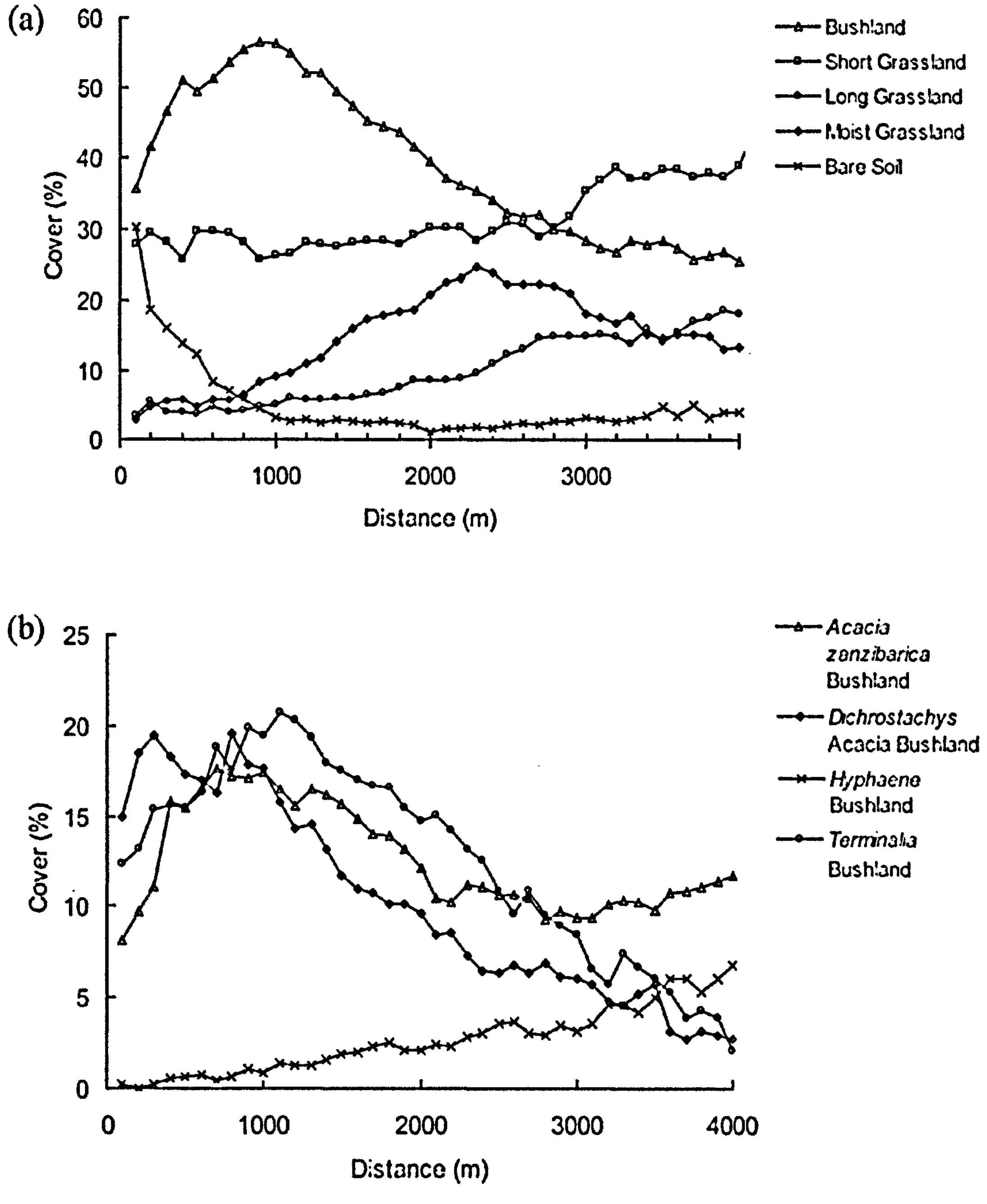

Fig. 6. (a) Changes in the mean cover of different grassland types and all bushland with distance from the paddocks; (b) Changes in the cover of various bushland types with distance from the paddocks.

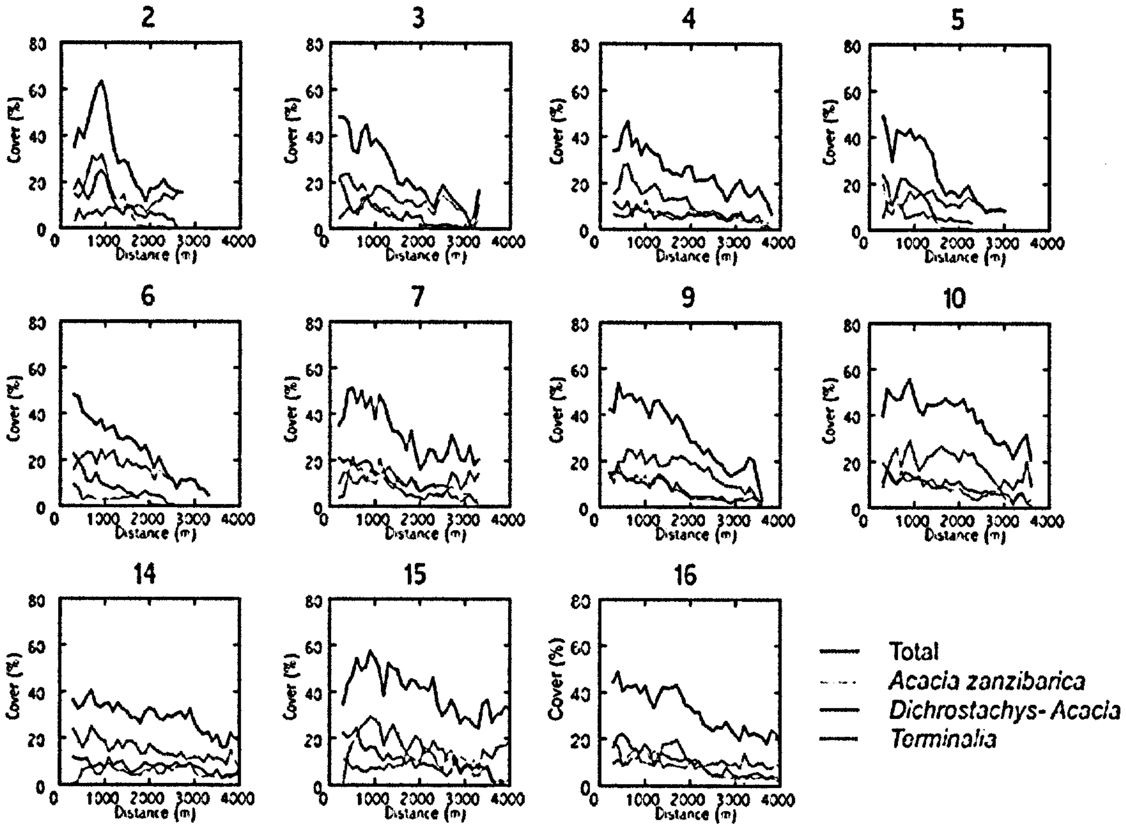

Fig. 7. Changes in the cover of three bushland types and in all bushland with distance from individual paddocks on Mkwaja Ranch.

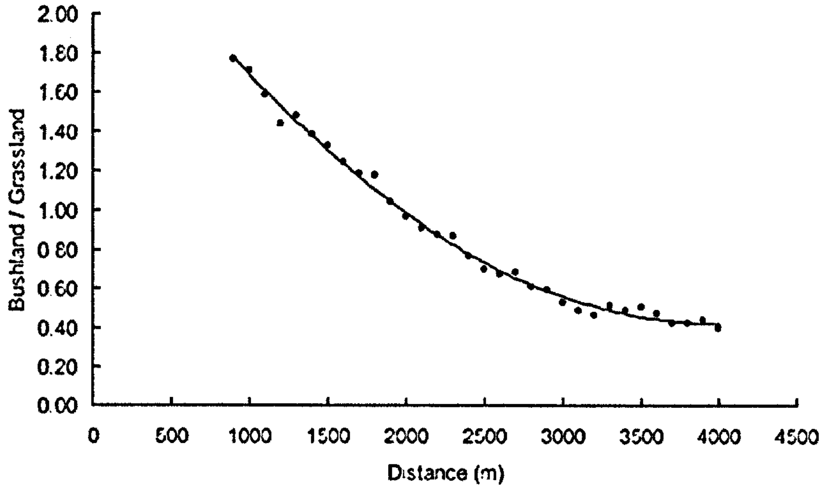

Fig. 8. Changes in the mean bushland/grassland ratio (y) with distance from the paddocks (x). The quadratic equation describing this trend is
$y = 1.42486E\text{-}7 * x^2 - 0.001136 * x + 2.6852$ ($R^2 = 0.995$, $P < 0.001$).

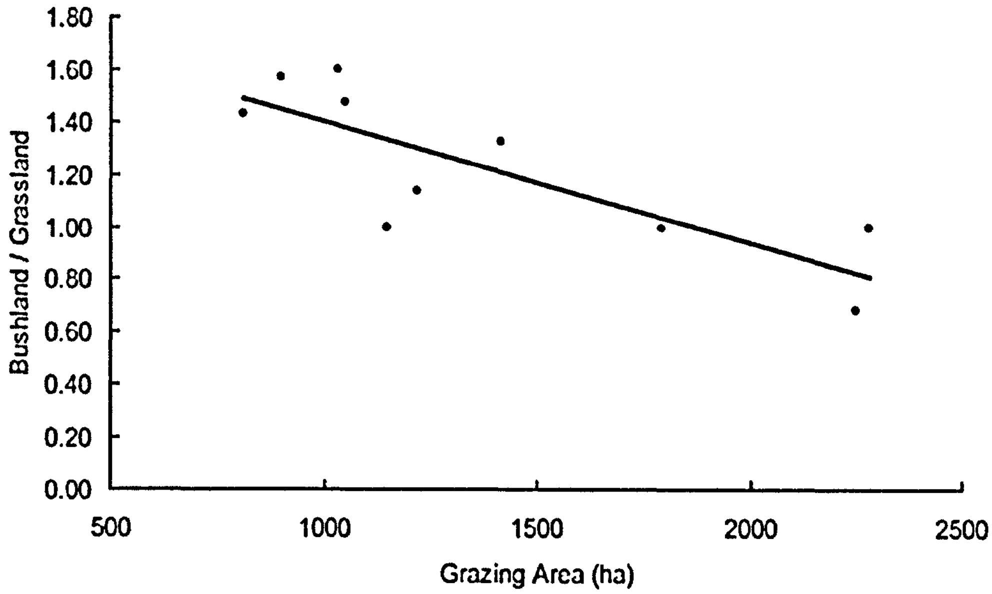

Fig. 9. Relationship between the area available for grazing and the bushland/grassland ratio for 10 paddocks on Mkwaja Ranch. The regression line equation is $y = -0.0005 * x + 1.859$ (R^2=0.662; P= 0.004).

Discussion

VEGETATION MAPPING

Previous studies using satellite imagery to investigate the ecological impact of ranching have characterised the condition of the vegetation by means of indices based on combinations of different spectral bands (Hanan *et al.* 1991; Pickup 1994). Such indices are sensitive to above-ground biomass and are therefore useful for monitoring the degradation of grasslands; they are less useful in structurally heterogeneous vegetation with a complex mix of grassland and bush. In this study we preferred to use the remote- sensed image to make a vegetation map. Although this is a more difficult and time-consuming procedure, such a map provides more useful information. In practice, several characteristics of savanna vegetation can make the classification of remotely sensed images difficult. For example, areas that have been recently burnt or intensively grazed may have a lower biomass than undisturbed areas and thus a different reflectance.

As a result, savanna types such as long- and short-grass savannas may be confused. To minimize such problems one could use an image taken in the late rainy season when the vegetation has had time to recover from disturbances, or develop a map from a series of two or more images taken a few months apart (Grignetti *et al.* 1997). In our study area, however, these solutions were not feasible due to the high cloud cover for much of the year.

Despite the 6-year interval between the dates of the image and the field survey, the multispectral classification of the Landsat TM image produced good results. The vegetation map we obtained gave reasonably reliable information on the abundance and distribution of the main vegetation types, and provided clear evidence about how cattle ranching has influenced the vegetation. An overall accuracy of 77% is sufficient for many uses and lies within the range obtained in other studies (e.g. 76.7% for blanket bog in Scotland, Reid & Qarmby 2000; 85% for Mediterranean vegetation, Grignetti *et al.* 1997; 40% for an arid grassland shrubland vegetation in Australia, Lewis 1998). The main problems were in distinguishing structurally similar vegetation types. For example, species dominating one type of bushland also occur in other types, while *Terminalia* bushland has many of the evergreen and semi-evergreen species found in semi-evergreen woodland. Relatively open bushland can be confused with grassland or thicket-grassland mosaics. *Echinochloa* wooded grassland and *Panicum* wooded grassland both occur in moist areas and are structurally similar. Tall stands of *Andropogon gayanus*, which can grow to > 2m, may resemble *Hyperthelia dissoluta* and so thicket-grassland mosaic can be wrongly classified as *Hyphaene*-dominated grassland. On the other hand, if the *Hyphaene*-dominated grassland is grazed the grass layer is similar to that of the thicket-grassland mosaic.

DISTRIBUTION OF BUSHLAND

The two main trends in the distribution of bushland are a decrease in abundance from north to south, and a concentration of bush in the neighbourhood of paddocks. While the decrease of bushland and woodland types from Mkwaja North to Mkwaja South could be partly a result of north-south gradients in rainfall, topography and soils, the local patterns of bush encroachment around former paddocks are undoubtedly of anthropogenic origin. The B/G ratio decreases at distances above 900 m from a paddock and reaches a value of 0.4 at 4000 m (i.e. the same value as the average for the Saadani Game Reserve in this study). This suggests that bush encroachment in Mkwaja is chiefly the result of ranching, and that the vegetation structure more than 3500-4000 m from a paddock has not been significantly affected by livestock. On Mkwaja Ranch, the distances between the paddocks are mainly between 4 and 8 km, so that >55% of the area of the ranch lies within the zones mostly affected by bush encroachment (300-2500 m). The significant negative correlation between the B/G ratio and the available grazing area per paddock may be best explained by the fact that, with increasing grazing area, the maximum distance to the paddock also increases.

Similar bushland distribution patterns have been found by Perkins & Thomas (1993a; 1993b) around artificial water holes in a semi-arid savanna rangeland in Botswana. They distinguished four, more or less distinct zones: a 'sacrifice' zone with low vegetation cover (0-400 m from water holes), a nutritious grass zone (200-800 m), a zone of high bush encroachment (200-2000 m), and a zone of shrub savanna. In a simulation model, Jeltsch *et al.* (1997) generated comparable spatial patterns using parameters appropriate for a semi-arid grazing system in the Kalahari (385 mm average annual rainfall). After a simulation period of 16 years, the pattern of bush cover strongly resembled that found in our study. From this we may conclude that the pattern of bush encroachment in this humid savanna is similar to that found in semi-arid savannas despite the expected differences in the balance between grasses and woody plants. Using the same model as Jeltsch *et al.* (1997), Weber *et al.* (1998) investigated the influence of stocking rate on bush encroachment and found that there was a threshold density of livestock below which bush encroachment was very low and above which it increased rapidly. A simulation of vegetation development over 50 years with an annual average rainfall of 300-400 mm and a stocking rate of >10 ha lsu^{-1} resulted in a maximum bush cover of > 60%, a level similar to that recorded at Mkwaja at an average distance of 900 m from paddocks. The stocking rates on Mkwaja were 1-7 ha lsu^{-1}, significantly higher than in many semi-arid grazing systems for which 9-16 ha lsu^{-1} are recommended (Perkins & Thomas 1993b), but the carrying capacity at Mkwaja may be higher due to higher rainfall (annual average of 900 mm). However, average stocking rate can be a poor predictor of the grazing pressure in an area. Particularly in grazing systems that are based on central points like paddocks or waterholes, the impact close to those points is significantly higher than it is in areas further away.

Other management factors have also influenced the development of scrub at Mkwaja. On Mkwaja North the brush cutter was used regularly from the 1960s to the 1980s to fight bush encroachment. According to several sources (Klötzli 1980; Lupi & Walther 1994, ranch reports), this had the effect of promoting both regeneration from seed and regrowth, particularly of *Acacia zanzibarica*, and actually promoted bush encroachment. Although brush cutting was finally abandoned in the 1980s, the effects of this management on the vegetation are still evident. For example, near paddocks 2 and 3 (Fig. 7) the area with the highest bush density probably represents the zone that was first invaded by *Acacia zanzibarica* as a result of intensive cattle grazing and was then repeatedly cut. In contrast, the paddocks in Mkwaja South were spared from brush-cutting and it can be assumed that the bush pattern is primarily grazing-induced. For example, around paddocks 14 and 16 the peak in bush density is less marked and closer to the paddocks than is the case for most northern paddocks.

Although there was a general increase in bush associated with ranching, there were noticeable differences in the distribution of the various types of bushland, which can be explained by differences in the ecology of the dominant bush species. For example, around paddocks 5, 6, 7 and 16 the mixed *Dichrostachys-Acacia* bushland is more abundant than *Acacia zanzibarica* bushland. The seed pods of *Dichrostachys cinerea* and *Acacia nilotica*, the most important species in this bushland type, are eaten by cattle and the seeds are thus dispersed in places where animals gather (cf. Van Staden, Kelly & Bell 1994; Miller 1996; Brown & Carter 1998; R. Cochard pers. obs.). In certain places (such as in paddock 7) high densities of seeds of *Acacia nilotica* and *Dichrostachys cinerea* could still be found 2 years after the paddocks were abandoned. *Acacia zanzibarica* has dehiscent pods which are not consumed by cattle. It appears to be favoured in areas of high to intermediate grazing, not because of enhanced dispersal but as a result of increased seedling recruitment and survival. *Acacia zanzibarica* seems to be well adapted to a wide range of conditions in this area and bushlands are not restricted to the vicinity of the paddocks. *Acacia zanzibarica* bushlands also occurs in Saadani where there has been no cattle grazing for many years, but native herbivores are relatively abundant. The factors that led to the formation of these stands are unknown, but grazing by animals such as hartebeest *Alcelaphus buselaphus* Pallas and the introduced wildebeest *Connochaetes taurinus* Burchell and/or fire management may be involved.

Terminalia spinosa has winged seeds which are wind-dispersed. It is a successful colonizing species, particularly in undulating terrain within the *Andropogon* thicket-grassland mosaic where soils are often visibly degraded by trampling and grazing (e.g. around paddocks 4, 9 and 14). In some areas that were cleared of forest or woodland (e.g. around paddocks 4, 7 and 9) it seems to be the first woody species to recolonize, perhaps restoring the shade and nutrient conditions needed for the establishment of forest species.

Although *Hyphaene compressa* is cited in the ranch reports and in the work of Klötzli and others (Klötzli 1980; Lupi & Walther 1994) as one of the most severe 'problem' species, *Hyphaene* bushland is not prominent near paddocks. This suggests that it was promoted less by cattle than by brush-cutting; this is consistent with its abundance in those parts of the fly belt which were probably

Hyphaene-dominated grasslands before the area became a ranch. According to ranch reports, infestations by *Hyphaene compressa* were intensively treated with arboricides followed by manual clearing. This could also explain why in 1994 there was relatively little *Hyphaene* bushland near the paddocks.

DISTRIBUTION OF GRASSLAND

The abundance of long grassland increases gradually from < 5 % cover near paddocks to about 15 % at 2800 m distance (Fig. 6a). Fire tends to favour long grassland; *Hyperthelia dissoluta*, the major species of long grasslands, is only grazed when young (Ibrahim & Kabuye 1988) while it is promoted by intense fires (Knapp 1973; Klötzli 1980). Fire also supresses most bush species other than the fire-adapted *Hyphaene* (Knapp 1973). Both factors, management for cattle pastures and subsequent fire control, may thus explain why this grassland type was replaced by short-grass types under heavy grazing. Short grassland was probably more susceptible to bush encroachment since it provides better pasturing for cattle, and occasional fires were probably not intense enough to kill off bush regrowth. Short grassland covers almost 30% of the areas close to paddocks and this proportion does not increase recognizably up to about 3000 m away from paddocks (Fig. 6a).

The short grass vegetation in the vicinity of paddocks contains many ruderals and invasive species (e.g. Barker, Thurow & Herlocker 1990; Young, Patridge & Macrae 1995; Cornelius & Schultka 1997; Rietkerk *et al.* 2000). The paddocks themselves were highly disturbed environments which received high inputs of animal excreta. The grass community within paddocks clearly represents a floristically distinct vegetation type, but due to its very confined distribution it was not distinguished from other short grassland types in this study.

CONCLUSIONS

The results of this study help us to understand why intensive livestock ranching as practiced on Mkwaja Ranch is unsustainable. The serious problems facing the ranch managers at Mkwaja became evident at a relatively early stage in the history of the ranch, and were described by Ford & Blaser (1971), writing just 16 years after the enterprise began (p. 77): 'It is still not possible to say whether management will succeed in controlling vegetation and disease at the same time or whether, in the end, these obstacles to cattle raising will prove too expensive for the ranch to continue'. For a few years, a stocking rate of 1-7 ha lsu^{-1} could be maintained. If, however, carrying capacity implies a 'continuing yield without environmental damage' (Allaby 1994, p. 70), an appropriate stocking rate for this type of single-species livestock systems is probably much lower and may be similar to that recommended for more arid savanna ecosystems. The climate in humid savannas is generally less erratic than in arid ecosystems. This implies that the potential for degradation of grass and soil resources is reduced, since degradation in rangelands is often aggravated during episodic drought events (Rietkerk 1998; Fynn & O'Connor 2000; Sternberg *et al.* 2000). However, the potential for gradual bush encroachment promoted by livestock may be higher in humid savannas that have been derived from woodland and forest and are mainly fire controlled.

In theory, highest stocking rates may be sustained under uniform grazing pressure over the whole area. In practice, however, grazing impact is never uniform, even in natural grazing systems. A discussion about an ecologically appropriate and sustainable stocking rate should therefore account for the spatial component of any ranching system. In this context, the advantages of traditional, nomadic livestock systems over modern intensive ranching are again being rediscovered (Behnke, Scoones & Kerven 1993). Even on confined private ranches there are ways to achieve a more regular grazing distribution. For example, paddocks should only be used for a limited period (1-2 years); grazing should then be transferred to an area that has not been recently used, thus reducing the dangers of long-term overgrazing in the surroundings of paddocks. Clearly this option is feasible for paddocks but not for dams or boreholes. The daily management of the herd is also important; herdsmen should quickly lead cattle away from the paddock in the morning, so that areas further away from the paddock are grazed with similar intensity.

More research on grazing patterns as well as on the ecological factors determining humid savanna vegetation is needed to understand their dynamics under different management regimes. The survey technique presented here provides a convenient way of monitoring the process of bush encroachment. Further, a comparison of the distribution patterns of the various bush species at the landscape level may be useful in developing improved management regimes targeted on particular species. In the particular case of Mkwaja Ranch, which will soon become part of the new Saadani National Park, it will also be interesting to observe how the vegetation changes when the natural factors such as fire and a diverse assemblage of herbivores resume their former importance.

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Again he started to read the newspaper, paid attention to the maps which were published, the names of towns, coasts and deserts where battles were still being fought. One evening he sat down to his table in front of a white sheet of paper. It was now spring. The window was open, in the mild air of the night. One branch of the big acacia which grew in the garden almost touched the wall, and he could see by the illumination of the lamp the branches with their feather-like leaves, which were trembling in front of the background of darkness, the oval folioles, coloured brightly green by the electric light, which by and then were swaying like feather tufts, suddenly quivering by a self-governing movement, as if the whole tree would awaken, breathing out, shaking itself, and then everything calmed down again, and they sank back to their stillness.

Claude Simon, The Acacia

Secondary *Acacia zanzibarica* woodlands in coastal Tanzania: 1. Structure and biomass along a woodland-savanna gradient

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Summary

1. Fifty years of intensive cattle grazing on Mkwaja Ranch in Tanzania have led to extensive bush encroachment of the coastal savanna vegetation by the myrmecophyte *Acacia zanzibarica.* Today extensive, almost mono-specific secondary woodlands cover an area of about 46 km^2 of the former ranching area. In this paper we describe changes in vegetation structure along a gradient from open savanna to dense bushland. The study site was near a former paddock in an area that was heavily used by cattle while the ranch was in operation. This woodland in this area has regenerated since the early 1980's when the bush was last cleared.

2. In June 2002, we established and surveyed 97 circular plots (4 m radius). Soil samples taken from each plot were analysed for texture, organic matter, and total phosphorus and nitrogen. The height and basal diameter of all trees were measured, and various components of aboveground biomass (wood, spines and foliage) were determined by allometric calculations. Tree foliage (biomass and leaf area index, LAI) and grass layer (total and living biomass, resp. LAI) were assessed (or estimated) on three occasions, twice during the wet season (June 2002 and 2003) and once in the dry season (February 2003).

3. Tree density reflected an underlying soil texture gradient, with few trees on more sandy soils and sometimes closed woodland on loamy-clayey soils. Levels

of soil organic matter and total phosphorus increased along this gradient, and nitrogen levels were highest in dense stands of *Acacia zanzibarica.*

4. Even in the virtual absence of large herbivores, spines were most strongly developed in the most vulnerable, lower parts of trees, and spinescence was highest on trees in open savanna. The abundance of pseudogalls and ant nests, however, increased with increasing tree size. Ant nest counts and tree living wood ratio (~ tree vigour) best explained foliage flush during the two wet seasons. During the dry season, when on average less than half of the foliage biomass was present, competition with the grass layer and other trees in dense stands had a higher influence on tree foliage.

5. The biomass, LAI and leaf water content of the grass layer were strongly influenced by fire. The average specific leaf area (SLA) of plant species was, in contrast, mainly influenced by soil nitrogen content and tree density, but not by fire. The living biomass and LAI of the grass layer also decreased with increasing tree density. Although tree layer LAI was on average about half of grass layer LAI, the overall transpiration rates were estimated to increase with increasing tree density.

6. By increasing total vegetation transpiration rates and decreasing grass growth, bush encroachment and woodland establishment had a significant impact on grazing resources available to cattle and native wildlife. However, the long-term impact of woodland on the savanna ecosystem appears to be less important than the factors soil and fire. *A. zanzibarica* woodlands may, therefore, be seen as a transitional state or as the extreme end of bush density in a still resilient humid savanna that in the absence of ranching is mainly fire-maintained.

Key-words: bush encroachment, East Africa, tree density, soil gradient, fire, tree-grass interactions, herbivore defences, multivariate

Introduction

Savannas are tropical vegetation types in which ecological processes such as primary production, hydrology and nutrient cycling are strongly influenced by woody plants and C_4 grasses, and only weakly by plants of other growth forms (Walker 1987). While savannas were once seen as intermediate, transitional states between tropical forests at one extreme and grasslands at the other, they are now regarded as rather stable vegetational states exhibiting a balance between woody and grass components. This balance between trees and grasses can be influenced by many factors including soil conditions, fire and grazing; availability of water appears to be particularly important (e.g. Huntley 1982, Tothill & Mott 1985, Walker 1987, Scholes & Walker 1993, Blösch 2002). To explain savanna structure Walker & Noy-Meir (1982) suggested a simple model of two-layer competition in the rooting zone, whereby the dense superficial root systems of C_4 grasses make them superior competitors for water during the wet season, while the deeper rooted trees have access to ground water and so may retain their foliage throughout the year. This model has been supported by some more recent empirical studies, but not by others (e.g. Knoop & Walker 1985, le Roux, Bariac & Mariotti 1995; c.f. Scholes & Archer 1997). For example, Higgins, Bond & Trollope (2000) suggested that long-term effects of fire on life history-disturbance interactions on tree demography may be more important for the understanding of tree-grass balance in many African savannas.

One of the most important elements in the flora of African savannas are the various species of *Acacia* (Ross 1981). The roots of most acacias are associated with symbiotic nitrogen-fixing bacteria, and their foliage therefore has a higher nitrogen content than many other savanna species (Coe & Beentje 1991, Odee *et al.* 1995, Harrier *et al.* 2000). The foliage of acacias is therefore a valuable food source for large herbivores; browsing species such as the giraffe feed on acacias throughout the year, while mixed feeders such as many antelopes (e.g. kudu and impala) use it mainly during the dry season when green grass is not available (Kingdon 1997). In view of the high nutritional quality of *Acacia* foliage, it is perhaps not surprising the genus exhibits a remarkable array of anti-herbivore defences including plant secondary substances, leaf nectary glands to attract ants (most acacias), simple spines of various forms, and swollen thorns which serve as the domatia for symbiotic species of ants on obligate ant-acacias (myrmecophytes) (Coe & Beentje 1991, Ross 1981). Defensive structures are present even in the absence of herbivores, but higher allocation to defence can be induced by browsing pressure (e.g. Young 1987, Milewski, Young & Madden 1991, Young, Stanton & Christian 2003, Huntzinger *et al.* 2004, Ward & Young 2002). In addition to direct herbivore defences, acacias exhibit several other features which have been related to resisting herbivory or the impact of fire, such as a high physiological adaptability, with a broad range of growth forms (e.g. Archibald & Bond 2003), and various regenerative traits including the ability to resprout from roots and stumps, or complex mechanisms of seed dispersal and seedling recruitment (Midgley & Bond 2001; c.f. Cochard, Edwards & Weber 2004).

When savanna ecosystems are used as rangeland, the diverse natural communities of large herbivores are usually replaced by a single introduced grazing species, the cow (Du Toit & Cumming 1999). This change in the structure of the herbivore community often leads to a change in the structure of the vegetation, with the development of dense stands of woody species in areas formerly dominated by grasses (Tobler, Cochard & Edwards 2001, Snyman 1998). There are various ways in which the spread of bush may affect savanna ecosystem processes and thus influences vegetation development. In most savannas, water is the most important limiting factor, and transpiration by trees can considerably reduce water availability to other plants (Scholes & Archer 1997). Tree encroachment can also alter soil nutrient conditions, especially if the trees are nitrogen-fixing leguminous species (Martin *et al.* 2003, Hibbard *et al.* 2003, Odee *et al.* 1995).

In some ranching areas, such as in northern Australian savannas and in Southern African fynbos, there has been severe encroachment by exotic, invasive

Acacia species which replace the native flora and radically alter important ecosystem processes (Humphries *et al.* 1991, Holmes & Cowling 1997). Such changes to those sensitive, dry vegetation types are often considered to be irreversible (c.f. Cochard & Edwards 2004a). East African savannas, however, seem to be more resilient under livestock grazing pressure than savannas on other continents, and until now alien tree species have rarely gained a stronghold (Solbrig, Medina & Silva 1996; but see Shiferaw *et al.* 2004). This may reflect the fact that African savannas evolved with a rich assemblage of large grazing and browsing ungulates (Du Toit & Cumming 1999, Lovett *et al.* 2000). There have been several studies on bush encroachment in Africa (c.f. listing in Tobler, Cochard & Edwards 2003) but few have investigated vegetation patterns and changes after ranching has been abandoned, and most of these have focused on herbage composition and nutrient conditions in former pastures or paddocks (e.g. Backéus, Rulangaranga & Skoglund 1995, Young, Patridge & Macrae 1995, Scholes & Walker 1993, Augustine 2003). We know only one study in East Africa (Reid & Ellis 1995) that investigated secondary acacia woodlands in a dry upland savanna rangeland in Kenya.

In this study we investigate the structure and biomass of secondary woodland in a former cattle ranch in Tanzania, where the dominant encroaching tree species was the myrmecophyte *Acacia zanzibarica* (S. Moore) Taub. var. *zanzibarica.* This species today forms extensive, almost mono-specific woodlands in many areas of the former ranch. *A. zanzibarica* is a common savanna tree of East Africa and one of several *Acacia* species popularly known as 'whistling thorn' acacias (Coe & Beentje 1991). The tree can grow to a height of > 15 m and has a strongly monopodial growth form, with a dominant main axis and relatively few, elongated primary branches which are held more or less horizontally and are themselves only sparsely branched. Compared to flat-topped 'umbrella' trees such as *Acacia nilotica*, the canopy of slender *A. zanzibarica* is very open and casts little shade, and even dense woodlands still support a continuous grass layer. Its trunks and branches bear large stipular, woody spines which partially form thick bi-lobed pseudo-galls at their base that are inhabited by symbiotic crematogastine ants. The leaves, which bear extrafloral nectaries (petiole glands), are held in tight clusters close to the main branches and are thus protected from browsers by the spines which normally protrude beyond the foliage.

Aspects of the ecology of four symbiotic ant species occurring on the related myrmecophyte *Acacia drepanolobium* have been well documented in several studies in Kenya (c.f. review in Cochard 2004a). Two of these ant species have been recorded on *A. zanzibarica* in Mkomazi Reserve, Northern Tanzania, namely *Crematogaster sjöstedti* Mayr and *Crematogaster nigriceps* Emery (Stapley 1999). *C. sjöstedti* (the black cocktail ant) is the only species which also lives within hollow tunnels in stems and branches leading down to the tree's roots (Stapley 1999, Stanton & Young 1999). In our study site the black cocktail ant also builds papery nests on branches. On Mkwaja ranch, *A. zanzibarica* was not browsed by cattle (Ford & Blaser 1971), and was also one of few savanna trees to be completely ignored by goats (Kozák 1980). In contrast, giraffe and other wildlife seem to have been little deterred by ant defences (pers. obs.; Madden & Young 1992).

Myrmecophytism (i.e. ant-plant mutualism) may be regarded as functionally analogous to chemical defences as levels of tannins are generally low in myrmecophytes compared to acacias lacking ant symbionts (Ross 1981, Ward & Young 2002). To maintain continuous protection from ant colonies all myrmecophytes need to produce leaves throughout the year so as to provide a continuing supply of food from foliar nectaries or tended scale insects (Ross 1981, Hocking 1970; c.f. Cochard 2004a). Myrmecophytism in the genus *Acacia* is only found in tropical America (14 species) and in Africa (16 species) (Hocking 1970). In contrast to America, ant-acacias in Africa do not produce protein bodies on their leaves, and ant colonies must therefore supplement their diet by foraging off trees (Stapley 1999, Hocking 1970). Ants and tree foliage, nevertheless, may be interpreted within a single systemic frame and in environmental context. Most of the recent research in Africa has so far emphasised the role of ants as defensive agents against browsing by mammalian herbivores (e.g. Madden &Young 1992, Stapley 1998, Huntzinger *et al.* 2004). It is, however, still debated whether myrmecophytism in acacias *actually* developed in response to mammalian browsing (Hölldobler & Wilson 1990) or had evolved before the appearance of mammals as a response to insect herbivory (Coe & Beentje 1991, Janzen 1966). It is clear that in modern ecosystems, however, ants play several defensive functions and may be important in protecting their host plants against mammalian browsing, insect herbivores, and climbing plants (Willmer, Stone & Mafunde 1999).

We surveyed stands of *Acacia zanzibarica* along a gradient of woodland density from open grassland to closed woodland. The main aims were to investigate variation in (a) stand structure and biomass, and (b) resource allocation of *Acacia zanzibarica* to foliage, woody biomass and defence. Specific questions were:

1. How does the density of *Acacia zanzibarica* woodland (in terms of tree counts and woody biomass) correlate with several measured soil variables in an area impacted by cattle?
2. How does tree growth form vary along the woodland density gradient, and how is tree biomass (branching, foliage and spines) stratified along the vertical axis?
3. How do the abundance of defensive structures of *A. zanzibarica* (simple spines and swollen thorns) and the abundance of ant nests vary along the woodland density gradient?
4. What is the seasonal variation in the leaf area index (LAI) and biomass of tree and grass foliage and how strong is the influence of fires?
5. How does the aboveground biomass of trees and grasses correlate along the density gradient?

Since there existed very little baseline data on the ecology of *A. zanzibarica* we used a strictly multivariate approach to investigate these individual questions and elucidate interdependencies and overall patterns.

Study site

The former Mkwaja Ranch in Tanzania occupied an area of 462 km^2 of coastal savanna grassland, woodlands and forest (Fig. 1; Tobler, Cochard & Edwards 2003). Before the area was grazed by cattle, the humid savannas on the Tanzanian coast were probably fire-maintained systems, with wildlife playing a secondary role. There has been some debate as to whether the savanna replaced an initially continuous coastal forest cover as a result of human interference during pre-historic times (e.g. Klötzli 1980); the savanna vegetation is still interspersed by patches of dense evergreen thickets and, in some parts, coastal forest. The ranch, which was established in 1954, was one of the largest in East Africa, and at peak times during the 1960's and 1970's supported over 13'000 head of cattle (That 2004). Bush encroachment on pastures became evident within a few years after the ranch began operation (Ford & Blaser 1971), and brush-cutting during the 1970's only made the problem worse, as encroaching trees resprouted from roots and the grass sward was weakened (Klötzli 1980). Brush-cutting was given up in the early 1980's, and by 1994, after 40 years of intensive cattle ranching, all night paddocks were surrounded by a zone of thick bushland which reached its highest density at a distance of around 900 m (Tobler, Cochard & Edwards 2003). In 2003 anthropogenic woodlands dominated by *A. zanzibarica* covered around 46 km^2, or about 12 % of the former ranching area.

The ranch was never profitable, and during the late 1990's the numbers of cattle were steadily reduced until operations ceased in August 2000. There followed two years of uncontrolled poaching, with the result that the already very low wildlife populations were further reduced. The former ranch has now been incorporated in the new Saadani National Park, and it is hoped that wildlife will colonise it from the former Saadani Game Reserve, now also part of the National Park, which shares a common border with the ranch to the south (Fig. 1). For the time being, however, the area provided a unique setting for a study of post-ranching vegetation dynamics with little disturbance by large herbivores. For example, whereas in Saadani giraffe density was estimated at more than 1.4 km^{-2}, in Mkwaja it was probably less than 0.15 km^{-2} (Treydte 2004, pers. obs.).

The study site was the *A. zanzibarica* woodland belt south of the former Mariamu paddock on Mkwaja Ranch (5°43'S, 38°47'E; Fig. 1). This was the oldest and most intensively used paddock and during the 1980's and 1990's held up to 1000 cattle. Because the surrounding areas were recurrently brush-cut until 1982, the trees were mainly not more than 20 years old, though some may have regenerated from stumps and roots. Soils at Mariamu were mostly grey vertisols derived from coral sands. Soils were all relatively uniform and unstructured to a depth of more than 1.5 m. Part of the site was burnt sometime in October/November 2001. High, intensive rainfall during only a few days in March and in April 2002 promoted intensive grass growth; some exceptional rains also occurred in July/August 2002 (Table 1). In October 2002, during the early dry season, about half of the study area was burnt, and there was a second, much hotter fire at the end of February which killed many trees in those parts of the site unaffected by the October fire (c.f. Cochard and Edwards 2004a). Records of rainfall during the wet season in 2003 were lost, but were below average, probably less than half of the mean annual records from 1955-1998 (Table 1).

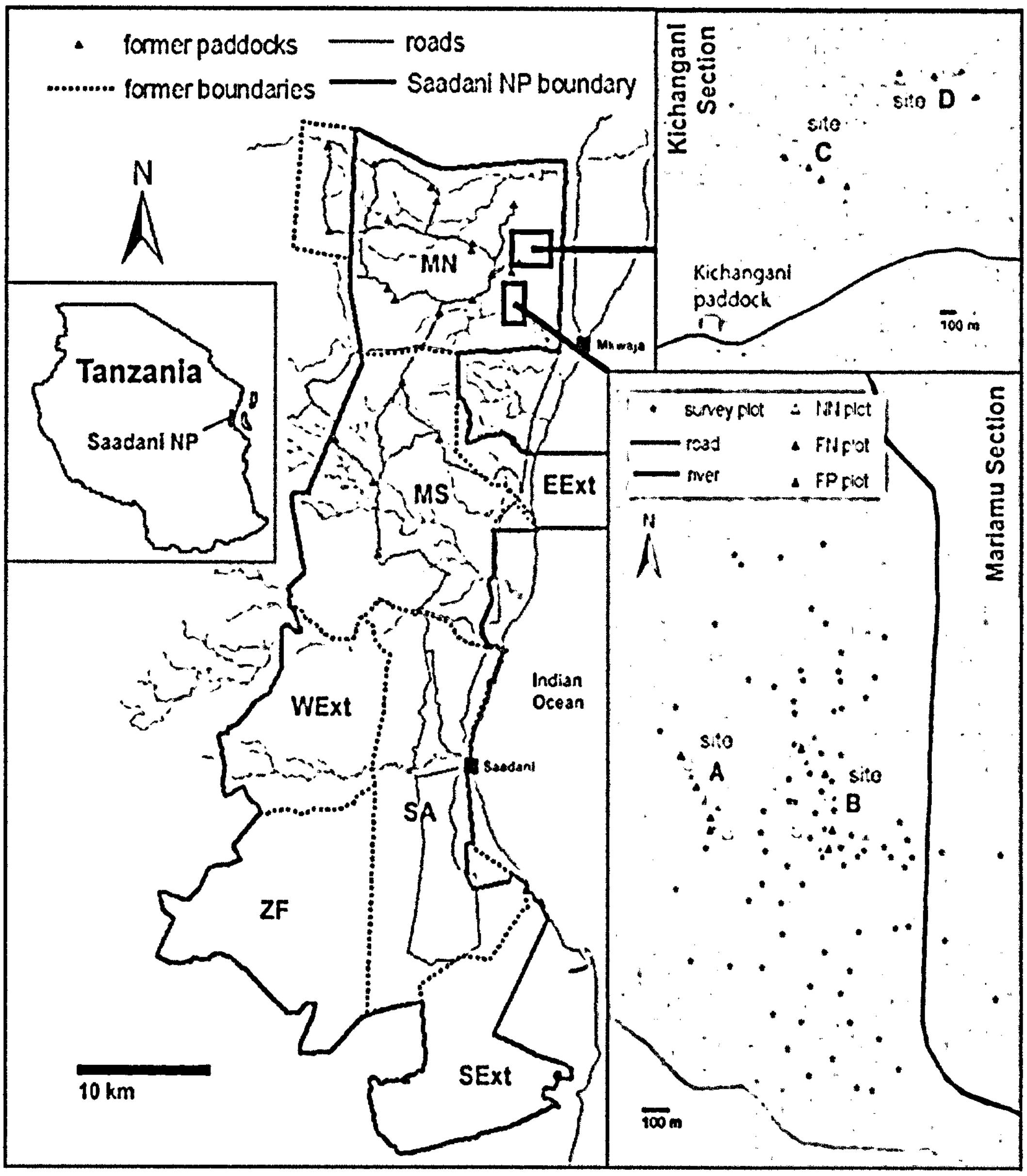

Fig. 1. Location of the study sites on the coast of Tanzania. The left side shows a map of recently created Saadani National Park with its constituent parts: the northern former ranching area of Mkwaja North [MN] and Mkwaja South [MS], former Saadani Game Reserve [SA] and Zaraninge State Forest [ZF], and additional extensions to the National Park in the East [EExt], West [WExt] and South [SExt]. The insets show the position of the study plots. 81 survey plots (Mariamu Section only) were used in the present study and in Cochard & Edwards (2004a, 2004b). 16 NN (control) plots (sites A, B, C and D in Mariamu and Kichangani Sections) were used in this study, Cochard & Edwards (2004a, 2004b) and Cochard, Edwards & Weber (2004). 16 FN (felled) and 16 FP (felled and poisoned) plots were used in the study by Cochard, Edwards & Weber (2004) and Cochard & Edwards (2004b), but not in the present study.

Table 1. Average monthly temperature (daily maximum and minimum) and rainfall for the years 1955-1998, and total monthly rainfall in the year 2002.

month	temperature °C		rainfall mm	
	daily max.	daily min.	average 1955-1998	year 2002
January	32.8	24.5	51	12
February	33.1	24.6	45	51
March	33.0	24.4	103	106
April	32.0	24.0	198	236.5
May	31.4	23.3	145	22.5
June	30.0	21.8	44	2
July	29.6	20.7	33	73
August	29.9	20.9	38	68
September	30.9	21.8	40	32.5
October	31.6	22.6	95	2
November	32.1	23.7	131	?
December	32.3	24.2	96	?
mean°; total*	31.6°	23.0°	1019*	> 605.5*

Methods

PLOT SELECTION

Using a GIS-based vegetation map prepared in an earlier study (Tobler, Cochard & Edwards 2003) we selected 60 points in *A. zanzibarica* woodland. In May 2002, these points were located in the field with the aid of GPS and the nearest *A. zanzibarica* tree to each point was tagged and taken as the centre of a circular plot of 4 m radius (area 50.3 m^2). In five cases, where other tree species were inside plots the centre of plots was shifted to another *A. zanzibarica* tree to provide pure stands of *A. zanzibarica*. Since only a few of the points proved to be in dense woodland, we selected an additional 40 points in the field so as to cover the full gradient from dense woodland to open savanna. Three study plots were abandoned because they could not be relocated.

ALLOMETRIC TREE BIOMASS ESTIMATES

With its regular growth form, *Acacia zanzibarica* lends itself well to allometric estimates of tree biomass based upon measurements of the length and diameters of the trunk and major branches. In July 2002, we cut 119 branches of different sizes from *A. zanzibarica* trees growing near Mariamu to obtain the necessary regression relationships between branch dimensions and components of biomass. For each branch, we recorded the basal diameter and the total length and number of branchings, and measured the dry weight with a 10 kg spring balance. The abundance of simple spines (referred to as 'spines') and pseudogalls (referred to as 'swollen thorns') and the density of foliage on each branch were assessed by eye using a system of four categories for each parameter. All leaves were then pulled from branches, dried in paper bags in a solar drying oven, and subsequently weighed. We measured the lengths of all spines and the diameters of the swollen thorns, and samples of both types of spine (100 of each) were removed, measured and weighed. From these data linear regressions were calculated relating biomass of leaves and spines to branch diameter and visual categorical estimates (eqs. 1-6; Appendix).

More detailed information on the vertical distribution of biomass was obtained for a sample of 40 trees felled in September and November 2002. The trunk diameter of each tree was measured at 1 m intervals from ground level up to the highest point in the canopy and its volume was calculated. The height above ground of each lateral branch was recorded as well as the branch diameter at base and the number of branchings; the degree of branching category, foliage density and abundance of spines and swollen thorns was recorded using the system of categories described above. For trees with multiple stems, each stem was first measured individually, and measurements were then added together. A sample of wood from the base of the trunk was taken to determine the wood density (eq. 7; Appendix). From these data, linear regressions were calculated relating total tree woody, foliage and spine biomass to tree bole diameter and visual categorical estimates (eqs. 8-12; Appendix). Only 34 trees > 6 m were used to illustrate relative vertical distribution of biomass.

Observations on root structure were made in a deep gully where the root system of one large *A. zanzibarica* tree was partially exposed. Following heavy rainfall it was possible to dig out more of the root system and describe its branching pattern.

PLOT TREE SURVEYS

In May 2002, the positions of all trees within or overhanging each plot were recorded using an X-Y coordinate system. For each tree, bole diameter at 20 cm height was measured and the percentage of the canopy within the plot was estimated. On a tree with multiple stems the average bole was calculated by the formula: $diameter = \sqrt{(bole_{(1)}^2 + bole_{(2)}^2 + \ldots)}$. A competition index was calculated from tree bole diameter and position within plots (see Cochard and Edwards 2004a). Tree heights (m), tree breadth-height ratios and the ratios of dead wood on trees were estimated by eye. The degree of branching was recorded on a four-point scale, ranging from category 1 for an erect tree with almost no branching to category 4 for a tree with spreading crown with a high level of branching. Visual assessments were also made of the abundance of simple tree spines, the proportion of swollen thorns (spines with pseudo-galls) and the density of foliage using scales from 0 to 4. To assist in these assessments, reference photographs were made to illustrate each category. If ants were present on trees the species was noted, and the number of ant nests was counted. Tree foliage density was surveyed in June 2002, February 2003 and June 2003, and on each occasion it was noted whether the trees were still alive. Using allometric equations 8-12 (Appendix) plot woody and foliar biomass were calculated.

GRASS LAYER BIOMASS AND LAI

Grass biomass in each plot was measured in June 2002 and in June 2003. All aboveground plant material was cut from four 41×41 cm^2 quadrats located 2 m from the centremost tree along the four cardinal points. The material from the four quadrats was pooled, weighed fresh in the field, and weighed again after drying. The ratio of dried green grass matter against total grass dry matter was calculated by multiplying the grass water content ((wet-dry)/dry grass weight ratio) by the factor of 1.65, which was about the mean water content of completely fresh grass. From this the living grass biomass was then calculated. The grass layer in February 2003 was sampled on the permanent plots of another study (Cochard, Edwards & Weber 2004), and from this we calculated the equations 13-16 (Appendix). Using these equations the grass biomass and grass water content were estimated on plots for February 2003.

For each plot an average grass specific leaf area (SLA) in $cm^2\ g^{-1}$ was calculated by multiplying estimated grass species ratios on plots (species cover/total grass cover) with the SLA of the respective grass species as provided in Table 2, which summarises data from Cochard & Edwards (2004b). Multiplying this average SLA with the total and living biomass data of June 2002, February 2003 and June 2003, the total and effective grass leaf area indexes (LAI) for the three dates were calculated.

SOIL SAMPLING AND ANALYSES

Time-domain-reflectometry (ThetaProbe type ML2x; Delta-T Devices) was used to measure soil water content at 10 cm depth. Eight measurements were made on each plot 1 to 3 hours after heavy rain on 28th July 2002. Average plot values were taken as estimates of field capacity. In June 2003, four soil samples (0-40 cm) per plot were taken using an augur from the points used to measure grass biomass. The samples from one plot were mixed and dried.

Subsamples were digested using the Kjeldahl method and total N and P contents determined using continuous flow spectrophotometry. Soil organic content was determined by loss on digestion with hydrogen peroxide H_2O_2, and percentages of sand, loam and clay were measured using the standardised suspension method in use by the Swiss Federal Agricultural Research Stations (FAL, FAW & RAC 2004).

STATISTICAL ANALYSES

In order to determine the main factors which influence a tested dependent variable, regression analyses were performed in an iterative process (for descriptions of statistics and methodology see Chatterjee, Hadi & Price 2000, Chatterjee & Hadi 1988, Minitab Inc. 2003). All variables were first checked for normality using P-P plots. A transformation to a natural logarithm provided normality of most data sets. Seedling and resprout data (Results in Cochard & Edwards 2004a) were normalised using the normal score function. All tested independent variables were first entered in the regression calculations. Extreme values with a high influence on the overall regression equation were repeatedly identified after the calculation using Welsch-Kuh's distance (DFITS) and Cook's distance. Additionally, outliers were identified in normal residual plots. Extreme values were deleted until the data had a similar overall influence on the equation. In that way, of the 781 data points for the tree variable analyses, on average 13 and maximally 30 data points were deleted during analyses. Of the 97 data points for the plot variable analyses, on average 6 and maximally 12 data points were deleted. Of the 119 data points for the branch variable analyses, on average 9 and maximally 18 data points were deleted.

Then a best subsets regression analysis was performed to identify the optimal set of predictor variables. As selection criterion we used Mallow's C_p measure (the lowest value). Redundant variables were removed from the new regression calculations, after which extreme values were again recurrently identified and deleted. Then again a new best subset analysis was performed, until the best equation with no extreme values was determined. We stated this final equation, and the stepwise inclusion of predictors with regard to the final equation. This stepwise inclusion does not necessarily follow the same path of a stepwise regression analysis. In stepwise regression, the next best predictor is always selected on the basis of the equation in the last step, therefore not always leading to the best equation, which will show up in best subsets analysis. After determination of the final equation, we performed a best subsets analysis only on the selected variables and included the variables according to their successive appearance on the next level. The statistical software Minitab 14 (Minitab Inc. 2003) was used for all statistical analyses.

The main results of all the regression equations are summarised in Table 3 for soil, tree layer and grass layer 'plot' variables, in Table 4 for individual 'tree' variables and in Table 5 for 'branch' variables. For each dependent variable tested the adjusted R^2 of the final model is listed, whereby higher values of R^2 indicate higher accuracies of the final models. The weights of predictor variables are stated as percentage contribution of the adjusted R^2 of the model at the variable inclusion step relative to the adjusted R^2 of the final model. This means that the weights, indicated by squares and triangles, must be read relative to the value of the final adjusted R^2 and may not be viewed as absolute weights. Triangles indicate whether the relation between a predictor and the dependent variable is positive (▲) or negative (▼) in the final equation. The triangle of the first variable included into the model is underlined. Variables that were not considered for analysis from the beginning are shaded in grey colour. In order to elucidate hidden correlations, more than one analysis was performed for some test variables, varying inclusion of predictor variables. By and large, the results of an analysis were interpreted in the light of the results of other analyses in order to elucidate overall interdependencies. All final regression equations were highly significant by $p < 0.001$. A detailed listing of all variables used in regression analyses, their descriptive statistics, the actual regression equations and values of the adjusted R^2 at any variable inclusion step are given in an Appendix in Cochard (2004b).

Results

GENERAL SITE CONDITIONS

The 98 plots were all situated in formerly open grassland vegetation which had been colonized to varying degrees by *A. zanzibarica*; apart from a few shoots of the palm *Hyphaene compressa* this was the only woody species present on plots above seedling size, though five plots had been moved to avoid including other tree species. Tree density in the plots varied widely from 2 to 50 *A. zanzibarica* trees 100 m^{-2} (c.f. Cochard & Edwards 2004a).

In June 2003, the herbaceous layer was dominated by a few grass species, mainly *Panicum infestum*, *Heteropogon contortus*, and by the sedge *Fimbristylis triflora* (Table 2). The grasses *Diheteropogon amplectens*, *Digitaria milanjiana* and *Hyperthelia dissoluta* were commonly encountered on rather sandy soils in open savanna areas. *P. infestum*, *H. contortus*, *Andropogon gayanus* and *F. triflora* were predominant in woodland areas on loamy soils, while *Bothriochloa* spp. and *Sporobolus pyramidalis* were mainly found on loamy-clayey soils (Table 2). The mean grass cover on plots was about 66.6 %, with the few herbs interspersed in the grass matrix accounting for less than 0.5 % of average plot cover (Table 2).

The soils of the study plots graded from predominantly sandy (max. sand content of 95.5 %) to loamy (min. sand content of 58.2 %; Table 3). Mean contents of soil organic matter (0.18 %) and nitrogen (0.022 %) were low and highly correlated with soil texture, lying close to a distinct sand-clay axis of PCA loadings (Table 3, Fig. 2). The mean concentration of total phosphorus was 0.021 %. Organic matter decreased with increasing sand content, whereas grass and tree biomass had a slightly positive influence (var. 3, Table 3). Soil water holding capacity at 10 cm depth was best predicted by organic matter, and also soil texture (var. 4, Table 3). Soil phosphorus was also best predicted by organic matter, but the fit was weak ($R^2 = 15.1$ %; var. 5, Table 3). Soil nitrogen, on the other hand, was well predicted by organic matter and soil texture ($R^2 = 77.3$ %), while tree density, grass biomass and fire explained an additional 8.7 % of variation (var. 6, Table 3).

Table 2. Listing of the most common plant species on study plots, indicating average estimated percent plot cover and specific leaf area (SLA) of tree foliage (foliage only, not whole plant), grasses and sedges.

species	Plot cover	SLA (cm^2/g)	
	June 2003	mean	st. dev.
1. trees			
Acacia zanzibarica (S. Moore) Taub.	-	72.94	7.48
2. grasses and sedges*			
Panicum infestum Andersson	18.6 %	90.71	23.98
Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult.	11.4 %	30.47	1.97
*Fimbristylis triflora** Schum. Ex. Engl.	11.1 %	61.22	11.00
Digitaria milanjiana (Rendle) Stapf	7.1 %	66.47	21.82
Diheteropogon amplectens (Nees) Clayton	5.2 %	36.85	4.47
Bothriochloa bladhii (Retz) S. T. Blake	1.9 %	37.95	3.10
Sporobolus pyramidalis (P. Beauv.) Veldkap	1.9 %	40.70	5.65
Eragrostis superba Peyr.	1.5 %	35.02	8.62
Andropogon gayanus Kunth	1.2 %	31.69	12.22
*Mariscus macropus** C. B. Clarke	1.2 %	~61.2	-
*Bulbostylis pilosa** Willd.	1.0 %	~61.2	-
Hyperthelia dissoluta (Steud.) W. D. Clayton	0.8 %	~37.0	-
Bothriochloa inscupta (Hocchst. ex A. Rich.) A. Camus.	0.6 %	~38.0	-
Cymbopogon caesius (Nees) Stapf	0.5%	~37.0	-
other grasses and sedges	2.1 %	~48.3	-
total grasses and sedges	66.1 %	~48.28	~9.45
total herbs	0.5 %	-	-

About half of the plots were burnt in October in what appears to have been a 'cold' fire which had little effect on the trees. From November 2002 to February 2003 very little rain fell, so that a fire in February was nourished by almost completely dry grass. The more intense fires in unburnt plots killed many trees. Thus the mean tree density per plot declined from 16.1 ± 12.4 trees 100 m^{-2} in June 2002 to 14.3 ± 12.1 in June 2003 (c.f. Cochard & Edwards 2004a). In the PCA of Fig. 2, the fire vectors are approximately orthogonal to the soil texture vectors, suggesting that soil factors and fire, the main determinants of vegetation, were independent of each other.

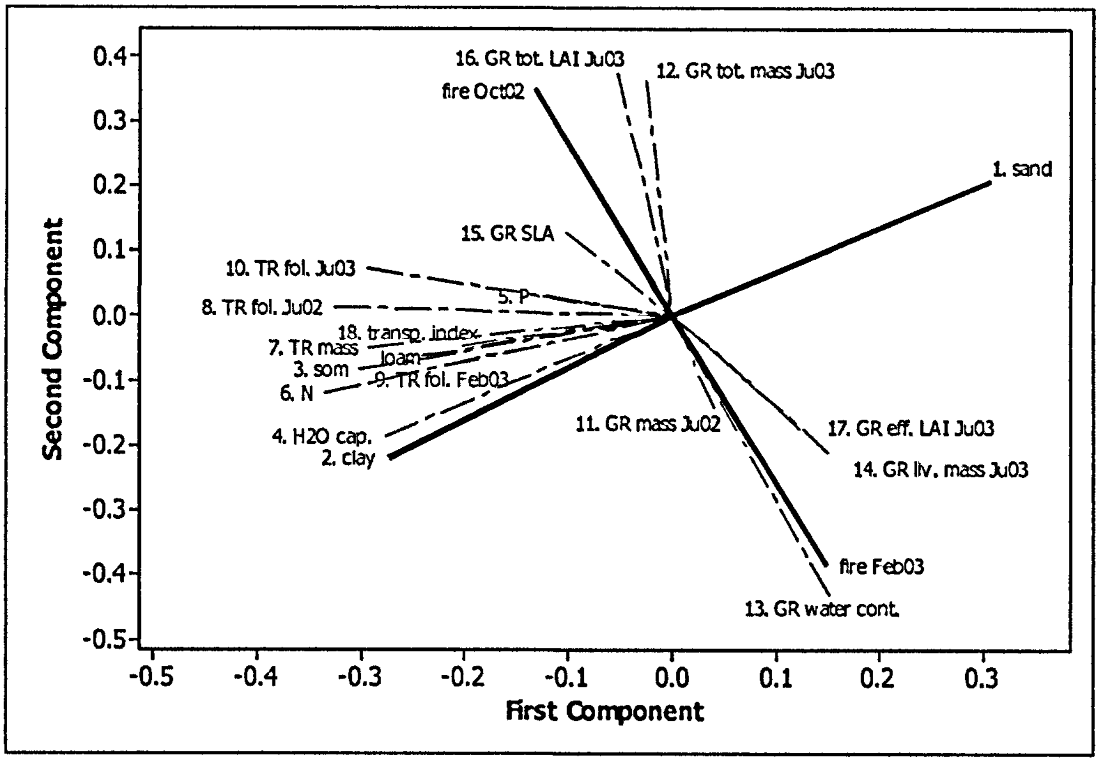

Fig. 2. PCA loadings of soil variables (sand, clay, loam, field water holding capacity (H2O cap.), soil organic matter (som), N, P), fire variables, tree (TR) variables (woody (mass) and foliage (fol.) biomass m^{-2}), grass (GR) variables (water content, specific leaf area (SLA), and total (tot.) and living (liv.) and biomass m^{-2} (mass), respectively total and effective (eff.) leaf area index (LAI)), and transpiration index. If no date is indicated, variables were sampled in or modelled for June 2003. The eigenvalue of the first component was 6.150, that of the second component 3.537.

Table 3: Summary of soil, tree and grass layer plot test variables, their descriptive statistics and main predictor variables in multiple regression models. Variables with a star (*) were calculated or modelled based on regression equations, with two stars (**) calculated also based on informed assumptions. For test variables 3-6, and 8-9 also total and effective grass LAI, and grass water content, and for variables 11-17 also ant nest count (n m^{-2}) and swollen thorn biomass of trees (g m^{-2}) were included in analyses with no effect as predictors (not shown).

Reading key				
			var. not used in analysis	
▲			var. with positive sign	
▼			var. with negative sign	
▼̲			1st included variable	
▪	▴	▾	< 3 %	rel ative contribution to final R^2
▪	▲	▼	3-10 %	
■	▲	▼	10-40 %	
■	▲	▼	> 40 %	
■			> 75 %	

	Dependent variables	Descriptive statistics				Summary of multiple regression analysis	relative stepwise contribution of predictor variables to R^2 of model																
							SUMMARY				Soil variables						Fire		Grass		Tree l.		
		average	standard deviation	maximum	minimum	adj. R^2 of final model	soil variables	fire impact	grass layer	tree layer	organic matter %	sand content %	clay content %	H_2O hold. cap. %	P content %	N content %	October fire °C**	February fire °C**	total biomass gm^{-2}	life biomass gm^{-2}	tree count 100 m^{-2}	tree biomass gm^{-2}*	foliage gm^{-2}*
Soil variables	1. sand content %	78.1	9.1	95.4	58.2	92.9	■̲						▼̲										
	2. clay content %	15.8	7.7	34.2	0.1	92.9	■̲					▼̲											
	3a. soil organic matter %	0.18	0.08	0.48	0.05	56.8	■̲					▼̲											
	3b.	"	"	"	"	64.3	■̲		▪	▪		▼̲							▴		▴		
	4. H_2O holding cap. %	25.4	5.8	38.9	14.9	80.3	■̲				▲̲	▾	▾										
	5a. phosphorus content ‰	0.21	0.02	0.24	0.16	15.1	■̲				▲̲												
	5b.	"	"	"	"	17.1	■̲	▪		▪	▲̲							▾			▲		
	6a. nitrogen content ‰	0.22	0.06	0.66	0.16	77.3	■̲				▲̲	▾											
	6b.	"	"	"	"	86.0	■̲	▪	▪	▪	▲̲	▾		▴				▴	▴		▲	▾	
Tree layer	7a. wood mass kg m^{-2}, 6.02*	1.85	1.06	5.02	0.12	29.4	■̲									▲̲							
	7b.	"	"	"	"	24.1	■̲						▲̲										
	8. foliage mass g m^{-2}, 6.02*	47.6	31.0	149	0.54	82.4	▪			■̲		▾	▾			▴						▲̲	
	9. foliage mass g m^{-2}, 2.03*	10.4	6.5	36.9	0.5	66.9	▪	▪	■	■̲		▾	▼	▼	▾		▼			▲	▴	▲̲	
	10. foliage mass g m^{-2}, 6.03*	33.0	24.0	111	0	76.9	▪		▪	■̲		▾	▼			▴				▾		▲̲	
Grass layer	11. total biomass g m^{-2}; 6.02	299	90	567	121	17.1	■̲					▲̲				▲							
	12a. tot. biomass g m^{-2}; 6.03	191	86	522	52.5	61.0	▪	■̲		▪			▾			▴		▼̲				▾	
	12b.	"	"	"	"	18.0	■̲			▪	▲			▼	▲						▴		▼
	13. water content ratio, 6.03	0.84	0.51	2.1	0.01	58.4	▪	■̲		▪		▴	▴				▼	▲̲					▼
	14. live biomass g m^{-2}, 6.03	83.4	47.0	306	0.91	49.4	▪	▪		■̲	▲			▼			▼				▼̲		▼
	15. SLA cm^2/g, 6.03*	60.1	8.2	77.3	38.3	32.7	■̲			▪			▲			▲̲					▼		
	16. total LAI cm^2/cm^2, 6.03*	1.15	0.58	3.86	0.32	62.3	▪	■̲		▪			▾			▲		▼̲					▾
	17. live LAI, 6.03*	0.50	0.29	1.92	0.01	33.3	■	▪		■̲	▲	▲		▼				▲					▼̲
π	18. transpir. index ~l/d/m^2**	0.052	0.02	0.103	0.006	63.2	▪	▪		■̲		▾	▼			▴		▴			▾	▲̲	

Table 3. Summary of soil, tree and grass layer plot test variables, their descriptive statistics and main predictor variables in multiple regression models. Variables with a star (*) were calculated or modelled based on regression equations, with two stars (**) calculated also based on informed assumptions. For test variables 3-6, and 8-9 also total and effective grass LAI, and grass water content, and for variables 11-17 also ant nest count (n m^{-2}) and swollen thorn biomass of trees (g m^{-2}) were included in analyses with no effect as predictors (not shown).

Reading key					
		var. not used in analysis			
▲		var. with positive sign			
▼		var. with negative sign			
▼		1st included variable			
•	▴	▾	< 3 %	relative contribution to final R^2	
▪	▲	▼	3-10 %		
▪	▲	▼	10-40 %		
■	▲	▼	> 40 %		
■			> 75 %		

	Dependent variables	Descriptive statistics			
		average	standard deviation	maximum	minimum
Soil variables	1. sand content %	78.1	9.1	95.4	58.2
	2. clay content %	15.8	7.7	34.2	0.1
	3a. soil organic matter %	0.18	0.08	0.48	0.05
	3b.	"	"	"	"
	4. H_2O holding cap. %	25.4	5.8	38.9	14.9
	5a. phosphorus content ‰	0.21	0.02	0.24	0.16
	5b.	"	"	"	"
	6a. nitrogen content ‰	0.22	0.06	0.66	0.16
	6b.	"	"	"	"
Tree layer	7a. wood mass kg m^{-2}, 6.02*	1.85	1.06	5.02	0.12
	7b.	"	"	"	"
	8. foliage mass g m^{-2}, 6.02*	47.6	31.0	149	0.54
	9. foliage mass g m^{-2}, 2.03*	10.4	6.5	36.9	0.5
	10. foliage mass g m^{-2}, 6.03*	33.0	24.0	111	0
Grass layer	11. total biomass g m^{-2}; 6.02	299	90	567	121
	12a. tot. biomass g m^{-2}; 6.03	191	86	522	52.5
	12b.	"	"	"	"
	13. water content ratio, 6.03	0.84	0.51	2.1	0.01
	14. living mass g m^{-2}, 6.03	83.4	47.0	306	0.91
	15. SLA cm^2/g, 6.03*	60.1	8.2	77.3	38.3
	16. total LAI cm^2/cm^2, 6.03*	1.15	0.58	3.86	0.32
	17. effective LAI, 6.03*	0.50	0.29	1.92	0.01
TL	18. transpir. index ~l/d/m^2 **	0.052	0.02	0.103	0.006

Table 3.
cont.

Summary of multiple regression analysis

	adj. R^2 of final model	relative stepwise contribution of predictor variables to R^2 of model																
		SUMMARY				Soil variables						Fire		Grass		Tree l.		
		soil variables	fire impact	grass layer	tree layer	organic matter %	sand content %	clay content %	H_2O hold. cap. %	P content %	N content %	October fire °C**	February fire °C**	total biomass gm^{-2}	life biomass gm^{-2}	tree count 100 m^{-2}	tree biomass gm^{-2}*	foliage gm^{-2}*
1.	92.9	■̲						▼̲										
2.	92.9	■̲					▼̲											
3a.	56.8	■̲					▼̲											
3b.	64.3	■̲		▪	▪		▼̲							▴		▴		
4	80.3	■̲				▲̲	▾	▾										
5a.	15.1	■̲				▲̲												
5b.	17.1	■̲	▪		▪	▲̲							▼			▲		
6a.	77.3	■̲				▲̲	▾											
6b.	86.0	■̲	•	•	▪	▲̲	▾		▴				▴	▴		▲	▾	
7a.	29.4	■̲									▲̲							
7b.	24.1	■̲						▲̲										
8.	82.4	▪			■̲		▾	▾			▴						▲̲	
9.	66.9	▪	▪	▪	■̲		▾	▼	▼	▾		▼			▲	▴	▲̲	
10.	76.9	•		•	■̲		▾	▼			▴				▾		▲̲	
11.	17.1	■̲					▲̲				▲							
12a.	61.0	•	■̲		▪			▾			▴		▼̲				▾	
12b.	18.0	■̲			▪	▲̲			▼	▲						▴		▼
13.	58.4	▪	■̲		▪		▴	▴				▾	▲̲					▼
14.	49.4	▪	▪		■̲	▲			▼			▼				▼̲		▾
15.	32.7	■̲			▪			▲			▲̲					▼		
16.	62.3	▪	■̲		•			▾			▲		▼̲					▾
17.	33.3	▪	▪		■̲	▲	▴		▼				▲					▼̲
18.	63.2	▪	•		■̲		▾	▼			▴		▴			▾	▲̲	

Table 4: Summary of tree variables, their descriptive statistics and main predictor variables in multiple regression models.

Reading key	
	var. not used in analysis
▲	var. with positive sign
▼	var. with negative sign
▲̲	1st included variable

				rel. contribution to final R^2
▪	▴	▾	< 3 %	
▪	▴	▾	3-10 %	
■	▲	▼	10-40 %	
■	▲	▼	> 40 %	
■			> 75 %	

		Descriptive statistics		Summary of multiple regression analysis																															
					relative stepwise contribution of predictor variables to R^2 of the final model																														
					SUMMARY								Plot variables												Tree variables										
					Plot vars			Tree variables					Soil variables						Fire		Grass layer				density		size		growth		vigour		defences		
	Dependent variables	average	standard deviation	adj. R^2 of final model	soil variables	fire impact	grass layer	stand density	tree size	growth form	foliage and vigour	tree defences	organic matter %	sand content %	clay content %	H_2O holding cap. %	P content %	N content %	October fire °C	February fire °C	total biomass gm^{-2}	living biomass gm^{-2}	total LAI	effective LAI	tree count 100 m^{-2}	competition index	bole diameter cm	tree height m	crown width	branching category	living wood ratio	foliage category	ant nest count	swollen thorn cat.	spine category
Tree form	1. tree height m	9.02	4.56	**74.1**	▪			■	■̲					▾	▾	▾		▴								▲	▲̲								
	2. bole diameter mm	64.5	28.9	**17.1**	■			■̲					▲			▼		▲								▼̲									
	3. crown width/height ratio	0.3	0.22	**14.1**	■			■̲	■					▴	▴	▴	▲	▼								▼̲	▼								
	4. branching category 1-4	2.4	0.8	**28.8**	■				■̲	■			▾					▲									▲̲	▼							
Tree defences	5a. spine category 1-4	2.3	0.8	**28.5**	■			■	▪	■		■̲	▲		▾											▼	▾		▲	▴				▲̲	
	5b.	2.3	0.8	**15.2**	■			■̲	■	■			▲	▾	▾											▼̲		▼	▴	▲					
	6a. swollen thorn cat. 1-4	2.11	0.80	**26.3**	■				■	■		■̲	▼	▼	▼		▴	▲									▲	▾		▲					▲̲
	6b.	"	"	**14.8**	■				■	■̲			▼	▼	▼			▲									▲	▼		▲̲					
	7. ant nest count per tree, 6.02	3.7	5.4	**62.6**	■		▪	▪	■̲	▪	■	▪		▴	▴	▴	▾	▴					▾			▾	▲̲	▴		▴		▲		▴	▴
Tree leaf phenology	8a. foliage category, 6.02	2.26	0.79	**36.0**	■		▪		▪		■	■̲		▾	▾	▾	▲					▲						▾					▲̲	▴	▴
	8b.	"	"	**32.2**	■		▪		■		■̲	▪				▾	▲	▴					▲				▲	▾			▲̲			▴	
	9a. foliage category, 2.03	0.84	0.52	**32.7**	■		■̲	■	▪		■	■		▾	▼	▼					▲̲				▼			▾			▲		▲	▴	▴
	9b.	"	"	**28.2**	■		■̲	■		▪	■	■		▾	▼	▾	▾		▴		▲̲	▴				▼			▴		▲			▲	
	9c.	"	"	**24.6**	■	■̲		■		▪	■	■		▾	▼	▾			▼̲						▼				▴		▲			▲	
	10a. foliage category, 6.03	1.65	0.9	**46.3**	■	▪	■	▪	▪	▪	■̲	■		▼	▼					▾		▼	▴		▴		▴	▾			▲̲		▲	▾	▴
	10b.	"	"	**42.8**	■	▪	■	▪	▪	■	■̲	▪		▼	▼					▾		▼	▲		▴		▴	▾		▲	▲̲			▾	▴
	10c.	"	"	**32.8**	■	▪		■	■	▪	■̲	▪		▼	▼	▾				▾					▲		▲	▼		▴	▲̲			▾	▴

Table 4. Summary of tree variables, their descriptive statistics and main predictor variables in multiple regression models.

Reading key				
	var. not used in analysis			
▲	var. with positive sign			
▼	var. with negative sign			
▲̲	1st included variable			
•	▴	▾	< 3 %	rel. contribution to final R^2
▪	▲	▼	3-10 %	
▪	▲	▼	10-40 %	
■	▲	▼	> 40 %	
■			> 75 %	

	Dependent variables	Descriptive statistics		Summary of multiple regression									
					relative stepwise contribution								
					SUMMARY								
					Plot vars			Tree variables					
		average	standard deviation	adj. R^2 of final model	soil variables	fire impact	grass layer	stand density	tree size	growth form	foliage and vigour	tree defences
Tree form	1. tree height m	9.02	4.56	74.1	•			▪	■̲			
	2. bole diameter mm	64.5	28.9	17.1	▪			■̲				
	3. crown width/height ratio	0.3	0.22	14.1	▪			■̲	▪			
	4. branching category 1-4	2.4	0.8	28.8	▪				■̲	▪		
Tree defences	5a. spine category 1-4	2.3	0.8	28.5	▪			▪	•	▪		■̲
	5b.	2.3	0.8	15.2	▪			■̲	▪	▪		
	6a. swollen thorn cat. 1-4	2.11	0.80	26.3	▪				▪	•		■̲
	6b.	"	"	14.8	▪				▪	■̲		
	7. ant nest count per tree, 6.02	3.7	5.4	62.6	▪		•	•	■̲	•	▪	•
Tree leaf phenology	8a. foliage category, 6.02	2.26	0.79	36.0	▪		▪		•		▪	■̲
	8b.	"	"	32.2	▪		▪		▪		■̲	•
	9a. foliage category, 2.03	0.84	0.52	32.7	▪		■̲	▪	•		▪	▪
	9b.	"	"	28.2	▪		■̲	▪		•	▪	▪
	9c.	"	"	24.6	▪	■̲		▪		•	▪	▪
	10a. foliage category, 6.03	1.65	0.9	46.3	▪	•	▪	•	•	•	■̲	▪
	10b.	"	"	42.8	▪	•	▪	•	•	▪	■̲	•
	10c.	"	"	32.8	▪	•		▪	▪	•	■̲	•

Table 4. continued

Summary of multiple regression analysis

relative stepwise contribution of predictor variables to R^2 of the final model

	Plot variables												Tree variables										
	Soil variables						Fire		Grass layer				density		size		growth		vigour		defences		
	organic matter %	sand content %	clay content %	H_2O holding cap. %	P content %	N content %	October fire °C	February fire °C	total biomass gm^{-2}	living biomass gm^{-2}	total LAI	effective LAI	tree count 100 m^{-2}	competition index	bole diameter cm	tree height m	crown width	branching category	living wood ratio	foliage category	ant nest count	swollen thorn cat.	spine category
1.		▾	▾	▾		▴								▴	▲̲								
2.	▲			▼		▲								▼̲									
3.		▴	▴	▴	▲	▼								▼̲	▼								
	▾					▲									▲̲	▼							
5a.	▲		▾											▼	▾		▲	▴				▲̲	
5b.	▲	▾	▾											▼̲		▼	▴	▲					
6a.	▼	▼	▼		▴	▲									▲	▾		▴					▲̲
6b.	▼	▼	▼			▲									▲	▼		▲̲					
7.		▴	▴	▴	▾	▴					▾			▾	▲̲	▴		▴		▲		▴	▴
8a.		▾	▾	▾	▲					▲						▾					▲̲	▴	▴
8b.				▾	▲	▴					▲				▲	▾			▲̲			▴	
9a.		▾	▼	▼					▲̲				▼			▾			▴		▲	▴	▴
		▾	▼	▾	▾		▴		▲̲	▴				▼			▴		▴			▲	
9b.		▾	▼	▾			▼̲						▼				▴		▲			▲	
10a		▼	▼					▾		▼	▴		▴		▴	▾			▲̲		▲	▾	▴
10b		▼	▼					▾		▼	▲		▴		▴	▾		▲	▲̲			▾	▴
10c		▼	▼	▾				▾		·			▲		▲	▼		▴	▲̲			▾	▴

In June 2003, 14 of the plots showed traces of grazing, probably from warthog, *Phacochoerus africanus* Gmelin. However, on only 3 plots was the area grazed > 3 % of the total area, and the maximum grazed area was 15 %. We saw no sign of any browsing within the plots.

TREE GROWTH FORM AND BIOMASS ALLOCATION

Average height of all trees sampled in plots was 9.0 ± 4.6 m, with a range from 1-20 m. Tree height increased with increasing bole diameter and with competition index (var. 1, Table 4). This indicates that trees were more slender in dense stands, since tree diameter actually decreased with increasing competition index (var. 2, Table 4; c.f. Cochard & Edwards 2004a). This is more directly demonstrated by the estimated height/crown width ratio, which decreased with increasing competition index, and also with increasing bole diameter (var. 3, $R^2 = 14.1$ %; Table 4). Tree branching category increased with tree diameter, but branching was higher on sturdy trees as tree height had a negative sign (var. 4, Table 4). Nitrogen was also a positive predictor of branching category (var. 4, Table 4).

A summary of the vertical distribution of biomass is presented in Fig. 3 for the 34 trees (6-15 m tall) investigated in detail. Tree bole mass decreased gradually with height while branch biomass was highest at 40-60 % tree height. Since leafiness of branches significantly increased with height up to 60-80 % tree height (ANOVA: $df = 4$, $F = 4.75$, $p = 0.001$; Fig. 3), foliage mass was about equal between 40-60 % and 60-80 % tree height (Fig. 3).

We found three types of roots for *A. zanzibarica* at the gully erosion site: a deep tap root (probably several meters deep), fine roots extending horizontally at 10-25 cm below surface, and very long, rope-like roots with a diameter of 2–5 cm and spreading horizontally > 20 m from the trunk.

The average length of simple spines was 2.4 ± 1.5 cm but some were > 10 cm long. Enlarged hollow bases of swollen thorns had an average diameter of 1.6 ± 0.6 cm with some reaching as much as 6 cm across. Biomass allocation to spines varied with position on the tree, being greatest near the ground and in the top canopy (ANOVA allocation relative to branch woody biomass: *df* = 4; $F = 5.3, p = 0.001$; relative to foliage biomass: *df* = 4; $F = 8.5, p < 0.001$; Fig. 3). Swollen thorn armour varied relative to foliage at different tree heights (ANOVA: *df* = 4, $F = 3.41, p = 0.011$; Fig. 3) but not relative to woody biomass (ANOVA: *df* = 4, $F = 2.19, p = 0.074$).

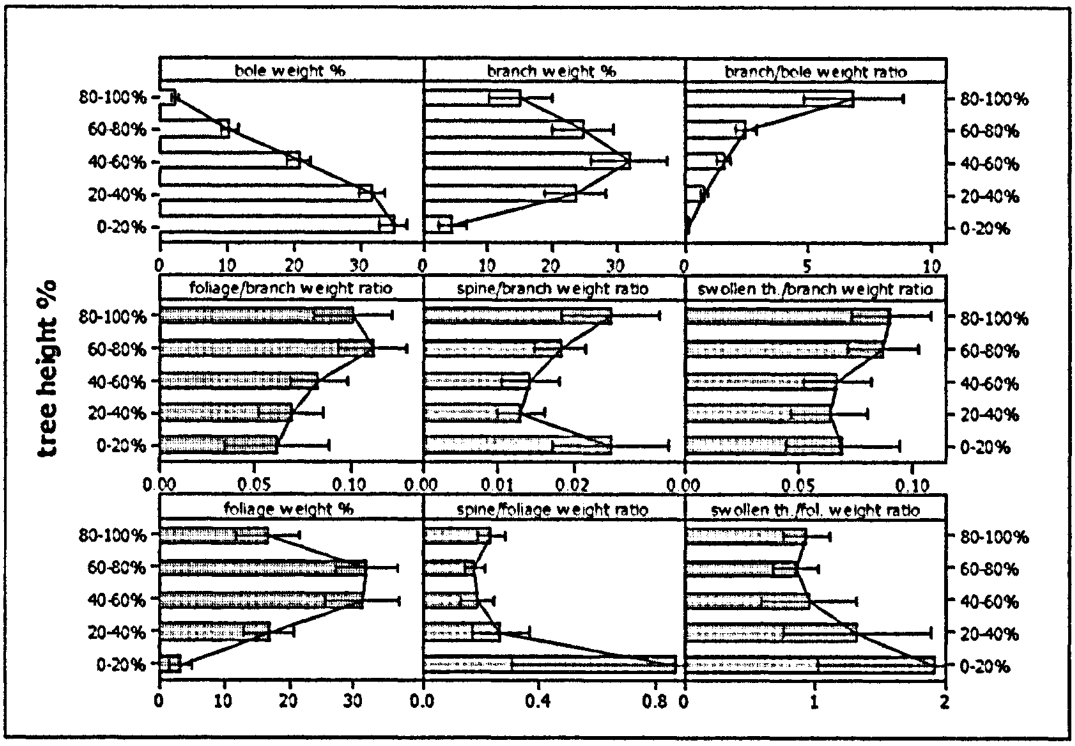

Fig. 3. The distribution of tree biomass variables from ground level (0 %) to tree canopy top (100 %) for 34 cut trees (6-15 m high). The three top panels show tree bole weight distribution (a) and woody branch weight (b), and the distribution of their ratios (c) along tree height ranges at intervals of 20 %. The three lower panels show the ratios of the total foliage (d), spine (e) and swollen thorn (f) weights over the weight of the supporting branches, whereas the bottom panels illustrate relative biomass distribution of foliage (g) along tree height with regard to total biomass (100 %), and the ratios of spine (h) and swollen thorn (i) weights over foliage weight.

About 24 % of spines and 11 % of swollen thorns on the branches collected had broken off leaving only scars. The measured spine biomass on the 119 sampled branches correlated weakly with increasing biomass of swollen thorns and of foliage, whereas potential spine biomass, i.e. allowing for the lost spines, was uncorrelated with swollen thorn biomass (vars 1-5, Table 5).

Tree spinescence as assessed visually for all 783 trees was positively correlated with swollen thorn density on trees (vars 5a and 6a, Table 4) and negatively with competition index (var. 5, Table 4). In contrast, swollen thorn category was unaffected by tree density, but was positively related to tree size and branching category, and was also affected by soil conditions (var. 6, Table 4). The already low R^2 of 26.3 % reduced to only 14.8 % if spine category was not included in the analysis (var. 6, Table 4).

Table 5. Summary of regression analysis for branch data.

Predictor variables Dependent variables	adjusted R^2 of final model	diameter cm	bracnhing count	obs. spine weight g	pot. spine weight g	obs. swollen thorns g	pot. swollen thorns g	foliage g
1. observed spine weight g	49.0		▲			▲		▲
2. potential spine weight g	63.5	▲	▲					▲
3. observed swollen thorn weight g	63.8	▲	▴	▲				
4. potential swollen thorn wgt g	74.3	▲						▴
5. foliage weight g	51.3	▲		▲				

On > 91 % of all trees, the swollen thorns contained a small black tree ant, probably *Crematogaster sjoestedti* Mayr, and ten trees were occupied by another species with a reddish-brown abdomen, probably *Crematogaster nigriceps* Emery. 67 % of trees had at least one ant nest of *C. sjoestedti*, whereas

C. nigriceps apparently did not construct nests. More ant nests were counted on larger trees, but analysis indicated that leafiness of trees also had a marked positive influence on ant nest presence and counts (var. 7, Table 4). The density of swollen thorns on tree branches appeared to have no influence on the presence of ant nests (var. 7, Table 4).

TREE BIOMASS AND LAI

Aboveground woody biomass in the 97 plots ranged from 0.1 to 5 kg m^{-2}, with an average of 1.85 ± 1.06 kg m^{-2} for all plots in June 2002, and 1.73 ± 1.94 kg m^{-2} in June 2003. Total soil nitrogen was the best predictor of woodland density (var. 7a, Table 3) while clay content took the first position when nitrogen was excluded (var. 7b, Table 3). In the PCA (Fig. 2) the vector for tree biomass is aligned with those for sand and clay, illustrating the negative correlation between tree biomass and soil sand content (see also Fig. 4).

Trees lost much of their foliage during the dry season, with the result that leaf biomass varied considerably during the year. Based on an assessment of tree foliage density, it was estimated that the mean biomass of tree foliage in the plots varied from 47.6 ± 31.0 g m^{-2} in the wet season of June 2002 to 10.4 ± 6.5 g in the dry season in February 2003 before the second fire, and to 33.0 ± 24.0 g in June 2003. There were strong positive correlations between foliage biomass and woody biomass (vars 8-9, Table 3; Fig. 5). Fig. 6 shows the mean vertical distribution of foliage biomass in the plots derived by extrapolation from the subset of 34 trees (Fig. 3). The analysis suggests that > 70 % of tree foliage in the woodland was between 3-12 m above ground, and that within this range leaf biomass was distributed fairly uniformly.

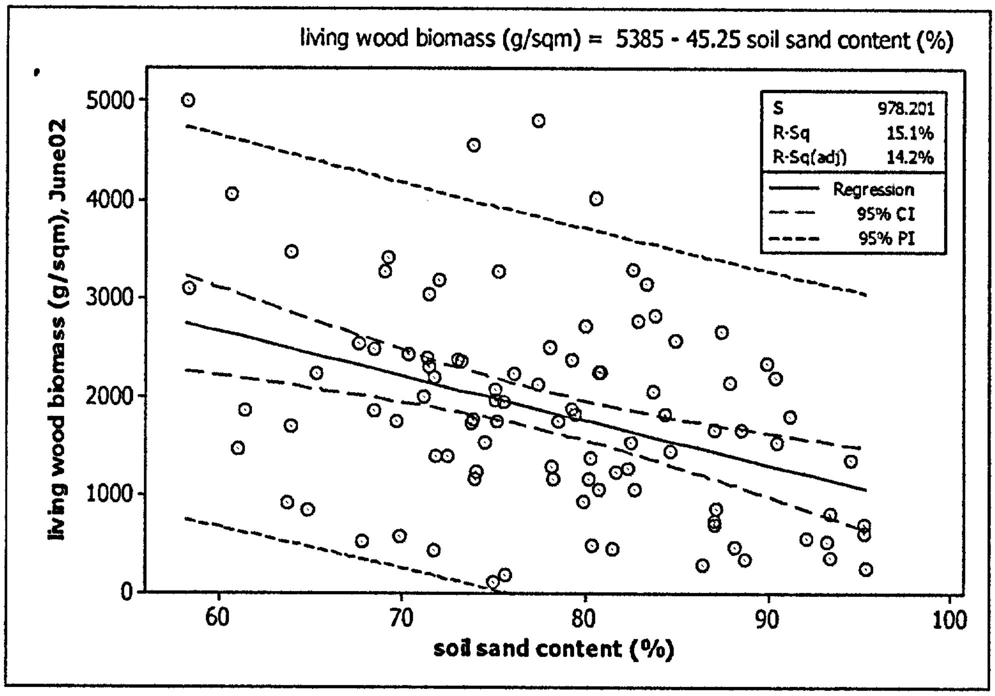

Fig. 4. Woody biomass (gm^{-2}) against soil sand content (%). The equations and main statistics of the regression relation are also indicated.

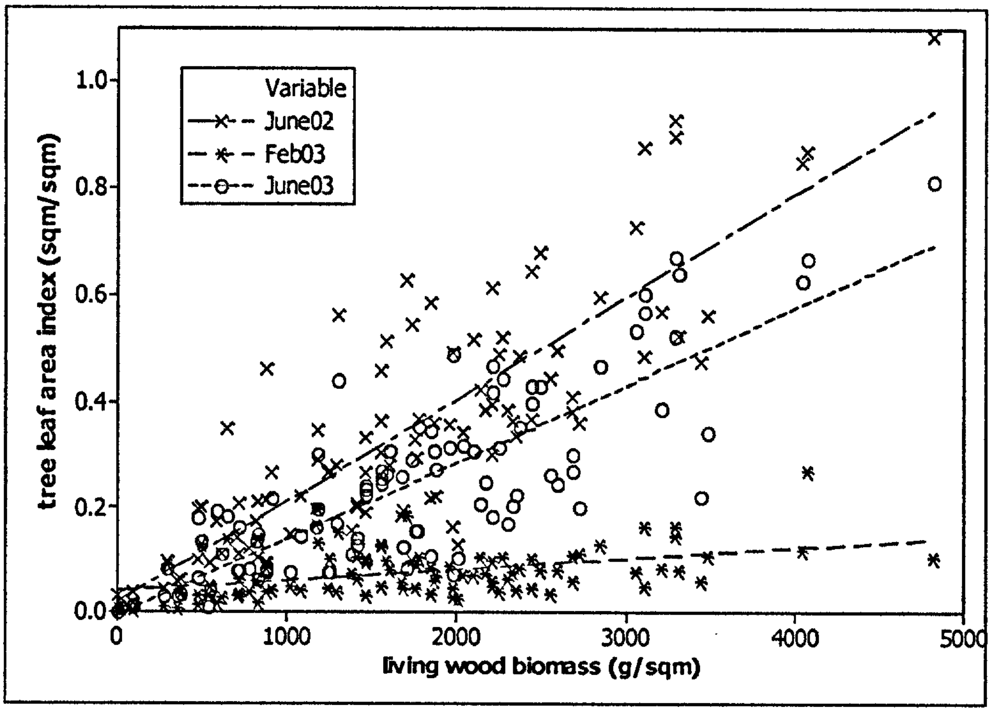

Fig. 5. Tree leaf area index increase with tree biomass increase during the wet season in June 2002 and 2003 and during the dry season in February 2003.

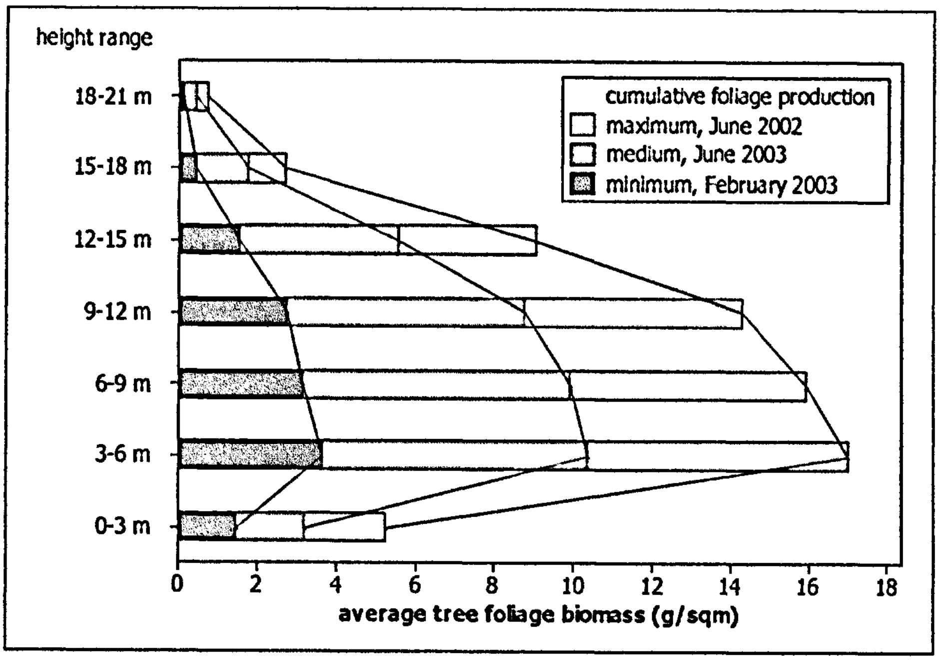

Fig. 6. Vertical foliage distribution averaged over all sampled trees on plots, expressed in terms of average foliage biomass per m^2 ground area. Steps from minimum to medium and maximum leafiness represent additional leaf biomass at the respective dates.

The multiple regressions indicate that, apart from correlation with woody biomass, the tree foliage biomass (or equally LAI) in the wet season (both June 2002 and 2003) was only influenced by soil texture and nitrogen (vars. 8 and 10, Table 3). In contrast, tree foliage in February 2003 was apparently influenced negatively by living grass biomass and also by the October fire (var. 9, Table 3). Soil texture, water holding capacity and phosphorus also appeared to be significant in the dry season (var. 9, Table 3).

At the level of individual trees, ant nest count was the most important predictor of foliage density in June 2002 (var. 8a, Table 4). Since this association probably reflects the dependence of ants upon extrafloral nectaries of acacia leaves, a second analysis was performed excluding ant nest count. In this case, tree vigour, as measured by living wood ratio, followed by tree size were the most important predictors of foliage density (var. 8b, Table 4).

In contrast, tree foliage density in the dry season was predicted first by grass biomass, with a positive sign, and secondly by ant nest count (var. 9a, Table 4).

Excluding ant nest count from the analysis, living wood ratio replaced it as the second best predictor (var. 9b, Table 4). As it was unclear why grass biomass was positively correlated with foliage category, a third analysis was performed without grass variables. The first variable, with a negative sign, was then the October fire (var. 9c, Table 4). Tree competition and density, and soil texture were also important variables influencing tree foliage during the dry season (var. 9, Table 4).

In June 2003, tree living wood ratio was the most important predictor before ant nest count, and the grass layer and soil texture variables also had a significant influence on tree leafiness (var. 10a, Table 4). Total grass LAI had a slightly positive influence, but living grass matter was negatively correlated with tree leafiness (var. 10ab, Table 4). In contrast to the dry season, fire was not important, if grass variables were not considered in the analysis (var. 10c, Table 4).

BIOMASS AND LAI OF THE GRASS LAYER

Average total grass biomass (i.e. both living and dead plant material) varied from 299 ± 90 g m^{-2} in June 2002 to an estimated 362 ± 169 g m^{-2} in February 2003 before the second fire, and to 191 ± 86 g m^{-2} in June 2003. In June 2003, average leaf water content was 84 ± 51 % of dry grass biomass weight, and from this the mean living grass biomass was calculated to be 83 ± 47 g m^{-2}.

Total grass biomass was strongly affected by fire. Thus, in the multiple regression using June 2003 grass biomass data, the R^2 decreased from 61.0 % to 18.0 % when fire was excluded from the multiple regression (var. 12, Table 3). Analysis of the 2002 data (for which recent fire history was unknown) yielded an equally low R^2 of 17.1 % (var. 11, Table 3). The importance of fire for the grass layer can also be gauged from the association in the PCA (Fig. 2) between the vectors for 'fire in October 2002' and 'grass biomass'.

Grass greenness in June 2003, as measured by leaf water content, was positively affected by the last fire (c.f. Fig. 2), but tree foliage biomass had a slightly negative influence (var. 13, Table 3). For living grass biomass fire was, therefore, only the second most important predictor, whereby living grass matter was higher on plots burnt in the last fire in February (vars 14 and 17, Table 3; Fig. 7). Living grass matter was mainly negatively affected by tree density and to a lesser extent by tree foliage (var. 14, Table 3).

Average grass SLA may be regarded as an indicator of functional species composition. It was mainly influenced by soil conditions, whereby grass populations on clayey soils with high nitrogen content had a higher SLA (var. 15, Table 3). Tree density, on the other hand, had a negative influence, keeping in mind that tree density also increases with soil nitrogen (var. 15, Table 3).

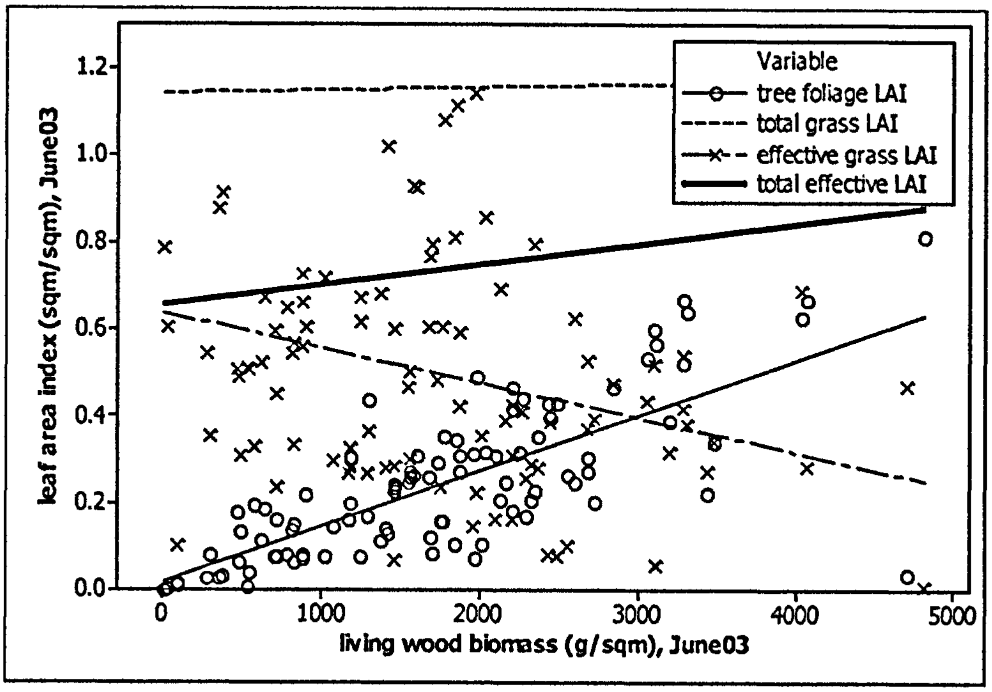

Fig. 7. Tree leaf, and total and living grass leaf area index against tree biomass during the wet season in June 2003.

Obviously grass LAI was closely correlated with biomass m^{-2} as can be seen in Fig. 2. The LAI's of the grass layer ranged between 1.79 ± 0.60 m^2/m^2 in June

2002 to an estimated 1.36 ± 0.61 m^2/m^2 in February 2003 before the second fire, and to 1.15 ± 0.58 m^2/m^2 in June 2003. Like total grass biomass, total grass LAI in June 2003 was mainly determined by fire, and additionally by soil nitrogen content (var. 16, Table 3). In contrast, effective grass LAI was best predicted by foliage biomass of trees in addition with soil organic matter and fire (var. 17, Table 3). Average effective grass LAI in June 2003 (0.50 ± 0.29 m^2/m^2) was higher than average tree foliage LAI (0.24 ± 0.18 m^2/m^2). Yet, grass layer decreased as foliage increased, and at high tree densities tree foliage LAI was generally higher (Fig. 7).

TRANSPIRATION ESTIMATES

Our extrapolation of transpiration data on mean LAI's suggests that ~ 0.03 $l/d/m^2$ of water may have been transpired on average in June 2003 by the tree layer and ~ 0.02 $l/d/m^2$ by the grass layer. According to our temptative model total water loss by overall transpiration may increase with increasing tree density up to ~ 0.1 $l/d/m^2$ in the plot with highest woody biomass m^{-2}, and tree biomass density and soil texture are the best predictors in the analysis of transpiration index (var. 18, Table 3).

Discussion

VARIATION IN TREE BIOMASS AND LAI IN RELATION TO SITE CONDITIONS

After 20 years of growth many secondary stands at Mariamu were probably close to maturity, with the largest trees being up to 20 m tall. Tree height was strongly correlated with tree bole diameter, which was commonly higher in open situations under low competition and especially on more sandy soils (c.f. Cochard & Edwards 2004a). Tree heights at Mariamu were comparable to those reported by Blösch (2002) in the Kagera region in North-Western Tanzania. At Mkomazi Reserve in Northern Tanzania, the maximum height recorded was 12 m (Stapley 1999), and Coe & Beentje (1991) indicate the maximum height of *A. zanzibarica* to be 7 m.

The mean LAI for all plots ranged from 0.076 in the dry season to 0.347 in the first wet season, values which are well below those of most other woodland types. For example, in the Kalahari, Botswana, *Brachystegia spiciformis* woodland (height of 11 m; cover of 64.8 %) had an LAI of 1.67, mopane woodland (height of 9.35 m; cover of 36.1 %) an LAI of 1.21, and acacia savanna (height of 7 m; fractional cover of 13.8 %), an LAI of 0.77 (Scanlon & Albertson 2004); in Australia, woodlands of *Acacia harpophylla* (biomass of 30 t ha^{-1}) had an LAI of 2-2.5 (Scanlan 1991) and eucalypt wooded grassland (height of 16 m; cover of 50 %) had an LAI of 0.6-0.95 (Hutley, O'Grady & Eamus 2001).

At 18.5 t ha^{-1} the average woody biomass was comparable to the value of 15.5 t ha^{-1} for dense mature *A. zanzibarica* stands at Bura in the Tana River Basin in Kenya (Vertanen *et al.* in Johansson & Kaarakka 1992), and to 18.3 t ha^{-1} in an 18-year old stand of *Acacia drepanolobium* in Laikipia, Kenya (Okello, O'Connor & Young 2001). Our data suggest that the average rate of biomass accumulation is around 850 kg ha^{-1} yr^{-1}. This is a much higher value than the 290 kg ha^{-1} yr^{-1} reported for *A. zanzibarica* woodland at Bura; however, those data were for a stand at less than 7 years after brush-cutting, when trees were only two meters high and had a biomass of 1.95 t ha^{-1} (Johansson & Kaarakka 1992).

The density of secondary woodland at Mkwaja was not uniform but reflected an underlying gradient in soil texture. The most important reason for this variation in density was probably that initial seedling establishment and survival were lower on sandy soils due to their lower water holding capacity and lower nutrient concentrations. Furthermore, competition between tree seedlings and grasses was probably more intense in sandy soils because grass roots commonly penetrate more deeply on such soils than in soils with clay (e.g. Fetene 2001). A second possible reason for the density gradient is that it reflected the feeding preferences of cattle. Bush encroachment was associated with, and probably caused by, a weakening of the grass sward in areas where cattle fed intensively (Klötzli 1980, Ford & Blaser 1971, That 2004), and two of the most important forage grasses, *Panicum infestum* and *Heteropogon contortus,* occurred predominantly on fine-textured soils (Kozák 1980, Cochard & Edwards 2004b).

Higher nutrient and organic matter concentrations at dense woodland sites are mainly correlated with soil clay content, but they may also have been affected by the presence of trees, as has been reported in other studies (e.g. Hudak, Wessmann & Seastedt 2003, Martin *et al.* 2003, Hibbard *et al.* 2003). The data suggest that soil nitrogen levels were raised by the presence of acacia, presumably through symbiotic nitrogen fixation. We did not observe nodules in our study, but Odee *et al.* (1995) recorded high levels of nodulation on *A. zanzibarica* at Bura, under similar soil conditions but drier climate than at Mkwaja (mean annual rainfall of 372 mm; Kaarakka 1996); in any case, the roots of most East African acacias seem to be colonized by nitrogen fixing *Rhizobia* even in the absence of nodules (Harrier *et al.* 2000). In the case of phosphorus, the low R^2 (17.1 %; var. 5b, Table 3) indicates that the variables investigated explained only a small proportion of variation. The fact that phosphorus levels were also higher could be because of increased organic matter beneath dense tree stands, and perhaps also through the activities of ants accumulating nutrient rich litter (Palmer *et al.* 2000). The former use of the site by cattle may also have influenced the present spatial variation in soil phosphorus.

VARIATION IN TREE GROWTH FORM

In contrast to the tall, monopodial *A. zanzibarica* at Mkwaja, the heavily browsed trees in the Saadani Game Reserve to the South were only 2 to 6 m tall, and had much branched, laterally spreading crowns; these trees were also more heavily defended by long spines and supported large populations of ants (pers. obs.). We conclude that tree stands at Mariamu were hardly affected by browsing, and growth forms and tree defences did not vary greatly within the area. However, there was a clear trend towards more slender tree stature under increasing tree density. Selection for rapid height gain occurs in forests or woodlands where light is a limiting resource (Archibald & Bond 2003). Average irradiation levels were certainly lower in *A. zanzibarica* woodlands than in savanna, but light was probably not the most important factor limiting tree growth. Fire, which acts as a non-selective defoliator, also increases height gain in various tree species (e.g. *Acacia karroo*; Archibald & Bond 2003). During and after the strong February fire trees of *A. zanzibarica* were defoliated to heights of over 10 m, and many smaller trees were killed (pers. obs., c.f. Cochard & Edwards 2004a). Probably more than 80 % of total tree foliage was lost in woodland affected by this fire (c.f. Fig. 6).

VARIATION IN ABUNDANCE AND FORM OF SPINES

For *A. drepanolobium*, as for other acacias, it has been observed that intense browsing pressure from large herbivores induces an increase in both the density and length of thorns produced (Young 1987, Milewski, Young & Madden 1991), and relaxation of spine defence production occurred after herbivore exclusion (Young, Stanton & Christian 2003). Clearly, high browsing explains high observed spinescence of trees at Saadani, whereas at Mariamu spine defences were generally much lower (pers. obs.). Spines and pseudogalls were often vestigial or completely broken off on older branches. It appears, nevertheless, that, even in the absence of tree browsing by giraffe and antelopes, spine defences were highest both close to the ground, which would be within the reach of small browsers, and at the top of the canopy, where young shoots of foliage are abundant and may need protection from giraffes. Trees in more open stands also had generally higher levels of spinescence. There appeared to be a slight decrease in total spine density on increasingly tall trees, a pattern that has also been reported by Gowda & Palo (2003) for *A. tortilis* and by Edwards & Ekins (1997) for *Ulex europaeus*.

A positive interaction between ants and thorns as means of defence against browsing by goats was observed by Stapley (1998): browsing on trees of *A. drepanolobium* where ants (*C. nigriceps*) had been removed was about eight times higher than on trees where ants were present. In contrast, Madden & Young (1992), found that adult giraffes were not particularly deterred by ant defences and suggested that giraffes learn when a branch can be browsed with minimum risk from ants. Huntzinger *et al.* (2004) ultimately demonstrated that, like simple spines, indirect ant defences were also induced by browsing on *A. drepanolobium*: trees protected from large herbivores, produced 24.8 % fewer swollen thorns on distal branches and 25.4 % fewer active nectarines than trees outside enclosures. Ants may also have a role in protecting acacias against insect herbivory; Janzen (1966) found that occupancy of shoots by herbivore insects increased from 2.7 % to 38.5 % if symbiotic ants were removed from branches of a Mexican acacia; similarly, the loss of ant colonies, for example by fire, often led to the death of the plant, probably due to increased insect herbivory (Janzen 1967). However, this role has hardly been acknowledged in the literature on East African acacias, despite circumstantial evidence that ants do affect insect-plant interactions. For example, many of the 169 insect species recorded by Hocking (1970) on *A. drepanolobium* showed morphological and behavioural ant mimicry or specially sclerotised carapaces.

The observed correlation between numbers of spines and swollen thorns may simply reflect the fact that both structures have the same origin as stipules. However, swollen thorn density as well as ant nest counts were mainly correlated with tree size and tree branching and, unlike simple spines, not directly influenced by tree density. Like simple spines, swollen thorn density was on average highest in the tree canopy and also slightly increased near ground level, but the patterns were much less marked than for simple spines. This suggests that the distribution of swollen thorns was less related to potential browsing patterns, but rather distributed relative to tree size, foliage density, and possibly nectar productivity on branches. Since ants are mobile and can reach any point of attack on the tree in a short time (c.f. Stapley 1998, Hocking 1970), the position of pseudo-galls on trees is certainly less important than that of spines. There appears, however, to be a defensive spatial structuring within ant colonies: according to Stapley (1999), new pseudo-galls at outer branches are mainly occupied by worker ants, whereas more protected galls at inner branches are more often occupied by young ants. Plants of *A. drepanolobium* also secreted more nectar on leaves near growing shoot tips where spines had not yet hardened (Stanton & Young 1999). On the other hand, the distribution of swollen thorns may also indicate the importance of ants for functions other than mammalian herbivory, such as defense against insect herbivory and cleaning functions (e.g. Willmer, Stone & Mafunde 1999).

The presence of carton ant nests on *A. zanzibarica* trees is not mentioned in the literature though Coe & Beentje (1991) noted *Crematogaster* nests on *A. bussei* in Kenya. Stapley (pers. comm.) did not note any ant nests on *A. zanzibarica* at Mkomazi, though Blösch (pers. comm.) did observe them at Burigi Game Reserve. In contrast to other *Crematogaster* spp. *C. sjoestedti* does not nest in swollen thorns but in hollow tunnels in branches and stems (Stanton & Young 1999, Stanton, Palmer & Young 2002), and possibly even in the root systems (Stapley 1999). Colonies of *C. sjoestedti* are polygynous (i.e. having more than one queen) and polydomous (i.e. often occupying more than one tree; Stanton, Palmer & Young 2002). Queens of *C. nigriceps* were repeatedly found in swollen thorns, whereas queens of *C. sjoestedti* were not found in swollen thorns (Stapley 1999, Palmer 2003). It is possible that carton nests on trees at Mkwaja indicate actual presence of queens, whereas trees without ant nests may predominantly be occupied by workers from colonies of neighbouring trees. It appears that ant nests are built irrespective of pseudo-gall availability, indicating that *C. sjöstedti* populations were neither absolutely dependent on, nor limited by, the presence of swollen thorns (c.f. Stanton & Young 1999).

Leaf phenological variation of *A. zanzibarica* trees between wet and dry season was marked, but healthy trees never lost all leaves. Flushes of new leaves were produced at the onset of the wet season, though flushing sometimes occurred earlier if they lost tree foliage by fire (Cochard, Edwards & Weber 2004). A seasonal pattern of leaf fall similar to that for *A. zanzibarica* was also observed in *A. drepanolobium* (Young, Stubblefield & Isbell 1997). In contrast, all the acacias studied by de Bie *et al.* (1998) in West African savanna were deciduous, with most of them sprouting in the latter part of the dry season.

The seasonal distribution of leaf biomass is clearly related to availability of water. The post-fire leaf flushing indicates that in our study area sufficient water was available to *A. zanzibarica* to allow new leaf growth even at the height of the dry season (c.f. Cochard, Edwards & Weber 200a). Possibly there is a complex trade-off between the need to avoid desiccation and benefits from retaining foliage throughout the year. The fact that most myrmecophyte acacias do not completely lose their leaves reflects the need to support ant colonies with petiole gland nectar (Ross 1981). In contrast, all the West African species studied by de Bie *et al.* (1998), which are probably mainly chemically defended, follow a different phenological strategy; the authors suggested that the observed complete leaf shedding occurs to avoid excessive drought stress, and could be regarded as an evolutionary alternative to the scleromorphy of other savanna trees. Le Roux, Bariac & Mariotti (1995) studied soil water use in a humid savanna in West Africa. They found that both grass and shrub species acquired most of their water from the top soil layer during both rainy and dry periods, and a shift of water uptake pattern towards deeper soil horizons was observed only in the late dry season.

Many factors including water availability, fire and both vertebrate and invertebrate herbivory may influence the foliage biomass of trees. In our study area the impact on foliage by mammalian browsers was negligible, but it is possible that insect herbivory had an effect and it was probably lower on trees with higher ant protection (c.f. Basset 1996, Krüger & McGavin 1998, Janzen 1966). Ant nest count was indeed the most important predictor after the heavy rains in June 2002, though it was less important at the other two sampling dates. In view of the complex interdependence of ants and foliage, it is clear that variation in the abundance of both needs to be interpreted within a single systemic frame and in an environmental context.

With ant defences excluded from the analysis, living wood ratio was the main predictor of foliage density in the wet seasons. Low living wood ratio can probably be understood as a direct indicator of low tree vigour, as branches have died off because of fire impact and/or infirmity due to insects (e.g. wood boring beetles), pathogens and resource restriction (c.f. Cochard & Edwards 2004a, Cochard 2004a). If leaves of such trees produce less nectar, there may be fewer ants to protect the tree against insect and mammalian herbivores, and tree vigour further decreases.

During the dry season (February 2002), both ant nest count and living wood ratio were less important than in the wet season, but it was mainly positively related to total grass biomass. Total grass biomass was, on the other hand, mainly determined by the last fire in October 2002, and if grass variables were not considered fire was in fact the first predictor. It appears, therefore, that indirectly or directly, fire had a major impact on tree foliage, tree vigour and tree mortality and there was not one single mechanism which influenced tree foliage, but rather a combination of factors (c.f. Cochard & Edwards 2004a).

GRASS PHENOLOGY, TREE-GRASS INTERACTIONS AND EXPECTED TRANSPIRATION

Grass roots on loamy-clayey soils were mainly concentrated between 5-30 cm depth (c.f. Cochard & Edwards 2004b), and during drier periods grass growth was directly stimulated by individual rainfall events (c.f. Bourlière & Hadley 1983, Deshmukh 1984, Boutton, Tieszen & Imbamba 1988). In this humid savanna, however, the grass layer rarely dried out completely even during the dry season (Klötzli, pers. comm., Ford & Blaser 1971), and in February 2003 grass greenness was at about 20 % of total biomass (Cochard, Edwards & Weber 2004). Wet season grass biomass production – 2990 kg ha^{-1} in June 2002 and 834 kg ha^{-1} in June 2003 – was in the range generally estimated for grasslands in East Africa: if precipitation data from March to June was applied to Deshmukh's (1984) equation, grassland production would have been estimated at 2919 kg ha^{-1} in 2002 (367 mm rainfall March), and at 820 kg ha^{-1} in 2003 (~ 120 mm rainfall). Klötzli (1980) estimated total stand crop at Mkwaja at 2890 kg ha^{-1} in 1975 (491 mm of rainfall) for *Heteropogon* savanna grassland.

During the study period the grass layer was strongly influenced by fires. Since the ranch closed down in August 2000 fires laid by poachers or spreading from adjacent villages were common in this grassland, and the impact at the study site probably reflects current fire frequencies of Eastern Mkwaja North. Living grass biomass in June 2003 was, however, mainly negatively influenced by tree density. Many studies in drier East African savannas have actually reported increased grass biomass underneath trees, as a result of water conservation by tree shading or nutrient accumulation (e.g. Belsky *et al.* 1993, Belsky 1994, Veetas 1992). Ludwig *et al.* (2004) noted similar grass production underneath *Acacia tortilis* trees compared to the savanna matrix, whereby increased grass biomass production by nutrient accumulation underneath trees was just about offset by water competition with trees. In *A. zanzibarica* woodland grass biomass production measurably declined with increasing tree density, and the grass layer was also distinctly drier in dense woodlands (with higher tree foliage) as compared to adjacent savanna. Although the humid savanna at Mkwaja experiences higher annual rainfalls than the savannas studied by cited authors, *A. zanzibarica* trees most negatively influenced the grass layer via competition for water (c.f. also Cochard, Edwards & Weber 2004).

In contrast to grass biomass, average grass SLA was not influenced by fire, but by soil parameters and by tree density, whereby soil nitrogen content was the best predictor. Grasses with a high SLA, such as the grass *Panicum infestum* seem to be rather nitrophilic, growing mainly in woodlands (Cochard & Edwards 2004b). The sedge *Fimbristylis triflora* on the other hand seems to dominate on clay soils in dense woodland which are probably seasonally xeric. *Heteropogon contortus* and *Andropogon gayanus* grew mainly in intermediate conditions between dense woodland and savanna, whereas other tall growing grasses, such as *Diheteropogon amplectens*, *Hyperthelia dissoluta* and *Cymbopogon caesius* were mainly found in open savanna (Cochard & Edwards 2004b). There is clearly a relationship between nitrogen availability and functional grass architecture, which is discussed in more detail in Cochard & Edwards (2004b).

Total grass LAI in June 2003 was, therefore, influenced not only by fire, but also by nitrogen content in soil. Trends in effective grass LAI were, however, not much different to living grass biomass, showing a negative relationship with tree foliage (~ woodland density), and a positive relationship with organic matter (~ nitrogen) content and the last fire. Total effective LAI (including acacia foliage) only slightly increased with increasing tree density, but water loss by transpiration was probably considerably higher in dense woodlands. Measurements of stomatal conductance in June 2002 indicated that transpiration of *A. zanziabrica* was about 4 times higher than that of the grasses *H. contortus* and *P. infestum*, whereby rates of water loss on stump resprouts in a woodland glade were only slightly higher than in dense woodland stands (Cochard, Edwards & Weber 2004). It may, therefore, be expected that our tentative analysis for the June 2003 data actually reflects general patterns of transpiration in the woodland. Our results are indeed comparable to modelling results by Simioni, Gignoux & le Roux (2003), which revealed about equal net primary productivity, but increasing rates of transpiration and photosynthetically active radiation absorption efficiency along a gradient of increasing tree density in West African humid savanna.

CONCLUSIONS

The *A. zanzibarica* woodlands at Mkwaja mainly established on heavily grazed pastures on loamy-clayey soils. While bush encroachment and woodland establishment clearly had a positive influence on the nutrient status of the soil, grass growth was nevertheless decreased, probably because of reduced availability of water. Also the water content of fresh matter was generally decreased inside dense woodlands. This may have represented a significant impact on grazing resources for cattle and native wildlife. After cattle were removed, and with an extremely low biomass of native large herbivores, accumulation of grass fuel in woodlands was apparently sufficient for hot fires which not only suppressed woodland regeneration but also had an impact on already established trees (c.f. Cochard and Edwards 2004a). Overall, the impact of the woodland did not appear to be very strong as compared to the main determinant savanna factors, soils and fire. *A. zanzibarica* woodlands may, therefore, be seen as a transitional state or as the extreme end of the range of bush density in a still resilient humid fire savanna (c.f. Cochard & Edwards 2004a).

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Appendix

Regression equations (with *adjusted* R^2 and number of data points n) for tree morphology and biomass calculations.

		R^2 *adj.*	*n*
	1.) Spine regression equations		
1.	*spine weight (g)* = exp (- 4.65 + 1.82 * ln *spine length (cm)*)	97.6	100
2.	*swollen thorn weight (g)* = exp (- 0.99 + 2.08 * ln *sw. thorn bulb diameter (cm)*)	83.7	100
	2.) Branch regression equations		
3.	*wood weight (g)* = exp (3.49 + 2.57 * ln *branch base diameter (cm)* + 0.277 * ln *branching count*)	93.5	119
4.	*foliage weight (g)* = exp (0.479 + 1.19 * ln *branch base diameter (cm)* + 0.336 * ln *branching count* + 1.49 * *foliage category (1-4)*)	92.3	119
5.	*branch spine weight (g)* = exp (- 0.983 + 0.95 * ln *branch base diameter (cm)* + 0.375 * ln *branching count* + 0.633 * *spine category (1-4)*)	79.6	119
6.	*branch swollen thorn weight (g)* = exp (- 0.004 + 1.23 * ln *br. base diameter (cm)* + 0.339 * ln *branching count* + 0.745 * *swollen thorn category (1-4)*)	91.0	119
	3.) Wood and tree regression equations		
7.	*wood weight (g)* = 0.889 * *wood volume (ml)*	100	38
8.	*tree weight (kg)* = exp (- 2.54 + 2.63 * ln *bole diameter (cm)*)	97.9	40
9.	*total branch weights (kg)* = exp (3.12 + 2.25 * ln *bole diameter (cm)* + 0.876 * ln *branching category (1-4)*)	90.8	40
10.	*foliage weight (g)* = exp (0.521 + 1.62 * ln *bole diameter (cm)* + 0.882 * ln *branching category (1-4)* + 1.48 * ln *foliage category (1-4)*)	96.7	40
11.	*spine weight (g)* = exp (- 0.868 + 1.51 ln *bole diameter (cm)* + 0.972 * ln *branching category (1-4)* + 0.629 * *spine category (1-4)*)	95.5	40
12.	*tree swollen thorn weight (g)* = exp (0.0259 + 1.64 * ln *bole diameter (cm)* + ln *branching category (1-4)* + 0.745 * *swollen thorn category (1-4)*)	96.1	40
	4.) Other equations		
13.	*No fire 10.2002: grass biomass (g), 2.03* = 225.4 + 0.9121 * *gr. b.mass (g), 6.02*	34.3	14
14.	*Fire 10.2002: grass biomass (g), 2.03* = 18.7 + 0.7377 * *grass biomass (g), 6.02*	39.7	22
15.	*No fire 10.2002: ratio of grass dry weight (g)/wet weight (g), 2.03* = 0.3263 – 0.00007 * *grass biomass (g), 2.03*	15.0	14
16.	*Fire 10.2002: ratio of grass dry weight (g)/wet weight (g), 2.03* = 0.8203 + 0.000654 * *grass biomass (g), 2.03*	27.7	22

When Jotham was told about this, he climbed up on the top of Mount Gerizim and shouted to them, "Listen to me, citizens of Shechem, so that God may listen to you. One day the trees went out to anoint a king for themselves. They said to the olive tree, 'Be our king.' But the olive tree answered, 'Should I give up my oil, by which both gods and men are honored, to hold sway over the trees?' Next, the trees said to the fig tree, 'Come and be our king.' But the fig tree replied, 'Should I give up my fruit, so good and sweet to hold sway over the trees?' Then the trees said to the vine, 'Come and be our king.' But the vine answered, 'Should I give up my wine, which cheers both gods and men, to hold sway over the trees?' Finally all the trees said to the thornbush, 'Come and be our king.' The thornbush said to the trees, 'If you really want to anoint me king over you, come and take refuge in my shade; but if not, then let fire come out of the thornbush and consume the cedars of Lebanon!'"

The Bible,
Judges 9, 7-15

Secondary *Acacia zanzibarica* woodlands in coastal Tanzania: 2. Woodland density, dieback and regeneration

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Summary

1. In a previous paper concerned with secondary *Acacia zanzibarica* woodland on a former ranch in Tanzania we reported the distribution of biomass in 97 plots along a gradient of increasing tree density. Here we consider aspects of tree mortality and regeneration in these woodlands following the giving up of cattle ranching. The positions and base diameter of all trees in the plots were recorded in June 2002, and tree survival was noted at later dates. In June 2002, and in February and June 2003, seedling numbers were counted, while resprouts (i.e. both root suckers and coppice shoots sprouting from tree bases or stumps) were recorded in June 2003. Flowering intensity of trees was estimated by eye in November 2002, and numbers of pods were assessed in February 2003.

3. Tree density tended to reflect a gradient in soil texture with higher numbers of trees on the heavier soils. A very high scatter in the relationship between tree density and mean tree weight (both on logarithmic scales) suggests that self-thinning was not a significant factor determining tree mortality except maybe in a few very dense stands. The tree size distribution suggests that the stands are not even-aged but that there have been several phases of recruitment or resprouting during the last 20 years.

4. The main cause of tree deaths (in terms of topkill) during the study period appears to have been a hot fire in the late dry season (February 2003). Tree mortality was related positively to soil water holding capacity and negatively to tree density. Some trees, especially those of low vigour (as measured by the living wood ratio) were probably directly killed by fire. However, our results suggest that most tree mortality was caused only indirectly by the fire, and resulted mainly from water stress on clayey soils where water probably did not percolate beyond the grass rooting zone during the subsequent wet season with below-average rainfall. A hypothetical model of the impact of fire on tree stands is presented and explained.

5. Flowering and pod production were highly correlated with tree size. In contrast to flowering, pod production decreased in dense stands, indicating intra-specific competition for resources. Seed production of about 7.4 m^{-2} was very low compared to other woodlands with invasive leguminous trees.

6. The mean density of seedlings on plots was 0.04 m^{-2}. Seedling density was significantly related to soil and grass layer variables but not to seed rain. No seedlings survived until the late dry season, probably because of drought. Half of the trees 'killed' by fire (i.e. topkill) responded by producing coppice shoots from the base. Some trees also produced root suckers, though this form of vegetative recruitment was not related to the death of the aboveground tree. The mean density of all resprouts, both coppice shoots and root suckers, was 0.054 m^{-2}.

7. The study illustrates that dieback of *A. zanzibarica* can occur even in the absence of large, destructive herbivores such as elephant. Under the prevailing conditions, with very low mammalian herbivory and regular fires, the woodland will probably revert to predominantly grassland vegetation within the next 10-20 years. However, if there are future changes in the numbers of large herbivores or the frequency of fires, the balance between grass and tree components could change again.

Key-words: East Africa, savanna dynamics, tree demography, competition, mortality, recruitment, fire, multivariate

Introduction

The vegetation dynamics of East African savannas are closely linked with the population dynamics of the herbivore communities. Bush encroachment, for example, has been observed in regions where the diverse wildlife communities have been drastically reduced by hunting or rinder pest (e.g. Prins & van der Jeugd 1993, Leuthold 1996, Lenzi-Grillini *et al.* 1996, Ruess & Halter 1990). This has led to increasing concern about irreversible vegetation changes and habitat loss in African savannas as native herbivore communities are increasingly being displaced by single-species livestock systems, and traditional ways of pastoralism are abandoned for modern private ranching (Du Toit & Cumming 1999, Tobler, Cochard & Edwards 2003). Nevertheless, compared to other continents, savannas in Africa also appear to be more *resilient* under livestock grazing pressure (Solbrig, Medina & Silva 1996, Cochard & Edwards 2004a), and many fears about long-term effects to the vegetation may prove to be unfounded. Few studies have so far investigated resilience in a savanna rangeland context, and these have mainly focused on soil degradation and species shifts within the grassland (e.g. Walker, Kinzig & Langridge 1999, Anderies, Janssen & Walker 2002, de Soyza *et al.* 2000), or on woodland regeneration in anthropogenic grasslands (e.g. Ludwig *et al.* 2001). To our knowledge there has been no study of how savanna rangeland that is heavily affected by bush encroachment develops following the abandonment of grazing.

Before the 1980's, conceptual models of vegetation change in rangelands rested predominantly on the Clementsian succession theory (Smith & Pickup 1993, Blösch 2002). The adequacy of succession theory to tropical non-equilibrium ecosystems has, however, more recently been contested, and attention has since shifted to the more complex 'state and transition model' proposed by Westoby, Walker & Noy-Meir (1989). In the debates about this model it has often been proposed that above a certain grazing threshold, changes may occur to the vegetation of tropical savanna ecosystems which are irreversible. Walker (1993, p. 84), for example, recorded that 'linear reversible changes in response to grazing pressure and fluctuation in rainfall, as assumed under the succession model, are mostly precluded by a combination of lag effects, thresholds and multiple trajectories'. Various limitations and shortcomings of 'state and transition' theories have, however, also been pointed out. Smith & Pickup (1993) criticised that they lack any spatial component, while Briske, Fuhlendorf & Smeins (2003, p. 601) maintained that 'equilibrium and non-equilibrium ecosystems are not distinguished on the basis of unique processes or functions, but rather by the evaluation of system dynamics at various temporal and spatial scales'. Clearly, contrasting conclusions about savanna rangeland dynamics are often influenced by differences in theoretical viewpoint and the context of particular studies. This may be illustrated by the concept of 'resilience', which has been defined by Holling (1973) as the capacity of an ecological system to *endure* under the impact of disturbances without changing into a different system, whereas Walker (1993) defined it as the ability of an ecological system to *recover* after it has been changed. If a secondary bushland does indeed revert back to the initial open savanna after impact, bushland may therefore be seen within the broad frame of the 'savanna system' in the first definition, or as a transition state that is changing towards the initial state in the second definition.

In order to understand tree-grass balance in savanna systems two main alternative explanations have recurrently been proposed: 1. competition between woody plants and grasses for water, with the two components differing in their ability to exploit soil water (the two-layer soil-moisture competition model by Walker & Noy-Meir 1982), and 2. plant life history-disturbance interactions, such as long-term effects of fire on tree demography (Higgins, Bond & Trollope 2000). Different ecological factors, however, often interact in complex ways and vary considerably in importance between savannas in humid and dry tropical regions (e.g. Backéus 1992, Blösch 2002). Empirical evidence to support ecological theories based on models about savanna rangeland dynamics is, in any case, still meagre, particularly for African savannas which are hardly affected by introduced exotic species (Midgley & Bond 2001, Cochard & Edwards 2004a).

While bush encroachment evidently poses a great challenge for range managers in Africa (Tobler, Cochard & Edwards 2003), its long-term ecological consequences may, however, not always be as drastic and irreversible as has often been assumed. In some cases, bush encroachment may still be a reversible ecosystem response that can be allowed for in pasture management. For example Coppock (1993), studying the Borana herding system in Southern Ethiopia, described how bush encroachment may be part of a potentially sustainable pattern of rangeland use built around spatial flexibility by pastoral producers. In contrast to other continents (c.f. Cochard & Edwards 2004a), serious range degradation in Africa is often described in pedological terms rather than through vegetation effects (e.g. Dahlberg 2000, Rietkerk 1998), whereby encroachment of bush, legumes and ruderals on African pastures may even be viewed within the frame of a possible long-term regeneration process that reconstitutes the soil status of the initial savanna (c.f. Backéus, Rulangaranga & Skoglund 1995, Reid & Ellis 1995, Belsky & Amundsen 1998, Cochard & Edwards 2004a).

Various species of *Acacia* form the dominant elements in the flora of many African savannas (Cochard & Edwards 2004a), and acacias are often the dominant components of encroaching bush (Midgley & Bond 2001). This is partly because most acacias are strongly defended against browsing by spines, chemical compounds and ants (Cochard & Edwards 2004a), but also because their population dynamics are favoured by other forms of disturbance. They exhibit, for example, various regenerative traits such the ability to resprout from roots and stumps, and mechanisms of seed dispersal and establishment which favour recruitment in areas impacted by large herbivores (Midgley & Bond 2001; c.f. Cochard, Edwards & Weber 2004). Furthermore, a high physiological adaptability to herbivory and other impacts with a broad range of growth forms can be found in some acacias (e.g. Archibald & Bond 2003).

The work described here was performed on Mkwaja Ranch, a former cattle ranch on the Tanzanian coast which closed in August 2000. The availability of detailed information on the ecology and management history of the area provided an excellent opportunity to study resilience of a savanna ecosystem following a phase of heavy impact by cattle. Before the ranch was opened in 1954, the humid savannas on the coast of Tanzania were probably fire-maintained systems, with wildlife playing a secondary role (Klötzli 1980, Cochard & Edwards 2004a). After 50 years of intensive cattle grazing, almost mono-specific woodlands of the myrmecophyte tree *Acacia zanzibarica* (S. Moore) Taub. var. *zanzibarica* had established in large areas with previously open savanna vegetation (Tobler, Cochard & Edwards 2003; for a description of various aspects of the tree's ecology see Cochard & Edwards 2004a). However, following the removal of cattle in 2001 and in the absence of large numbers of wildlife, we observed that there was vigorous growth of grasses in woodland areas. We hypothesised that the increased vigour of the grass layer might affect tree density in the longer run by 1. promoting tree dieback of established trees (due to increased competition and/or hotter fires), and 2. suppressing tree regeneration and further recruitment (c.f. Cochard & Edwards 2004a).

In a previous paper (Cochard & Edwards 2004a) we described how soil factors influenced the density of trees in areas impacted by cattle, and presented data on the aboveground biomass of trees and grasses under post-ranching conditions. Based on those baseline data, we record here demographic changes in the tree populations during one year along a gradient of increasing tree density. Specific questions addressed here are:

6. What are the patterns of tree density and size distribution and what can we infer from them about stand history and development?
7. What are the main factors that determine tree mortality?
8. Do flowering intensity and seed production change along the tree density gradient?

9. What are the main factors that determine seedling recruitment and resprouting?

Study site

The former Mkwaja Ranch in Tanzania occupied an area of 462 km^2 of coastal savanna grassland, woodlands and forest (Cochard & Edwards 2004a). The Ranch was established in 1954, and at peak times during the 1970's supported over 13'000 head of cattle. Bush encroachment became evident within a few years after the ranch began operation (Ford & Blaser 1971), and brush-cutting during the 1970's only made the problem worse as encroaching trees resprouted from roots and the grass sward was weakened (Klötzli 1980). In August 2000 cattle ranching was finally abandoned, and since then the area has remained almost empty of large mammalian herbivores.

The spatial distribution of bushland on Mkwaja Ranch in 1994 was investigated by Tobler, Cochard & Edwards (2003) using a combination of satellite imagery and field survey. Two main spatial trends were detected in the vegetation. One was a large-scale decrease in the cover of bushland from the most intensively used parts of the ranch through more extensively used areas to the game reserve; a second trend was a radial vegetation pattern associated with the enclosures where cattle were herded at night. High amounts of *Acacia zanzibarica* bushland (as well as two other bushland types) occurred in a zone between 300 and 2500 m from the paddocks, with a peak in bush density at about 900 m (mean value for 18 paddocks). Since then most of the *A. zanzibarica* bushlands have grown into woodlands (Cochard & Edwards 2004a).

During ranching times, efforts to combat bush encroachment under cattle ranching were recurrently met with failure (That 2004). Lupi & Walther (1994), for example, reported that ringbarking of *A. zanzibarica* only killed about half of tree tops, whereas application of Tordon killed less than 40 %. Only the combination of ringbarking and Tordon had an effect of more than 90 %

mortality in tree tops. Nevertheless, *A. zanzibarica* resprouts vigorously from stumps (i.e. coppicing) and from roots (i.e. suckering) if the tree above ground is killed by brush-cutting or fire (Klötzli 1980, Cochard, Edwards & Weber 1994). In the absence of effective grazing exclusion and fire management, the control measures thus led to vigorous vegetative regrowth (Lupi & Walther 1994).

The study was conducted in the *A. zanzibarica* woodland belt south of the former Mariamu paddock on Mkwaja Ranch (5°43'S, 38°47'E). The areas surrounding the paddock were recurrently brush-cut up until 1982, so the trees in our study were mainly not older than about 20 years. The soils in the study area graded from predominantly sandy (max. sand content of 95.5 %) to loamy (min. sand content of 58.2 %). Average organic matter (0.18 %), phosphorus (0.021 %) and nitrogen (0.022 %) contents were distinctly low, and in the case of organic matter and nitrogen were highly correlated with soil texture, being highest on the loamy soils (Cochard & Edwards 2004a). At the time of this study in 2002, the *Acacia zanzibarica* woodland was on average 9 m high, and appeared to be relatively even-aged. The density of trees was extremely variable and followed the underlying gradient in soil texture, with high numbers of trees on the loamy/clay soils but few trees in areas with sandy soil (Cochard & Edwards 2004a). Grazing pressure on plots was negligible during the study period.

Methods

STUDY PLOTS

Initially 60 plots were selected at random in an area of predominantly *A. zanzibarica* bushland, but a further 40 points were chosen in the field so as to provide an adequate representation of the gradient from very dense woodland to open savanna. The locations of 3 study plots were lost and these plots were abandoned. The nearest *Acacia zanzibarica* tree to each point was taken as the centre of a circular plot of 4 m radius. A detailed site description and map showing the location of study plots is given in Cochard & Edwards (2004a).

PLOT SURVEYS

For each tree, position within plots, bole diameter, crown overlap, height, breadth-height ratio, the proportion of living wood (living wood ratio), branching category, spine category, swollen thorn category, foliage category in June 2002, February 2003 and June 2003, and ant nest counts were assessed as described in Cochard & Edwards (2004a).

Most *A. zanzibarica* trees flower during the early dry season (November to December), while a few trees flower at other times during the year. The dehiscent fruits ripen and split open in early February and the hard, disc-like seeds may directly fall from the tree. More often seeds remain attached to open pods which eventually are dispersed by wind in the vicinity of maternal trees (up to 20 m). In November 2002 the extent of flowering was noted on a categorical scale from 0 to 4, and in February 2003 the number of pods per tree was counted (or estimated to about ± 30 when the number was >100). All seedlings of *A. zanzibarica* were counted on plots in June 2002 and in June 2003. Resprouts from roots were counted in June 2003.

The biomass and LAI of grasses were assessed in June 2002, February 2003 and June 2003. Soil samples were also collected for the determination of sand and clay content, soil organic matter, total nitrogen and phosphorus contents. The water content of soils was measured in the field. All methods are described in Cochard & Edwards (2004a).

CALCULATIONS AND STATISTICAL ANALYSES

A detailed description of tree allometric biomass calculations and equations used is given in Cochard & Edwards (2004a). As an approximation measure of intra-specific tree competition pressure a simple competition index was calculated from the recorded position of trees within the plot by the equation, as proposed by Stoll, Weiner & Schmid (1994):

$$\textit{competition index} = \Sigma\,(\textit{bole diameters (mm)}\text{ of neighbouring trees} / \textit{distances (mm)}\text{ to respective trees})$$

Due to the sampling regime, the competition index was underestimated in the outer ring of plots (4.26 ± 0.14 for plots with more than 19 trees 100 m^{-2}) compared to the inner 0-3 m distance from the plot centre (4.61 ± 0.12). However, compared to the overall variation of competition index this effect was considered minor, and all trees were included in the analyses.

In October 2002 (early dry season), much of the study area was affected by a relatively weak fire, while a second, much hotter fire at the end of February 2003 killed many trees in those parts of the site where the grass fuel had not burnt in the October fire. During the latter fire, temperatures at ground level were measured with Thermax® colour markers (see Cochard, Edwards & Weber (2004). Using these data the following relationship between fire temperature and grass biomass was calculated:

$$\textit{fire intensity (maximum temperature in °C)} = 3.46 + 0.487 * \ln \textit{grass dry biomass (g)} - 0.839 * \textit{grass dry weight (g)} / \textit{grass wet weight (g)}$$

This equation was then used to estimate fire intensity in all plots in February 2003 and also in October 2002 (in this case using grass biomass data from June 2002). As a check, all analyses were performed using both estimated 'fire intensity' values (fire absent = 25°; fire present: temperature value between 150°-650° C), and 'fire occurrence' (fire absent = 0; fire present = 1) as predictor variables.

Statistical analyses are described in detail in Cochard & Edwards (2004a). The main results of the regression analyses are summarised in Table 1 for 'plot' variables and in Table 2 for individual 'tree' variables. For each dependent variable the adjusted R^2 of the final model is listed, whereby higher values of R^2 indicate higher accuracies of the final models. The weights of predictor variables are stated as percentage contribution of the adjusted R^2 of the model at the variable inclusion step relative to the adjusted R^2 of the final model. This means that the weights, indicated by squares and triangles, must be read relative to the value of the final adjusted R^2 and may not be viewed as absolute weights. Triangles indicate whether the relation between a predictor and the dependent variable is positive (▲) or negative (▼) in the final equation. The triangle of the first variable included in the model is underlined. Variables that were not considered for analysis from the beginning are shaded in grey colour. In order to elucidate hidden correlations, more than one analysis was performed for some test variables, varying inclusion of predictor variables. All final regression equations were highly significant by $p < 0.001$. A detailed listing of all variables used in regression analyses, their descriptive statistics, the actual regression equations and values of the adjusted R^2 at any variable inclusion step are given in an Appendix in Cochard (2004).

Results

FIRE INTENSITY

The October fire was apparently a relatively 'cold' fire which burnt the grass on about half of the plots but had little effect on the trees. From November 2002 to February 2003 very little rain fell, so that a fire in February was nourished by almost completely dry grass. This second fire affected 39 of the 45 previously unburnt plots (the remainder being protected by a road) but only 15 of the 52 plots burnt in October. Based on estimated grass fuel loads and dryness, the average temperature of the October fire was calculated approximately to 359° ± 53° C, while the temperature of the February fire was 249° ± 37° C for the plots already burnt in October, and 526° ± 48° C for the previously unburnt plots. The more intense fires in previously unburnt plots killed many trees.

TREE DENSITY AND SIZE DISTRIBUTION

The average tree density in the 60 randomly selected plots recorded in June 2002 was 8.5 ± 5.8 trees 100 m^{-2}, while the mean for all 97 plots (including those selected to represent higher tree densities) was 16.1 ± 12.4 trees 100 m^{-2}. The density of trees in individual plots ranged from 2-50 trees per 100 m^2. Tree density was log-normally distributed in the woodland, as seen by the cumulative density function of randomly selected plots in Fig. 1. Tree density on all plots, including non-randomly selected plots, fitted better to a gamma distribution as depicted in Fig 7.

In June 2002 mean woody biomass ranged from 121 g m^{-2} to over 5 kg m^{-2}, with an average of 1.85 ± 1.06 kg m^{-2}. Although tree density and total woody biomass m^{-2} were significantly correlated, much of the variation in biomass was attributable to tree size variation within stands (Fig. 2). By June 2003 woodland density had declined to 1.73 ± 1.94 kg/m^2, or 14.3 ± 12.1 trees 100 m^{-2}, mainly as a result of fire (vars 2 and 4, Table 1). In the multiple regression analyses, soil nitrogen was the best predictor of woodland density (vars 1-4, Table 1). Likewise, nitrogen was the first predictor of competition index in the analyses for individual trees (vars 1-2, Table 2). Plot mean and maximum bole diameter were well predicted by the two tree density variables (vars 5 and 6, Table 2), the relationship with tree number being negative and that with tree biomass being positive. Plot mean tree height was related to mean bole diameter, but was also influenced by other variables including soil conditions (var. 7, Table 2).

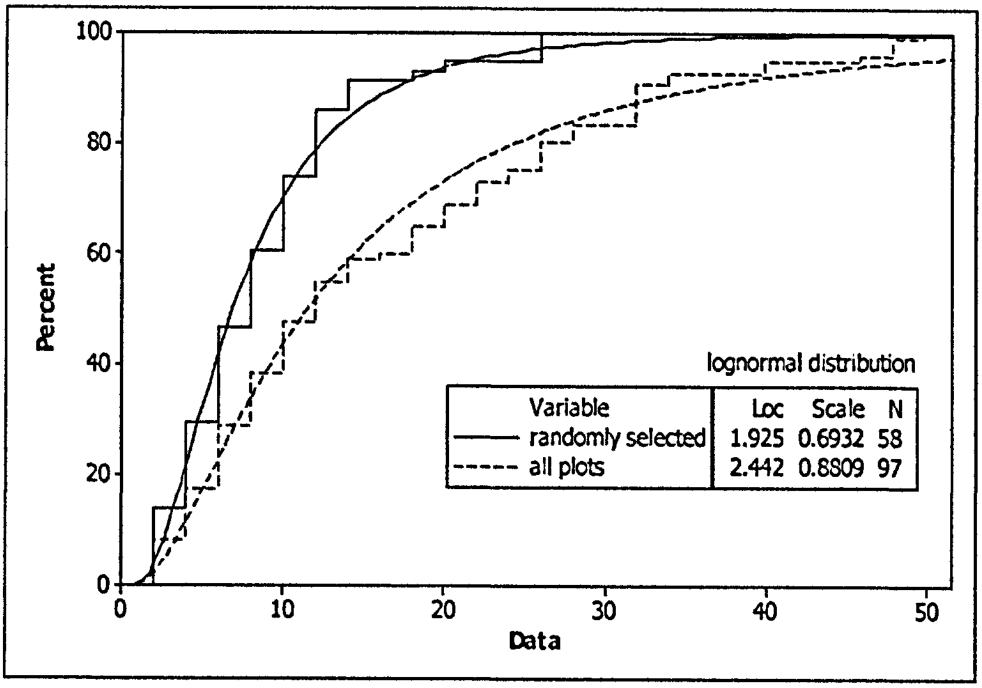


Fig. 1. Cumulative density function with lognormal distribution fit of tree density on randomly selected and on all plots.

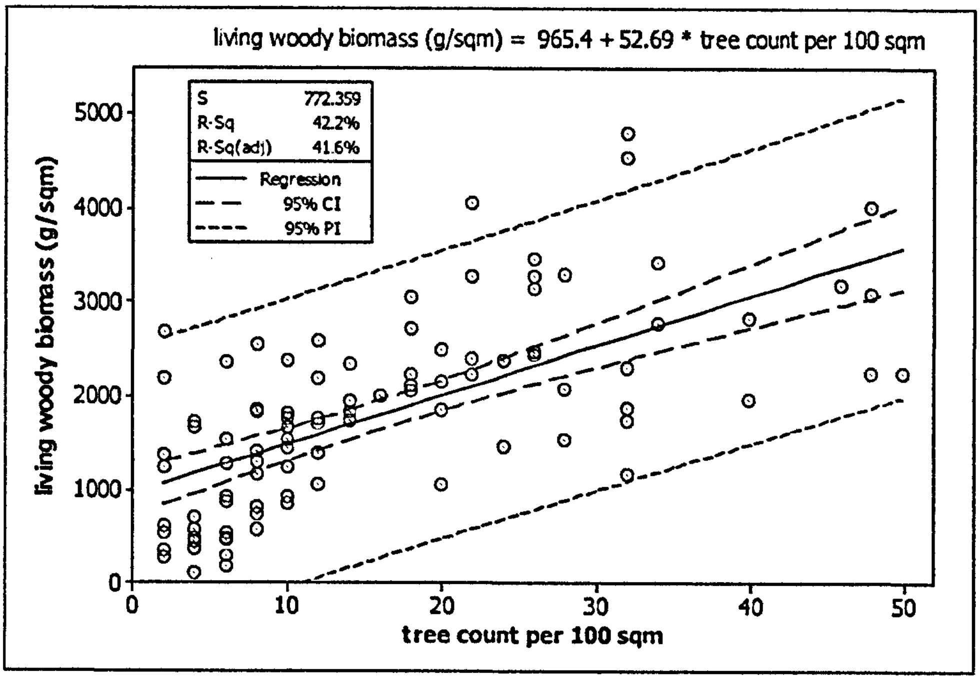


Fig. 2. Plots of June 2002 woody biomass (g m^{-2}) against tree count/100 m^2.

Table 1: Summary of tree layer and tree recruitment plot test variables, their descriptive statistics and main predictor variables in multiple regression models. Variables with a star (*) were calculated or modelled based on regression equations.

Reading key				relative contribution to final R^2
	var. not used in analysis			
▲	var. with positive sign			
▼	var. with negative sign			
▼̲	1st included variable			
▪	▴	▾	< 3 %	
▪	▴	▾	3-10 %	
■	▲	▼	10-40 %	
■	▲	▼	> 40 %	
■			> 75 %	

	Dependent variables	Descriptive statistics				Summary of multiple regression analysis	relative stepwise contribution of predictor variables to R^2 of the final model																						
							SUMMARY				Soil variables						Fire		Grass layer					Tree layer						
		average	standard deviation	maximum	minimum	adj. R^2 of final model	soil variables	fire impact	grass layer	tree layer	organic matter %	sand content %	clay content %	H_2O hold. cap. %	P content %	N content %	October fire °C *	February fire °C *	tot. biomass g m^{-2}	liv. biomass g m^{-2}	tot. leaf index m^{-2} *	eff. leaf index m^{-2} *	H_2O content	tree count 100 m^{-2}	wood mass g m^{-2} *	mean tr. diam. cm	max. tree diam. cm	mean tree height m	foliage g m^{-2} *	tree death 100 m^{-2}
Woodland density	1. tree count 100 m^{-2}, 6.02	16.1	12.4	49.7	2	44.7	■̲								▴	▲̲														
	2. tree count 100 m^{-2}, 6.03	14.3	12.1	47.8	0	39.0	■̲	▪			▼		▴			▲̲		▼												
	3. tree biomass gm^{-2}, 6.02*	1851	1056	5018	121	29.4	■̲									▲̲														
	4. tree biomass gm^{-2}, 6.03*	1738	1941	4819	2.86	24.1	■̲							▾		▲̲	▼	▼												
	5. mean tree diameter cm	75.5	19.1	145	44	75.4	▪			■̲					▾									▼̲	▲					
	6. max. tree diameter cm	111	29.9	220	46.6	61.2	▪			■̲					▲									▼	▲̲					
	7. mean tree height m	9.9	2.5	17.6	3.7	48.8	▪			■̲	▾	▼	▼		▼	▲											▲̲			
Thinning	8a. rel. tree survival 02-03	0.88	0.22	1	0	49.3	▪̲	▪	▪	▪	▼	▾		▼̲	▴			▼	▼							▴	▾			
	8b.	"	"	"	"	44.5	■̲	▪		▪	▼	▼		▼̲	▴			▼						▴		▲	▼			
	9. rel. biomass survival*	0.92	0.2	1	0	41.0	■̲	▪	▪	▪		▼		▼̲	▲			▼	▼							▲				
	10a. tree death 100 m^{-2} 02-03	1.47	2.95	0	13.9	25.9	■	▪̲	▪	▪				▲				▲̲	▲					▴						
	10b. tree death (hot Feb. fire)	2.64	4.25	0	13.9	42.7	■̲			▪	▲		▼	▲̲	▾									▴						
	11. life wood ratio, 6.02	0.85	0.14	1	0.2	17.2	■̲			▪			▼̲	▾		▼									▲					
Recruitment	12a. pod count m^{-2}, 2.03	4.14	5.17	32.0	0	45.5	▪			■̲			▴		▾	▼										▲̲			▲	
	12b.	"	"	"	"	26.1	▪			■̲					▼	▾								▼	▲̲				▴	
	13a. seedlings 100 m^{-2}, 6.02	3.71	7.46	61.7	0	31.2	■		▪̲	▪	▼	▴	▲		▼	▲			▼̲									▼		
	13b.	"	"	"	"	25.0	■		▪̲	▪	▼	▴	▴		▼	▲			▼̲					▴	▾					
	14a. seedlings 100 m^{-2}, 6.03	3.96	9.62	79.6	0	28.7	▪	▪	▪	■̲						▲	▼			▲								▼̲		
	14b.	"	"	"	"	28.1	▪̲		■	▪	▼					▲̲			▲	▼	▾	▴	▲	▴	▾					
	14c.	"	"	"	"	25.9	■̲	▪				▲	▲̲		▲		▼													
Resprouting	15a. resprouts 100 m^{-2}, 6.03	5.42	6.75	29.8	0	60.5	▪	▪		■̲			▴		▾	▲	▼								▴	▼̲				
	15b.	"	"	"	"	47.9	▪	▪		■̲		▴	▴		▼		▼							▲	▾				▴	▲̲
	16. coppices 100 m^{-2}, 6.03	1.62	4.09	29.8	0	55.3	▪	▪	▪	■̲			▴					▴			▴									▲̲
	17a. suckers 100 m^{-2}, 6.03	3.84	5.80	25.9	0	49.6	▪	▪		■̲	▴	▴	▲				▾									▼̲			▲	
	17b.	"	"	"	"	27.6	▪			■̲		▴	▲											▲̲	▼				▴	

Table 1. Summary of tree layer and tree recruitment plot test variables, their descriptive statistics and main predictor variables in multiple regression models. Variables with a star (*) were calculated or modelled based on regression equations.

Reading key				
	var. not used in analysis			
▲	var. with positive sign			
▼	var. with negative sign			
▼̲	1st included variable			
·	▴	▾	< 3 %	relative contribution to final R^2
•	▲	▼	3-10 %	
▪	▲	▼	10-40 %	
■	▲	▼	> 40 %	
■			> 75 %	

Dependent variables		Descriptive statistics				Summary	SUMMARY			
		average	standard deviation	maximum	minimum	adj. R^2 of final model	soil variables	fire impact	grass layer	tree layer
Woodland density	1. tree count 100 m^{-2}, 6.02	16.1	12.4	49.7	2	44.7	■̲			
	2. tree count 100 m^{-2}, 6.03	14.3	12.1	47.8	0	39.0	■̲	•		
	3. tree biomass gm^{-2}, 6.02*	1851	1056	5018	121	29.4	■̲			
	4. tree biomass gm^{-2}, 6.03*	1738	1941	4819	2.86	24.1	■̲			
	5. mean tree diameter cm	75.5	19.1	145	44	75.4	·			■̲
	6. max. tree diameter cm	111	29.9	220	46.6	61.2	•			■̲
	7. mean tree height m	9.9	2.5	17.6	3.7	48.8	•			■̲
Thinning	8a. rel. tree survival 02-03	0.88	0.22	1	0	49.3	▪̲	▪	▪	•
	8b.	"	"	"	"	44.5	▪̲	▪		▪
	9. rel. biomass survival*	0.92	0.2	1	0	41.0	▪̲	▪	▪	•
	10a. tree death 100 m^{-2} 02-03	1.47	2.95	0	13.9	25.9	▪	▪̲	▪	•
	10b. tree death (hot Feb. fire)	2.64	4.25	0	13.9	42.7	■̲			•
	11. life wood ratio, 6.02	0.85	0.14	1	0.2	17.2	▪̲			▪
Recruitment	12a. pod count m^{-2}, 2.03	4.14	5.17	32.0	0	45.5	▪			■̲
	12b.	"	"	"	"	26.1	•			■̲
	13a. seedlings 100 m^{-2}, 6.02	3.71	7.46	61.7	0	31.2	▪		▪̲	•
	13b.	"	"	"	"	25.0	▪		▪̲	·
	14a. seedlings 100 m^{-2}, 6.03	3.96	9.62	79.6	0	28.7	▪	▪	•	▪̲
	14b.	"	"	"	"	28.1	▪̲		■	▪
	14c.	"	"	"	"	25.9	▪̲	▪		
Resprouting	15a. resprouts 100 m^{-2}, 6.03	5.42	6.75	29.8	0	60.5	▪	▪		▪̲
	15b.	"	"	"	"	47.9	▪	•		■̲
	16. coppices 100 m^{-2}, 6.03	1.62	4.09	29.8	0	55.3	•	•	•	■̲
	17a. suckers 100 m^{-2}, 6.03	3.84	5.80	25.9	0	49.6	▪	•		▪̲
	17b.	"	"	"	"	27.6	▪			■̲

Table 1. continued

Summary of multiple regression analysis

relative stepwise contribution of predictor variables to R^2 of the final model

	Soil variables						Fire		Grass layer					Tree layer						
	organic matter %	sand content %	clay content %	H_2O hold. cap. %	P content %	N content %	October fire °C *	February fire °C *	tot. biomass g m^{-2}	liv. biomass g m^{-2}	tot. leaf index m^{-2} *	eff. leaf index m^{-2} *	H_2O content	tree count 100 m^{-2}	wood mass g m^{-2} *	mean tr. diam. cm	max. tree diam. cm	mean tree height m	foliage g m^{-2} *	tree death 100 m^{-2}
1.					▴	▲̲														
2.	▼		▴			▲̲		▼												
3.						▲̲														
4.				▾		▲̲	▼	▼												
5.					▾									▼̲	▲					
6.					▲									▼	▲̲					
7.	▾	▼	▼		▼	▲											▲̲			
8a.	▼	▾		▼̲	▴			▼	▼							▴	▾			
8b.	▼	▼		▼̲	▴			▼						▴		▲	▼			
9.		▼		▼̲	▲			▼	▼							▲				
10a.				▲				▲̲	▲					▲						
10b.	▲		▼	▲̲	▾									▲						
11.			▼̲	▼		▼									▲					
12a.			▲		▾	▼										▲̲			▲	
12b.					▼	▾								▼	▲̲				▴	
13a.	▼	▴	▲		▼	▲			▼̲									▼		
13b.	▼	▴	▲		▼	▲			▼̲					▴	▾					
14a.						▲	▼			▲								▼̲		
14b.	▼					▲̲			▲	▼	▾	▴	▲	▲	▼					
14c.		▲	▲̲		▲		▼													
15a.			▲		▾	▲	▼								▴	▼̲				
15b.		▲	▲		▼		▼							▲	▼				▴	▲̲
16.			▲					▲			▲									▲̲
17a.	▲	▲	▲				▼									▼̲			▲	
17b.		▲	▲											▲̲	▼				▴	

Table 2: Summary of tree variables, their descriptive statistics and main predictor variables in multiple regression models. The predictor 'foliage category' was included for analyses of variables 6-8, but since it was not significant it is not shown in the table.

Reading key				
		var. not used in analysis		
▲		var. with positive sign		
▼		var. with negative sign		
▲̲		1st included variable		
·	▴	▾	< 3 %	rel. contribution to final R^2
▪	▴	▾	3-10 %	
■	▲	▼	10-40 %	
■	▲	▼	> 40 %	
■			> 75 %	

		Descriptive statistics		Summary of multiple regression analyses																															
					relative stepwise contribution of predictor variables to R^2 of the final model																														
					SUMMARY								Soil variables						Fire		Grass layer				Tree variables										
					Other			Tree variables																	density		size		growth		vigour		defences		
	Dependent variables	average	standard deviation	adj. R^2 of final model	soil variables	fire impact	grass layer	stand density	tree size	growth form	vigour & survival	tree defences	organic matter %	sand content %	clay content %	H_2O holding cap. %	P content %	N content %	October fire °C	February fire °C	total biomass gm^{-2}	living biomass gm^{-2}	total leaf index m^{-2}	living leaf index m^{-2}	tree count 100 m^{-2}	competition index	bole diameter cm	tree height m	crown width ratio	branching category	living wood ratio	tree survival (y/n)	ant nest count	swollen thorn cat.	spine category
Density	1. tree competition index, 6.02	0.36	0.17	**37.7**	■̲				■				▼	▴		▾	▴	▲̲									▼								
	2. tree competition index, 6.03	0.34	0.18	**46.1**	■̲	■			■					▾	▴	▾	▲	▲̲	▲	▼							▼								
	3. bole diameter mm	64.5	28.9	**17.1**	■			■̲					▲			▾		▴								▼̲									
Mortality	4a. tree survival 02-03 (yes/no)	0.89	0.31	**23.5**	▪	■̲	▪	▪	·	▪	■	▪					▴	▾	▴	▼̲	▾				▴		▴	▾		▴	▲			▾	▾
	4b. survival (Feb. fire = 0)	0.96	0.19	**26.1**							■̲																				▲̲				
	4c. survival (Feb. fire = hot)	0.77	0.42	**29.9**	■̲			■	■		▪			▲	▴	▲	▲	▼̲							▲		▲	▼			▴				
	5. living wood ratio, 6.02	0.88	0.17	**16.4**	▪			■	■̲	▪				▴	▾										▲			▲̲	▴	▼					
Recruit.	6. flowering category, 2.03	1.08	1.30	**56.2**	·		·	·	■̲	·	·		▾		▴	▾							▴		▴	▾	▴	▲̲		▴	▴				
	7. pod counts per tree	13.5	50.4	**50.5**	·		▪	■	■̲	·		▪	▴					▾					▴	▼		▼		▲̲	▴				▲		▾
	8. coppicing (yes/no)	0.10	0.17	**32.1**	·	▪	·	▪	·	·	■̲			▾					▾	▲		▴	▴		▼			▾	▾			▼̲			

Table 2. Summary of tree variables, their descriptive statistics and main predictor variables in multiple regression models. The predictor 'foliage category' was included for analyses of variables 6-8, but since it was not significant it is not shown in the table.

Reading key					
		var. not used in analysis			
	▲	var. with positive sign			
	▼	var. with negative sign			
	▲̲	1st included variable			
	·	▴	▾	< 3 %	rel. contribution to final R^2
	•	▲	▼	3-10 %	
	▪	▲	▼	10-40 %	
	■	▲	▼	> 40 %	
	⬛			> 75 %	

	Dependent variables	Descriptive statistics		Summary of multiple regression								
					relative stepwise contribution							
					SUMMARY							
					Other			Tree variables				
		average	standard deviation	adj. R^2 of final model	soil variables	fire impact	grass layer	stand density	tree size	growth form	vigour & survival	tree defences
Density	1. tree competition index, 6.02	0.36	0.17	37.7	■̲				▪			
	2. tree competition index, 6.03	0.34	0.18	46.1	■̲	▪			▪			
	3. bole diameter mm	64.5	28.9	17.1	▪			⬛̲				
Mortality	4a. tree survival 02-03 (yes/no)	0.89	0.31	23.5	•	■̲	•	•	·	•	▪	•
	4b. survival (Feb. fire = 0)	0.96	0.19	26.1							⬛̲	
	4c. survival (Feb. fire = hot)	0.77	0.42	29.9	■̲			▪	▪		•	
	5. living wood ratio, 6.02	0.88	0.17	16.4	•			▪	■̲	•		
Recruit.	6. flowering category, 2.03	1.08	1.30	56.2	·		·	·	⬛̲	·	·	
	7. pod counts per tree	13.5	50.4	50.5	·		•	▪	■̲	·		•
	8. coppicing (yes/no)	0.10	0.17	32.1	·	•	·	•	·	·	⬛̲	

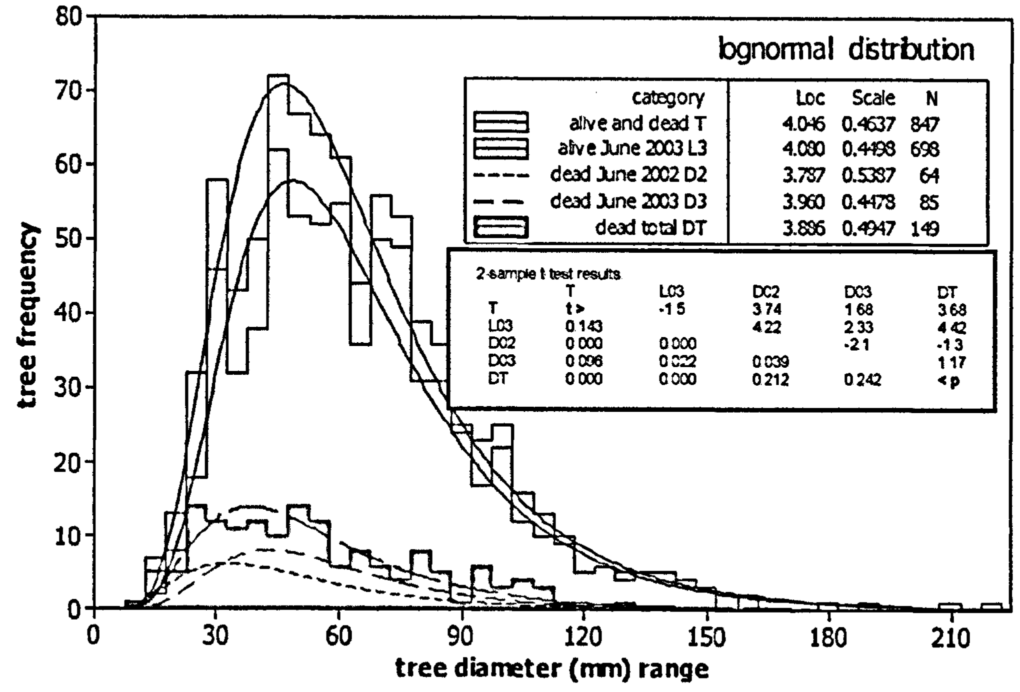
Table 2. continued

Summary of multiple regression analyses

relative stepwise contribution of predictor variables to R^2 of the final model

Soil variables						Fire		Grass layer				Tree variables										
												density		size		growth		vigour		defences		
organic matter %	sand content %	clay content %	H_2O holding cap. %	P content %	N content %	October fire °C	February fire °C	total biomass gm^{-2}	living biomass gm^{-2}	total leaf index m^{-2}	living leaf index m^{-2}	tree count 100 m^{-2}	competition index	bole diameter cm	tree height m	crown width ratio	branching category	living wood ratio	tree survival (y/n)	ant nest count	swollen thorn cat.	spine category
▼	▴		▼	▴	▲̲									▼								
	▾	▴	▼	▲	▲̲	▲	▼							▼								
▲			▼		▲								▼̲									
				▴	▼	▴	▼̲	▼				▲		▴	▾		▴	▲			▾	▾
																		▲̲				
	▲	▴	▲	▲	▼̲							▲		▲	▼			▴				
	▴	▾										▲			▲̲	▴	▼					
▾		▴	▾							▴		▴	▾	▲	▲̲		▴	▴				
▴					▾					▴	▼		▼		▲̲	▴				▲		▾
	▾					▾	▲		▴	▴		▼			▾	▾			▼̲			

In June 2002 the 97 plots contained 783 living and 64 dead trees; one year later 11% (85) of those trees alive in 2002 had died (Fig. 3). The average diameter of living trees in June 2002 was 64.5 ± 28.5 mm with a range from 13 mm to 220 mm. The frequency distribution of bole diameter was approximately log-normal (Fig. 3), but there were small peaks at 30, 45 and 70 mm bole diameter which may have represented distinct cohorts. Tree mortality was distributed across the range of tree sizes though it was highest amongst trees of < 30 cm diameter. Thus, the average bole diameter of all dead trees in June 2003 (54.7 ± 2.12 mm) was significantly lower than that of surviving trees (63.4 ± 1.0 mm), and there was a slight increase in average bole diameter until June 2003, caused mainly by the death of smaller trees (surviving tree average: 65.2 ± 1.1 mm; Fig. 3).



category	Loc	Scale	N
▭ alive and dead T	4.046	0.4637	847
▭ alive June 2003 L3	4.080	0.4498	698
---- dead June 2002 D2	3.787	0.5387	64
— — dead June 2003 D3	3.960	0.4478	85
▭ dead total DT	3.886	0.4947	149

2-sample t test results

	T	L03	DC2	D03	DT
T	t>	-1.5	3.74	1.68	3.68
L03	0.143		4.22	2.33	4.42
D02	0.000	0.000		-2.1	-1.3
D03	0.096	0.022	0.039		1.17
DT	0.000	0.000	0.212	0.242	<p

Fig. 3. Frequency distribution of bole diameter (at 20 cm above ground) of the 783 living trees plus the 64 dead trees measured in June 2002 on the 97 study plots (T), the 698 living trees in June 2003 (L3), dead trees in June 2002 (D2), dead trees from June 2002 until June 2003 (D3), and the total of dead trees in June 2003 (DT). A t-test matrix table for a cross-comparison of the different categories is also shown.

A multiple regression analysis based on data for individual trees revealed the competition index to be the most important predictor of bole diameter, though with an R^2 of only 17.1% (var. 3, Table 2); conversely, tree bole size was the second best predictor of competition index (vars 1-2, Table 2). The negative relationship between tree diameter and competition index is illustrated in Fig. 4a, which also reveals a relatively clear upper boundary to the scatter of points as depicted, suggesting that the maximum size that a tree can reach is related to the level of competition.

Fig. 4b shows the positive relationship between competition index and tree count 100 m^{-2}. An approximate upper and lower bound of competition pressure variation within plots of different tree densities may be drawn as illustrated. Based on the drawn lines in Figs 4a and 4b a maximum, mean and minimum 'size boundary line' was plotted correspondingly in Fig. 4c. The maximum line therefore represents the line of maximum bole diameter that may be found at a given plot tree density under lowest competition within plots, and the minimum line under highest competition within plots. It can be seen that the highest plot maxima of bole diameter are actually close to the average boundary line, but most plot maxima are even below the minimum boundary line (Fig. 4c). It can also be seen that the tree stands are relatively even-aged along the woodland-savanna gradient: plot maxima of tree bole diameter are almost constant while plot means decreased slightly with increasing tree density (Fig. 4c). Plot means were only above the minimum tree thinning line at very high tree densities (Fig. 4c). On most plots tree density therefore appeared to be well below the level potentially possible in this environment. That most of the tree stands in this woodland were apparently not undergoing density-dependent self-thinning was also supported by the relationship between log mean tree weight and log tree number per plot which in the regression had a slope of about -1/2 (Fig. 4d).

TREE MORTALITY

The trees which died between June 2002 and June 2003 tended to be smaller than average and occurred across a wide range of competition conditions (Fig. 4a). A multiple regression analysis indicates a small but positive influence of tree density on survival (vars 4a, 4c, Table 2), confirming the earlier suggestion that competition was not a major factor influencing tree mortality. In fact, the most important factor was fire (var. 4a, Table 2): in the 39 plots burnt only in February, 22.7 % of trees were killed (by fire or other factors), while in plots burnt in both fires 7.2 % of trees were killed and 3.7 % of trees died in plots burnt only in October; no trees died in the six plots which escaped fire altogether.

Another important factor, negatively related to tree mortality, was the initial living wood ratio (var. 4a, Table 2). This parameter, which may be seen as a measure of tree health and vigour at the time of sampling, was predicted by tree height and tree density (both positive relationships; var. 5, Table 2). When tree survival was analysed only for the 58 plots that were either not burnt, or only hit by 'cold' fires, living wood ratio was the only significant predictor (var. 4b, Table 2). In contrast, tree survival on the 39 plots which experienced the 'hot' February fire was mainly predicted by soil variables, tree size and stand density (var. 4c, Table 2).

Analyses at the plot level indicated that soil water holding capacity was the most important predictor of tree thinning as expressed in tree individual and tree biomass survival ratios (vars 8 and 9, Table 1). Unexpectedly, the relationships were negative, implying that increasing water holding capacity of the soil was associated with lower survival. In those analyses fire was only the second most important predictor, while the third was total grass biomass in June 2003. Since grass biomass may, however, have been influenced by tree mortality before June 2003 rather than *vice versa*, a second analysis was performed of the tree survival ratio, this time excluding grass variables; in this analysis, tree density emerged as a positive predictor in combination with mean and maximum tree bole diameter (var. 8b, Table 1). Fire was the first predictor when tree thinning was expressed in terms of the absolute numbers of tree deaths; as might be expected, there were more deaths in stands with more trees (var. 10a, Table 1). If only the 39 plots were analysed that were hit by the hot February fire, water holding capacity was again clearly the best predictor of mortality (var. 10b, Table 1). That tree mortality was higher under hotter fires, and on soils with higher water holding capacity, particularly in more open stands, is also illustrated in Fig. 5. Stand vigour measured as living wood ratios in June 2002 decreased with both, increasing soil clay and soil nitrogen content, while tree density appeared as a positive factor (var. 11, Table 1).

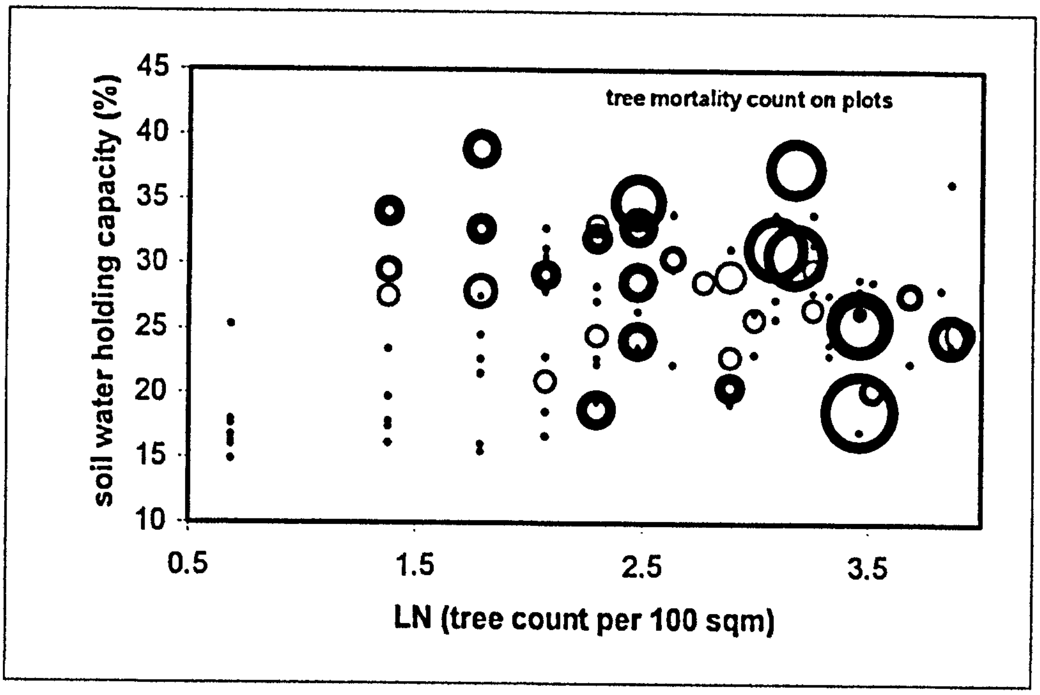


Fig. 5. Relative tree mortality on plots as indicated by bubble size (area indicating counts of dead trees), along the tree density gradient (x-axis) and soil water holding gradient (y-axis). The border of bubbles indicates whether a plot had been hit by hot February fire (thick lines), cold February fire (intermediate line) or the October fire only (thin line).

FLOWERING AND POD PRODUCTION

In November/December 2002, 55% of all trees were observed to be in flower (i.e. to have at least one flowering inflorescence), and by the following February 34% of all trees (and 61% of those observed to flower) had produced at least one pod.

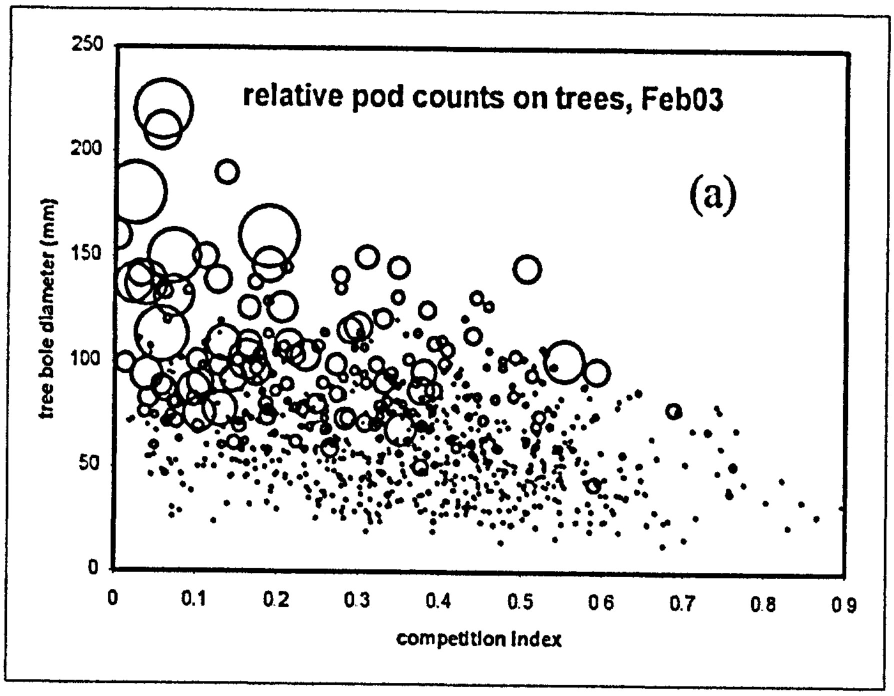
Flower production was strongly correlated with tree size but no other variables were important (var. 6, Table 2). Pod production was also positively related to tree size, and few trees of < 60 mm bole diameter produced pods (var. 7, Table 2; Fig. 6a). The maximum pod production was estimated at 560 pods on a large savanna tree. In contrast to flowering, final pod production was negatively related to both stand density and biomass of the grass layer (var. 7, Table 2; Fig. 6a). There was a weak positive association between pod production and numbers of ant nests per tree (var. 7, Table 2).

Pod production per plot ranged from 0 to 32.0 pods m^{-2}, with a mean value of 4.1 ± 5.1 pods m^{-2}. Mean bole diameter was the best predictor of pod counts on plots (var. 12a, Table 1). If this parameter was excluded from analysis it was replaced by the two tree density variables, and the R^2 decreased markedly from 45.5 % to 26.1 % (var. 12b, Table 1). It can be seen in Fig. 6b that pod production was generally highest on plots with a small number of trees but a high woody biomass. There was also a negative relationship between soil nutrients and pod production, but other factors may have been masked by nutrients (var. 12, Table 1).

Pods contained from 0 to over 10 seeds with a mean value (for a sample from closed woodland) of 1.8 ± 1.5 seeds per pod. Given that flowering occurred only during the early months of the year, mean annual seed production was, therefore, estimated to be 7.4 seeds m^{-2} or 24.3 seeds per tree.

RECRUITMENT BY SEEDLINGS

Seedlings were scarce, and numbers in June were considerably lower than adult tree counts on most plots (Fig. 7). At 0.040 ± 0.096 m^{-2}, the mean seedling density in June 2003 was slightly higher than that in June 2002 (0.037 ± 0.075 m^{-2}). However, there were no seedlings on 38 plots in June 2002 and none on 50 plots in June 2003. The maximum density found on any plot was 0.80 seedlings m^{-2}. The highly skewed distribution in seedling density could be approximately described by a gamma distribution as depicted in Fig. 7. No seedlings were found on plots during a rapid survey in February 2003.



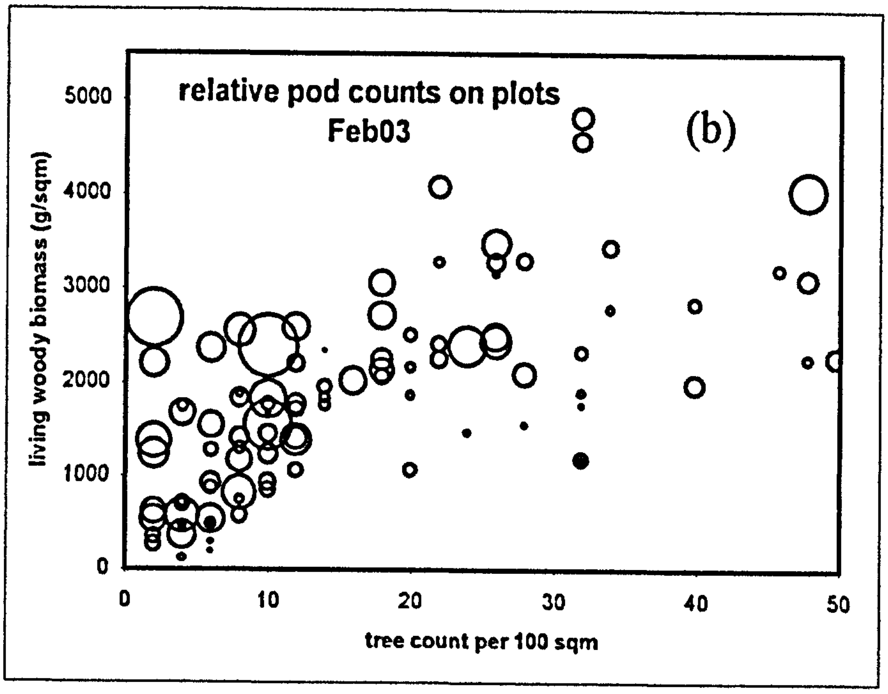


Fig. 6: Pod production and seedling establishment. **Upper panel (a)**: Relative pod counts (as indicated by bubble size) with regard to tree size and competition index in February 2003. Trees with no pods are indicated by smallest dots. **Lower panel (b)**: Relative pod counts with regard to woody biomass and tree count on plots in February 2003.

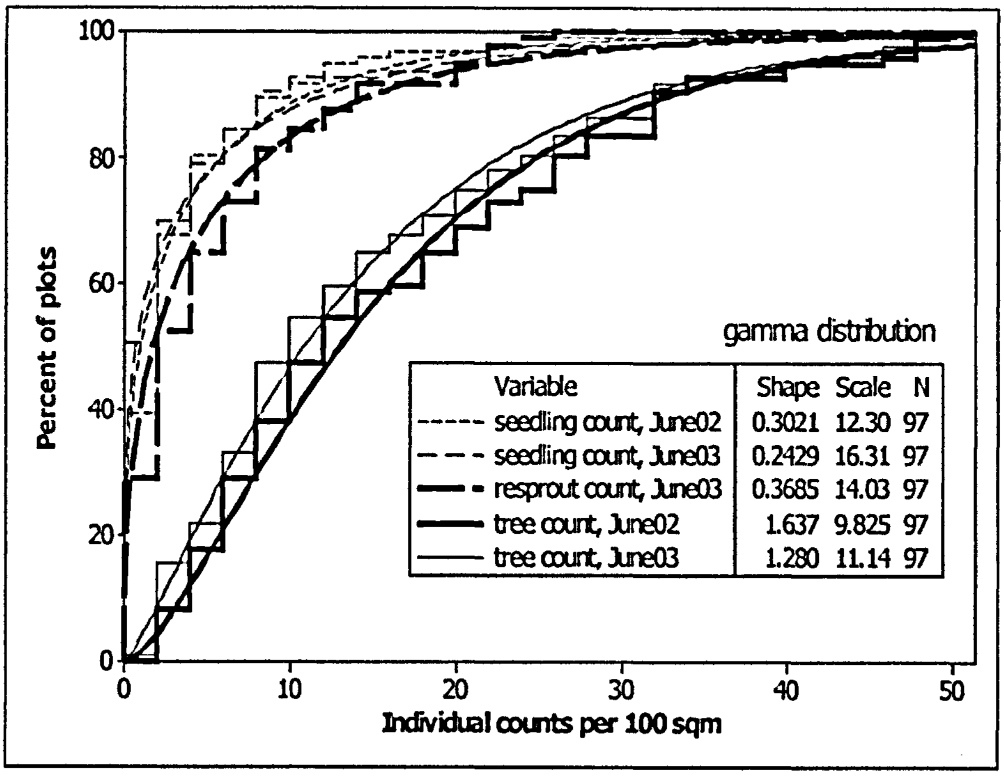


Fig. 7. Cumulative density function with Gamma distribution fit for seedling and resprout counts, and actual tree counts on plots in June 2002 and 2003.

The seedlings counted in June 2003 represented around 0.5 % of seed input in that year, and the numbers per plot did not correlate with pod production in February 2003; indeed, in contrast to pod production, seedling number was negatively related to average tree size in stands (vars 13a and 14a, Table 1). This may be explained by hidden correlations with other factors such as tree stand density, and ultimately soil factors. If mean tree size was deleted from the analyses it became apparent that soil variables and fire in interaction with the grass layer were more important than tree stand density in explaining seedling presence at both survey dates (vars 13b and 14b, Table 1). In June 2002, seedling numbers decreased with increasing grass biomass (var. 13, Table 1). In June 2003 seedling-grass relationships were more intricate (var. 14b, Table 1). Particularly grass water content on plots was strongly influenced by fire impact (c.f. Cochard & Edwards 2004a). If excluded from the analysis, soil texture variables and fire were the most important variables to emerge, and grass biomass variables were not included in the final equation (var. 14c, Table 1).

TREE PERSISTENCE AND RECRUITMENT BY RESPROUTING

One half of all trees (or strictly, tree parts above ground) that died during the study period produced coppice shoots from their stem bases, with the mean diameter of trees which resprouted (50.4 ± 23.0 mm) being significantly smaller ($t = 2.64$, $p = 0.01$, $df = 82$) than the diameter of those which did not (64.4 ± 25.8 mm). In contrast, only 5.2 % of surviving trees produced shoots, and there was no significant size difference compared to non-coppicing trees. Tree survival was therefore the main predictor in the analysis, with fire having an additional positive effect and tree density having a slight negative influence (var. 8, Table 2).

On 69 plots there was at least one resprout (coppice or sucker) in June 2003, and the average density was 0.052 ± 0.063 m^{-2} and the maximum 0.259 m^{-2} (Fig. 7). The main predictor of resprout density was mean plot tree size (var. 15a, Table 1). When this was excluded from the analysis, tree death, woodland density and soil variables were important factors (var. 15b, Table 1). There were fewer resprouts on plots burnt in October 2002 and thus spared from high fire temperatures in February 2003 (vars 15 and 17, Table 1). If analyses were split between coppice and sucker counts, it became obvious that tree death was only important with regard to coppicing (var. 16, Table 1). In contrast, suckering was mainly predicted by tree stand density and structure as well as soil texture, and only slightly by fire (var. 17, Table 1).

Discussion

WOODLAND DENSITY IN SPACE AND TIME

The distribution of trees was related both to soil texture, with higher tree densities in heavier soils, and also to soil nitrogen content. However, these relationships do not explain the high degree of clumping of trees which is evident from the log-normal distribution of woodland density in the randomly selected plots. Possibly, the impacts of cattle management have also left their traces in the present distribution of trees. Tobler, Cochard & Edwards (2003) suggested that the spread of *A. zanzibarica* in the late 1950's first followed a pattern of cattle grazing and trampling impact around paddocks, and that this initial paddock invasion was probably mainly by seed propagation (c.f. also Cochard & Edwards 2004a, 2004b). It was only in the 1970's that brush cutting was introduced, which had the effect of removing established trees while stimulating vigorous regrowth from trunk bases and roots. Even in 2002 the consequences of clonal regeneration from roots could be discerned in the form of rings of even-aged trees around small gaps (presumably representing the position of the former parent tree). Some dense clumps of trees may therefore be the result of clonal regeneration after brush cutting. Klötzli (1980) found that the success of clonal regeneration varied according to soil conditions and grassland type, being strongest in *Heteropogon* and *Panicum infestum* grassland.

Most of the woodland established some time after the last brush cutting in the early 1980's, while some very large individual trees may be older, having escaped brush cutting. Where acacias could establish in open savanna areas without much competition from neighbouring trees, size increase was probably higher than in dense woodland stands. For example, Smith & Goodman (1986) reported that, compared to controls, bole increment rates of *Acacia nilotica* were four times higher in trees released from intra-specific competition. Also trees in even-aged, initially rather uniform natural stands typically vary widely in size increment due to differential tree vigour, soil and canopy micro-environments and stochastic stand thinning (e.g. Gourlay, Smith & Barnes 1996, Okello, O'Connor & Young 2001, Stoll, Weiner & Schmid 1994). However, the stands of *A. zanzibarica* are probably not even-aged; we suppose that the peaks in the bole size distribution (Fig. 3) represent either favourable years for tree recruitment under continued heavy grazing, or resprouting of trees which have for some reason been killed. Higher tree increment of trees in open savanna (generally on more sandy soils) compared to trees in dense woodland stands (more clayey soils), and higher resprouting capacity in woodland stands (c.f. section about resprouts), probably explain why regression models of tree counts had a higher R^2 than models of tree biomass (vars 1-4, Table 1). In any case, our data indicate that while at least 17.6 % of trees died since August 2000 there was virtually no tree recruitment during this period (and probably very little in the last few years of ranching).

The variation in tree mortality among the plots did not follow the '-3/2 self-thinning rule' of mean tree biomass against tree stand density commonly observed for dense woodland stands and in plantations (Sackville Hamilton, Matthew & Lemaire 1995). This indicates that competition amongst trees was probably a less important mortality factor than it is in other woodlands where light is the main limiting resource; on the other hand, other factors which do not operate in a positive density dependent fashion – for example, competition with the grass layer, fire, and possibly also herbivory – may have been more important (c.f. Cochard & Edwards 2004a, Cochard, Edwards & Weber 2004).

TREE MORTALITY AND WOODLAND THINNING

Trees only died on plots which were burnt at least once during the study period, and particularly so on plots burnt by the second, hotter fire in February 2003. The ways that fire influences the structure of savanna vegetation are complex and various aspects of the nature and effects of fire must be considered to understand its impact. Fig. 8 attempts to graphically illustrate how a first and a second fire may affect the vigour of trees and eventually cause tree death. The black arrows indicate the effect of different types of fire, with the thickness of the arrow denoting the importance of the effect. The model is generally consistent with the inferences drawn from or results, though the weight of arrows may vary considerably according to tree sizes, stand density and possibly some environmental conditions.

A first major aspect of complexity concerns the intensity of fires and the fire history at a site. The effect of an individual fire is somewhat arbitrary, depending as it does on chance events such as starting point, and the direction and intensity of wind (Whelan 1995). As our results show, the path and intensity of fire are also highly influenced by the quality and quantity of fuel (illustrated by small, hatched arrows in Fig. 8; c.f. also Cochard & Edwards 2004a, Cochard, Edwards & Weber 2004); where grass has been partly consumed by an earlier fire or by grazing, the new fire is weak and likely to die off or to continue in a mosaic pattern. Thus fire history strongly affects which trees will subjected to a particular fire.

A second major aspect of complexity is how fire affects the survival and vigour of individual trees, either directly or indirectly by interaction with other components of the environment. Compared with some savanna trees, *A. zanzibarica* is not very resistant to fire; the smooth bark of this species is only 3-6 mm thick, which is much less than the 10-15 mm bark thickness reported for other fire-prone acacias (Eriksson, Teketay & Granström 2003). Thus, strong, hot fires may kill *A. zanzibarica* trees directly by damaging the stems (§1 in Fig. 8), and we observed that many of the smaller trees were killed during the hot fire in February.

Trees exposed to fire but not killed exude prolific amounts of resin at burnt parts of the stems and, as is the case for ringbarking (c.f. Introduction), are able to regenerate large sections of burnt bark. However, this bark regeneration may only be successful under optimal conditions (§2 and §3+§4, Fig. 8), and many trees which apparently survived the fire and produced resin or started resprouting again were nevertheless found to be dead in June 2003 (pers. obs.). Most of tree mortality following fire may therefore be attributable to a chain of other factors which negatively affect the vigour of trees and reduce their ability to regenerate, even in the absence of a second fire (§3+§5, Fig. 8). It appears that the living wood ratio in June 2002 may have been negatively affected by previous unrecorded fires, so that fire impact was probably higher on smaller trees under hotter fires such as those fuelled by higher grass biomass in more open areas. Our data clearly indicate that the ability of trees to survive fire varies according to their vigour (§6 and §7 in contrast to §1, Fig. 8), and for trees not affected by the hot fire in February 2003, living wood ratio was the only important predictor of survival.

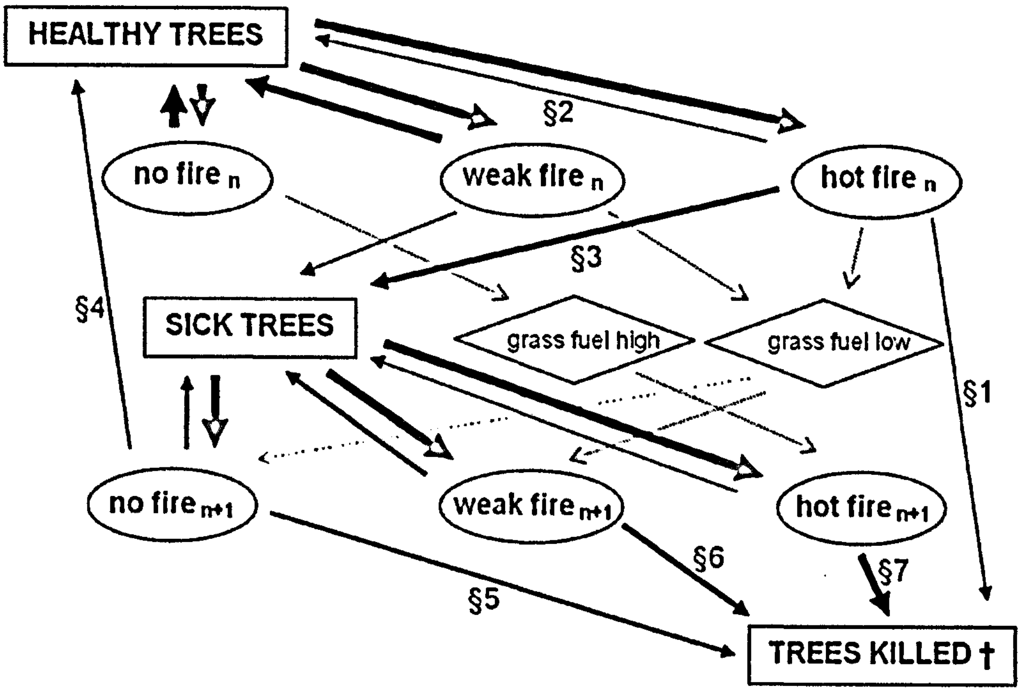


Fig. 8. Schematic model of the influence of fire on tree health and survival.

The most important factors predicting tree death in the February fire were, however, tree size, tree density and, in particular, soil parameters. That tree size is positively related to survival of savanna fires is not surprising (c.f. Archibald &

Bond 2003). Similarly it seems reasonable to suppose that the fire was less strong inside dense woodland due to lower grass biomass (c.f. Cochard & Edwards 2004a). More difficult to interpret are the negative relations that exist at the plot level between survival and both water holding capacity and clay content; indeed the latter two parameters were even more important predictors of mortality than fire. If we consider the overall patterns in this study and in the other two associated studies (Cochard & Edwards 2004a, Cochard, Edwards & Weber 2004), we suggest a model of cascading stress emanating from fire impact as is depicted in Fig. 9 (all § numbers in the following section refer to Fig. 9).

Hot fires, such as occurred in February 2003, cause debarking of the lower stem (§8) and defoliation of the tree canopy to more than 10 m above ground (§9; pers. obs.). The trees may also lose a large portion of the resident ant colony either as a direct result of the fire (§10) or through the loss of foliage, on which ants depend for nectar (§11). Fire also has several impacts on the environment in which the trees grow. The loss of grass biomass may change water levels in the upper soil layer (§12). While most insects have become victims of flames (§13), many others manage to escape the fire and can often be observed on trees where they may look for the few remaining plant resources still available for food (§14).

Particularly the loss of foliage on trees may ultimately lead to tree mortality by cascading effects of tree stress and resource depletion. According to Cochard & Edwards (2004a), trees and the defensive ants they support should be viewed within a single systemic frame; factors influencing tree health (§15) and resource availability (§16) affect foliage production, while the vigour of trees is dependent on the biomass of foliage (§17) and the abundance of ants (§18). In contrast to acacia trees whose foliage are chemically defended against insect herbivores, myrmecophyte acacias may therefore pass a critical period after fire, when foliage and symbiotic ant populations are just starting to regenerate (§19), yet insect herbivores are even more common (§20; c.f. also review and suggestions in Cochard 2004a). A similar pattern of post-fire tree stress and mortality has, for example, been described on myrmecophyte acacias in Central America by Janzen

(1967). Even though we made no observations on insect populations during this study we did observe vigorous flushes of new leaves on trees following the fire in February 2003 (§21); as a result, foliage levels were considerably higher on trees about three weeks after burning compared to trees measured at the same time on unburnt sites (Cochard, Edwards & Weber 2004). We suppose that such flushing is necessary in *A. zanzibarica* to maintain ant colonies (Cochard & Edwards 2004a). However, in the case of the February fire, it happened at a time when water resources in the soil were very low and may have led to increased water stress (§16).

In contrast to the trees, grasses resprouted very slowly after burning (§22, Fig. 9). Grass regrowth is mainly dependent on rainfall (Cochard & Edwards 2004a), and we suppose that as leaf transpiration area of the grass layer progressively increased competition between trees and grasses for water became increasingly intense (§23, Fig. 9). Since grasses can exploit water in the upper soil layers more effectively than can trees (Knoop & Walker 1985, Dodd & Lauenroth 1997; c.f. also Cochard, Edwards & Weber 2004), it seems probable that trees, and especially the fire-affected trees with abundant new foliage, became increasingly drought stressed (§25). The wet season in April-June 2003 was characterised by only minor precipitation events (Cochard & Edwards 2004a), and the water probably hardly penetrated beneath the top soil layers, particularly on clayey soils with a high water holding capacity (§26). On clay soils trees may therefore have come into even greater water stress than shortly after the fire; this could ultimately explain the negative relation between survival and water holding capacity (§27).

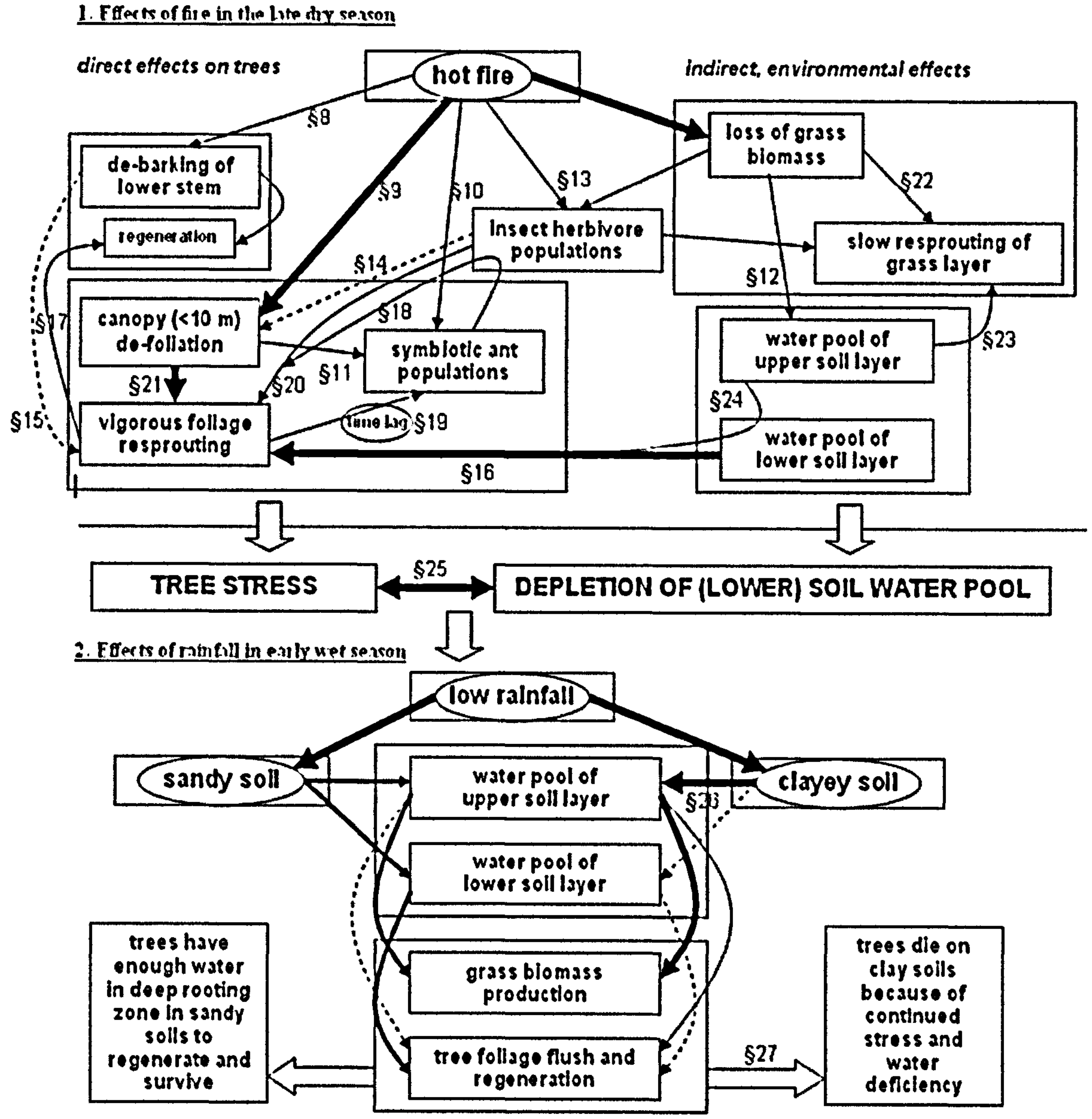


Fig. 9. Hypothetical model of the influence of hot fire on *A. zanzibarica* tree viability by direct impacts, indirect impacts and subsequent cascading effects.

Cochard, Edwards & Weber (2004) showed that the grass layer was particularly high in artificially created woodland gaps, which are generally enriched in nitrogen compared to adjacent savanna. It is therefore sound to assume, that once a dense stand of *A. zanzibarica* is opened up by fire (or other processes), the surviving trees do not necessarily benefit, either because of increased competition with the grass layer or because they are exposed to more severe fires in the future. Of course, this will only hold if the grass layer is not again affected by large herbivores. According to Cochard, Edwards & Weber (2004) it is those nutrient-rich woodland gaps where grasses seem to be particularly palatable to large herbivores. In summary, our data indicates that both, the two-layer soil-moisture competition model (Walker & Noy-Meir 1982) and the life-history-fire-disturbance interaction model (Higgins, Bond & Trollope 2000), retain their justification with regard to woodland decline and durable savanna resilience.

FLOWERING AND SEED PRODUCTION

While tree density had apparently no effect on the living wood ratio and mortality, trees in dense stands tended to produce fewer seeds than those in open areas, suggesting resource competition inside dense tree stands as has been observed in other studies (e.g. Smit & Rethman 1998). Equally, levels of foliage were decreased under high tree density in February 2003 (Cochard & Edwards 2004a). Both flowering and pod production increased exponentially with increasing tree size, and tree size was by far the most important predictor. Mean tree size was, therefore, also the first predictor in analyses at the plot level, and the R^2 decreased significantly if this variable was excluded from analyses. Competition index was, however, the second most important predictor of pod production on trees, while stand density did not significantly explain flowering category in November 2002, except in the sense that tree size generally decreased in denser stands. This probably reflects flower and pod abortion during the very dry conditions from December 2002 to February 2003. We made no detailed quantification of flowering success, but 38 % of trees initially flowering finally produced no pods at all. Hence seed abortion was probably higher than in the acacia species studied by Tybirk (1993): he observed about 22-48 % of seed abortion in three species with dehiscent pods, and about 5 % in two species with indehiscent pods. Willmer & Stone (1997) observed typical seed sets of between 1 and 4 seeds per flower in *A. zanzibarica* at Mkomazi Game Reserve.

The number of ant nests on trees had apparently a slightly positive influence on pod production. Willmer & Stone (1997) described how seed-set was assisted by *Crematogaster* ants on *A. zanzibarica.* Ants were deterred from young flowers by a signal, probably a volatile chemical. As soon as flowers were pollinated, ants returned to protect the developing ovules. Wagner (1997) found that seed set on *Acacia constricta* was about twice as high if there were *Formica perpilosa* ant nests underneath trees than if there were none, though she attributed this effect mainly to increased nutrient levels or soil biotic activity beneath ant nests. In our study the mean values of seed production - 7.4 seeds m^{-2} and 24.3 seeds per tree - were low compared to other invasive leguminous trees, e.g. 230-520 seeds m^{-2} for *Parkinsonia aculeata* (Cochard & Jackes 2004) and on average 992 seeds per individual on *Acacia nilotica* and 1628 on *A. tortilis* trees (Walters & Milton 2003). They were also lower than in the rare pyrophytic Australian acacias for which an average production of between 70 and 290 seeds per tree has been reported (Brown, Enright & Miller 2003).

SEEDLING RECRUITMENT

In June 2002 seedling presence was apparently decreased in dense grass, probably by direct competition for water and light. Seedling presence was increased by nitrogen content, but grass biomass was also slightly increased by nutrients. Grass growth was prolific after the exceptional rainfalls in the wet season from March to May 2002 and possibly more limited on plots with low nutrients than in June 2003, when water availability had probably been more important (Cochard & Edwards 2004a). In June 2003 the grass layer was still mainly influenced by the last fire, and total biomass was more than one third lower than in June 2002, with living biomass making up less than one third of this total (Cochard & Edwards 2004a). With tree size variables excluded from the analysis, grass layer variables emerged as significant predictors of seedling presence in June 2003. It appears that seedling numbers were higher on plots where there was less competition with grasses for soil water: seedling presence was negatively related to living grass biomass, but it seemed to be nevertheless increased on greener plots, indicating more soil water, and also on plots with high total biomass, indicating more shading and water retention. Yet, particularly grass water content on plots was strongly influenced by fire impact (Cochard & Edwards 2004a). If excluded from analysis, soil texture variables and fire were the most important variables to emerge, and grass biomass variables were not included in the final equation.

Soil texture is probably important for seedling establishment and early survival (c.f. Sanchez-Bayo & King 1994, Wilson & Witkowski 1998). Fire may also affect seedling germination and early establishment, as was observed for *A. zanzibarica* by Cochard, Edwards & Weber (2004). Yet, more important in explaining the June 2003 data was probably the effect of fire on the grass layer, and thence competition effects between seedlings and grasses; this relationship may have differed between the two sampling dates (c.f. Cochard, Edwards & Weber 2004). Complex competitive interactions between tree seedlings and grasses under different soil water and nutrient levels have, for example, been shown by Davis *et al.* (1999) for two *Quercus* species in Minnesota grassland and by Cohn, van Auken & Bush (1989) in a greenhouse experiment with *Acacia smallii.* In their study of several American acacia species, Zitzer, Archer & Boutton (1996) showed how light and soil properties affected root infection by symbiotic N_2-fixing *Frankia* and *Rhizobium* strains. Phosphorus availability is known to be an important factor affecting mycorrhizal fungi on roots of leguminous tree seedlings (e.g. Michelson & Rosendahl 1990), but in East Africa mycorrhizae are also found on the roots of many savanna grasses (Newman, Child & Patrick 1986). Phosphorus was negatively related to seedling counts in June 2002, but positively related in June 2003.

RESPROUTING AND TREE PERSISTENCE

Tree persistence by resprouting has been described as a key attribute of the resilience and productivity of savannas, and there is some evidence for a tradeoff between sprouting capacity and seed production (Bond & Midgley 2001, Shackleton 2001). Especially in fire-maintained savannas, resprouting may be favoured over regeneration by seed, since resprouts are more fire- and drought-resistant (Hoffmann 1998). At our site, there appears to have been a gradual shift in the regeneration strategy of *A. zanzibarica* from high resprouting capacity at young age to predominantly seed production at mature, old age. This seems also to be a common pattern for other savanna species (c.f. Cochard, Edwards & Weber 2004). It probably explains the high correlation with average tree bole diameter in the analyses at plot level: while the aboveground parts of smaller trees were more often killed by fire, they also had the highest vigour to resprout by coppicing or by suckering (c.f. Cochard, Edwards & Weber 2004). Apart from this, the correlations of resprouting with soil texture and nutrients seemed to be similar to those for seedling establishment.

As could be expected, coppice shoots were mainly recruited after tree topkill. Further coppicing was probably triggered in surviving trees by de-barking of tree boles after fire impact. Increased tree density probably had a slightly negative effect on coppicing. Studies in miombo woodland have also shown higher levels of resprouting in highly disturbed areas than in dense, self-thinning stands (Luoga, Witkowski & Balkwill 2004). Root suckering, in contrast, seems to be a less variable process in young tree stands, and was apparently not increased by current tree mortality in stands. Former recruitment patterns may have been different, however. In particular, heavy brush cutting until the early 1980's probably promoted suckering by uprooting trees and crushing soil (F. Klötzli, pers. comm.). The effect of cattle trampling may also have stimulated root suckering.

CONCLUSIONS

We conclude that the secondary *A. zanzibarica* woodlands at Mkwaja Ranch do not represent an alternate stable state to the initial savanna vegetation. The woodlands may rather be seen as the upper extreme of tree density in a still resilient savanna environment that can fluctuate within a broad range. Ranching may be seen as an intermittent disturbance which changed fire and water regimes in the savanna, thereby causing bush encroachment. Bush encroachment by *A. zanzibarica* decreased visibility for cattle mustering and reduced grazing resources; as a result, affected ares were less used by cattle and a new grazing equilibrium probably established at some point. The established trees prevented further tree recruitment of *A. zanzibarica* or other tree species, presumably by reducing water availability. The one woody species that was apparently able to colonise *A. zanzibarica* woodland in recent times was the doum palm *Hyphaene compressa*, a typical tree of the open fire-dominated savanna; the only signs we saw of woody succession was thicket formation beneath scattered large trees of *Terminalia spinosa* (pers. obs.). In contrast, we observed how other types of bushland, for example *Terminalia* bushland and *Dichrostachys-Acacia* bushland, were colonised by various woody species including rainforest species, suggesting that these bushland communities may in some parts represent succesional stages to forest vegetation (Tobler, Cochard & Edwards 2003, c.f. also Smith & Goodman 1987).

Our study also illustrates that the terminology of "stable states" and "transitions" may actually be misleading, since savannas are dynamic systems by nature, and relative stability may more often be the exception rather than the rule, particularly in fire-maintained humid savannas. Now that cattle have been removed, fire and competition with grasses have become the most important ecological factors determining woodland development; under these conditions the *A. zanzibarica* woodland seems to be opening up at a relatively fast rate and there is no regeneration. Providing that these determinants remain as they are, we suppose that most parts of the *A. zanzibarica* woodlands will return to open savanna within about the next 10-20 years. However, if sufficient grazing animals colonise the area, the ecological balance may again shift in favour of *A. zanzibarica*, as appears to have happened in large areas of the former Saadani Game Reserve. In this case the spread of bushland was presumably the result of heavy grazing by hartebeest, *Alcelaphus buselaphus*, and introduced wildebeest, *Connochaetes taurinus*, though early season burning (i.e. with cold fires) for wildlife management may also have played a role (Tobler, Cochard & Edwards 2003). Grass flushes after fire attract herds of ungulates (e.g. Brian 1996), and for this reason early burning is often practised for wildlife management in National Parks. In the longer run this often happens to be a bad recipe with regard to bush encroachment (Tobler, Cochard & Edwards 2003, Bond & Archibald 2003). Since extensive acacia woodlands in the national park are hardly in the interest of wildlife-oriented tourism and management, fire management for wildlife should either be completely abandoned, or only used in the late dry season when fires may be sufficiently strong to have an impact on woody vegetation.

This study provides some important lessons about why ranching was not sustainable at Mkwaja Ranch (for discussion see Cochard, Edwards & Weber 2004), and about the complexities of savanna ecosystems. The results show that several interacting factors influence whether or not bush encroachment occurs, and whether secondary woodlands are able to persist after ranching impact. The activities of large herbivores clearly play a central role; in the case of Mkwaja Ranch, grazing livestock caused large-scale encroachment of *A. zanzibarica*. However, with their recent withdrawal the stands appear to be declining rapidly. Particularly in humid coastal areas, anthropogenic fire may be sufficient to open up vegetation and maintain savanna even after large-scale transformation by bush encroachment promoted by the intensive activities of livestock. Fires may have long been used by people of the East African coastal savannas, and may have strongly influenced both ecological and evolutionary processes in these ecosystems.

Very little is yet known about the role of insect herbivory and wood borers in East African acacias and savannas in general (c.f. Lewinsohn & Price 1995). In a recent review of the topic, only bruchid seed beetles were mentioned as being important for acacia demography (Midgley & Bond 2001). However, our own limited observations lead us to suppose that insects may be a significant factor, among others, in *A. zanzibarica* woodland dieback (c.f. Cochard 2004a).

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The moonlight showed it all iron gray, except where some elephants stood upon it and their shadows were inky black. Little Toomai looked, holding his breath, with his eyes starting out of his head, and as he looked, more and more and more elephants swung out into the open from between the tree trunks. Little Toomai could only count up to ten, and he counted again and again on his fingers till he lost count of the tens, and his head began to swim.

Outside the clearing he could hear them crashing in the undergrowth as they worked their way up the hillside, but as soon as they were within the circle of the tree trunks they moved like ghosts.

Rudyard Kipling
The Jungle Book

Secondary *Acacia zanzibarica* woodlands in coastal Tanzania: 3. Regeneration potential in cut woodland gaps

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Summary

1. In two previous studies we investigated the structure, biomass and regeneration of secondary *Acacia zanzibarica* woodland at Mkwaja Ranch, coastal Tanzania. In this paper we present an experimental study to investigate how the creation of woodland gaps affects environmental conditions, vegetation development and tree regeneration.

2. In each of four study areas, twelve plots were selected and assigned to three treatments: control plots (NN), plots where all trees were felled by chain saw (FN), and cut plots where tree stumps were poisoned (FP). In November, before the gaps were made, tree stand density and seedbank were assessed on each plot. The foliage biomass and leaf area index (LAI) in the grass layer were estimated twice in the wet season (June 2002 and 2003), and once in the dry season (February 2003), and the same parameters were also measured for trees in the control plots. Seedling numbers were counted in all plots in March and June 2002 and in June 2003, while resprouts (coppicing from tree bases or stumps and suckering from roots) were counted and measured in February 2002 and in June 2003. Soil samples were taken and analysed for texture and main nutrients. Analyses of variance (general linear models) were used to test for differences between treatments and sites, and to determine important co-efficients.

Additionally, in June 2002 transpiration rates of acacia and grass leaves were measured in a cut plot and in a woodland plot. In February 2003, fire temperature was measured on two plots, and the effects of fire on acacia seeds were assessed.

3. Grass biomass and LAI during the wet seasons (June 2002 and 2003) were significantly higher in cut plots than in the control plots, while in the dry season (February 2003) there was no significant difference for grass biomass. In June 2003, grazing by wild animals was markedly higher on cut plots than on uncut controls.

4. Soil water content measured 14 days after rainfall was higher on cut plots compared to controls. This difference was apparently due to much higher rates of transpiration by trees than by grasses. Porometer studies revealed that the mean stomatal conductance of *A. zanzibarica* was more than three times higher than that of the grasses investigated.

5. Seedling establishment in March 2002 was significantly higher on cut plots than on controls. We also observed more seedlings on recently burnt sites. Seeds were scarified by low intensity fires but killed in hot fires. Very few viable seeds were present in soil samples collected in November 2001, indicating that the seedbank is transient and probably much influenced by fires. Seedling presence in the late wet season was still significantly higher on cut plots. However, no seedlings were found during a survey in February 2003, confirming other observations that there is presently no successful recruitment.

6. There was little evidence of successful vegetative propagation. On FN plots 68 % and on FP plots 11 % of stumps had coppice shoots in February 2002, and 28 % of all shoots were still alive in June 2003. Stumps of smaller trees were more likely to coppice and also to survive until June 2003. However, there was no increase in shoot length between February 2002 and June 2003, suggesting that the shoots were unable to escape above the grass layer. Root sucker counts were similar in June 2002 and 2003, and mainly differed between sites. Counts generally were neither affected by treatments nor by fire impact, but suckering appeared to be part of spontaneous vegetative propagation.

7. The study illustrates that savanna regeneration is possible in secondary woodlands relieved from ranching impact, and that regeneration can be accelerated by wood cutting which does not disturb the soil and affect tree roots (probably leading to increased root suckering). Nevertheless, savanna regeneration may be faster or slower or even be halted under varying rainfall conditions, fire frequencies and intensities, and regimes of herbivory. Some suggestions are made for successful management in a nature conservation and a ranching context.

Key-words: East Africa, savanna dynamics, grass flush, recruitment, seedling, sprouting, fire, transpiration

Introduction

African savanna ecosystems can be highly dynamic, with the vegetation alternating between woodland and grassland states (Cochard & Edwards 2004a, 2004b). Much emphasis has traditionally been placed on the role of elephant *Loxodonta a. africana* Blumenbach (van de Koppel & Prins 1998) to explain such transformations, and there are indeed many well documented examples of elephants having important impacts on woody savanna vegetation, either by browsing and other destructive behaviour (e.g. Laws 1970, Pellew 1983, Dublin 1995, Ben Shahar 1998) or through direct and indirect effects on regeneration (e.g. Dudley 1999, Goheen *et al.* 2004). Changes in elephant numbers have often led to dramatic effects on tree density in several protected areas (e.g. Leuthold 1996, Trollope *et al.* 1998, Duffy *et al.* 2002). It is fair to assume that many African savannas have been highly influenced by elephant over evolutionary times, even though elephants may no longer be present (e.g. van de Koppel and Prins 1998, Cochard & Edwards 2004b).

At Mkwaja Ranch, in coastal Tanzania, extensive secondary woodlands of the myrmecophyte tree *Acacia zanzibarica* (Moore) Taub. var. *zanzibarica* have established following bush encroachment on former rangelands during 50 years (1954-2000) of intensive grazing by Boran cattle *Bos indicus* L. (Tobler, Cochard & Edwards 2003, Cochard & Edwards 2004a). Bush encroachment was caused by changes in grass biomass, altered fire regimes, and probably also by displacing native wildlife which formerly controlled bush encroachment, both at the seedling stage (e.g. kudu *Tragelaphus strepsiceros* Pallas, bush duiker *Silvicapra grimmia* L. and other smaller antelopes) and at the tree stage (e.g. elephant and giraffe *Giraffa camelopardis* L.). Compared to current estimates (c.f. Treydte 2004) wildlife was still comparatively common during ranching times (e.g. Trail *et al.* 1985). Before and after abandonment of the Ranch in August 2000 numbers of wildlife were considerably reduced by poaching from neighbouring villages. In July 2002 the area was finally placed under protection and has now been incorporated into the newly created Saadani National Park.

Elephant have apparently always been present, though numbers have been relatively low, perhaps because of hunting for ivory in the coastal areas since pre-colonial times. Rough estimates of the numbers present in the Mkwaja-Saadani area during and after ranching range from about 50 to 300 individuals (A. Sanga pers. comm., F. Klötzli pers. comm., Robinson 1999, Treydte 2004); however, the elephants were rarely venturing into open savanna, but kept mainly to areas of savanna-forest mosaic. In contrast to some other wildlife species, elephant populations seem to be slowly recovering: in June 2003, after a year of anti-poaching controls by the new National Park authority, a single herd of over 80 elephants was observed in a large open area at Mariamu paddock, the largest former paddock at Mkwaja Ranch. Even so, their impact upon the adjacent *A. zanzibarica* woodlands was until recently very minor; thus, only one tree out of 847 surveyed in 2003 (Cochard & Edwards 2004b) was thought to have been pulled over by elephant.

In anthropogenically altered savannas such as in those of the humid coastal areas of Tanzania, frequent fires are more important in controlling tree density than are elephants. In fact, Cochard & Edwards (2004b) showed that after abandonment of ranching secondary woodlands of *A. zanzibarica* at Mkwaja Ranch were slowly opening up again even in the absence of megaherbivores. It was estimated that under current, post-ranching conditions woodlands may revert to a savanna typical of pre-ranching conditions within about 10-20 years due to thinning by fire and the declining vigour of older trees. This trend is likely to continue unless there is a marked increase in the number of larger grazers, for example the introduced wildebeest *Connochaetes taurinus* Burchell, which stimulate a new phase of acacia regeneration. According to Cochard & Edwards (2004c) the most palatable grasses for wildlife were generally correlated with high woodland density.

Under high cattle grazing established *A. zanzibarica* woodlands have a great potential to recover from resprouts and/or from seeds, as has been documented by several earlier studies (e.g. Klötzli 1980, Lupi & Walther 1994, That 2004). Repeated efforts to combat bush encroachment by brush-cutting were met with failure (Cochard & Edwards 2004b) because removal of aboveground parts of trees actually promoted the growth of resprouts and saplings, while fire management in the absence of effective longer-term grazing exclusion was hardly effective (Klötzli 1980, That 2004). Resprouting of trees is often seen as a key attribute of savanna resilience, particularly in savannas where mechanic tree damage, such as by elephant, may be common (Shackleton 2001, Bond & Midgley 2001, Pellew 1983). The effectiveness of resprouting as well as seedling recruitment may be decreased, however, under post-ranching conditions, particularly in humid savannas, where grass fuel is comparatively high.

In woodland gaps, grass biomass may be particularly high since these sites are commonly richer in nutrients than open savanna (Cochard & Edwards 2004a, Ludwig *et al.* 2004). This higher biomass reduces tree regeneration in various ways: competition with the grass layer reduces growth of seedlings and resprouts, while the higher amounts of grass fuel mean that any fire is more likely to kill young plants. On the other hand, seedling recruitment may be promoted by fires, as seeds in the soil are scarified and triggered to germinate in the next rainfalls (e.g. Sabitii & Wein 1988). According to Cochard & Edwards (2004b) seed production on *A. zanzibarica* trees was low, comparable to some Australian pyrophytic species. Nevertheless, initial invasion of grasslands by *A. zanzibarica* was probably by seed dispersal (Tobler, Cochard & Edwards 2003). Since the cattle were removed the numbers of large mammalian herbivores has remained low, and fire has regained its former importance in the ecology of this ecosystem. This provided a unique opportunity to test whether gap formation, e.g. by elephant, promotes woodland regeneration in the absence of high grazing pressure. This question has practical importance for bush management on cattle ranches; if regeneration does not occur under these conditions then it suggests that the spread of bush could perhaps be suppressed by brush cutting followed by effective grazing exclusion and fire management.

In an earlier paper we described the structure of secondary *A. zanzibarica* woodlands, and showed how fire affected stand structure and the distribution of grass and tree foliage biomass (Cochard & Edwards 2004a). It was shown that grass growth was lower in dense woodlands, probably because of competition with trees for water. We subsequently focused on demographic aspects of the woodland-forming tree *A. zanzibarica*, and demonstrated how tree and seedling mortality can be affected by the grass layer, both directly by increasing fire temperatures and indirectly through competition (Cochard & Edwards 2004b). In this third study we describe various experiments to investigate the regeneration potential of *A. zanzibarica* woodlands under post-ranching conditions. In the main experiment we created woodland gaps by cutting down trees; in half of the gaps the stumps were then poisoned. Regeneration by resprouting from stump bases (coppicing) and roots (suckering), and by seeds only was investigated in uncut control plots and in the two types of gap. We hypothesised that grass growth and soil nutrient status would differ between treatments and on control plots, and that grass and soil variables would change during the experiment, provided regeneration would occur.

Methods

STUDY SITES, PLOT SELECTION AND CUTTING TREATMENTS

In November 2001, four study sites were selected in dense *A. zanzibarica* bushland (a site map is presented by Cochard & Edwards 2004a); two sites (A and B) were south of the former Mariamu paddock and two sites (C and D) were in the bushland between Kichangani paddock and the airstrip. Mariamu was the oldest and most intensively used paddock, with up to 1500 cattle at peak times. Areas surrounding the paddock were recurrently brush-cut until 1982; thus the bushland in sites A and B is not older than about 20 years, though it may have regenerated from stumps and roots which established earlier. The paddock was closed in September 1998. Kichangani paddock, 1 km north of Mariamu, was opened in 1979 and was the last paddock to be closed, in August 2000. It supported up to 800 head of cattle. Site A was situated on a gentle eastward slope while site B was on even terrain. Site C and site D were both on gentle south to south-westward slopes.

At each site four sets of three 8×8 m^2 plots were selected and their corners marked with painted iron stakes. All plots supported dense stands of trees of similar age and structure (c.f. Table 1). The plots of one triplet, which were at least 30 m apart, were each assigned at random to one of three treatments: control (NN), trees felled (FN), and trees felled and stumps poisoned (FP). A buffer ring at least 3 m wide was additionally cut around the felled plots, and the trunks and branches of the cut trees were removed at least 3 m from the plot. All the tree stumps in the FP plots were poisoned shortly after felling by applying a mixture of 75 % of the herbicide Garlon® 120 (Dow AgroSciences, D.) and 25 % of the wetting agent Etalfix® (Maag Agro).

PLOT SURVEYS

In November 2001 a rough assessment was made of the soil seedbank in each plot by scraping up the top 2-3 cm of soil in 8 randomly selected 20 × 50 cm^2 quadrats and counting any seeds present. The diameters of trees and tree stumps on plots were measured in February 2002. Bole diameter was measured at 15-20 cm height. On a tree with multiple stem branching the average bole was estimated with the formula: $\textit{bole diameter} = \sqrt{(\textit{bole}_{(1)}^2 + \textit{bole}_{(2)}^2 + \ldots)}$. On the control (NN) plots various parameters describing tree growth were determined as described in Cochard & Edwards (2004a). Density of tree foliage was recorded in four categories (0-4) in March 2002, June 2002, February 2003 and June 2003. Tree foliage biomass was calculated using the following equation:

$$\textit{tree foliage weight (g)} = \exp(0.521 + 1.62 * \ln \textit{tree diameter (cm)}$$
$$+ 0.882 * \ln \textit{branching category (1-4)} + 1.48 * \ln \textit{foliage category (0-4)})$$

For the derivation of the equation see Cochard & Edwards (2004a).

The incidence of resprouting from stump bases (coppicing) and roots (suckering) was recorded in February 2002 and June 2003 on all plots. On felled plots lengths of resprouts from stumps were measured. An initial seedling count was made on plots after a heavy rainfall beginning of March 2002. A second survey of seedlings was performed in June 2002, and a third in June 2003. In February 2003 no seedlings were found during a cursory survey of all plots. Seedlings and resprouts could normally be told apart by size and growth form.

Grass biomass was measured in each plot in June 2002 and June 2003. All herb and grass biomass within six randomly placed 0.4 × 0.4 m^2 quadrats (but not closer to each other than 1.5 m) was cut at ground level and separated into species. The plant material was weighed when fresh in the field, and again after sun drying to determine the water content. Leaf area indices (LAI in m^2/m^2) were determined for each species using the specific leaf area (SLA) data provided in Cochard & Edwards (2004a). The total grass LAI on plots was also calculated.

SOIL SAMPLING AND ANALYSES

On each plot eight soil samples were taken in November 2001 and again in June 2003. Soil samples to a depth of 40 cm were taken with a soil auger, and the mixed sample for each plot was dried, initially in the sun and later in a laboratory oven. Samples were analysed for texture and nutrients (organic matter, nitrogen and phosphorus) as described in Cochard & Edwards (2004a). Soil water content at 10 cm depth was measured for each plot on two occasions using time-domain-reflectrometry (ThetaProbe type ML2x; Delta-T Devices Ltd.). The first occasion was about 14 days after heavy rainfall on 14th May 2002 and the second about 4-8 hours after a heavy rainfall on 27th June 2002. On 27th June 2002 soil samples to a depth of 15 cm were collected for analysis of nitrate content, which was performed three days later. Nitrate was extracted with calcium chloride from subsamples (FAL, FAW & RAC 2004) and then analysed photometrically using a FIAstar 5000 analyser (Foss Tecator© AB 2000, Höganäs, Sweden).

STOMATAL CONDUCTANCE, TRANSPIRATION AND TREE-GRASS COMPETITION EFFECTS

Stomatal conductance of both trees and grasses was measured using an AP4 porometer (Delta-T Devices Ltd.) at site A. After a pilot study in May 2002 more detailed measurements were made in July 2002 in a control plot ('woodland') and in a nearby FN plot ('gap'). At each site three trees of *A. zanzibarica,* three resprouts of the same species, and three tussocks each of the two most common grass species, *Heteropogon contortus* (L.) P. Beauv. ex Roem. & Schult. and *Panicum infestum* Andersson, were selected. Stomatal conductance of each plant was measured every 30 minutes between 09.00 and 18.00. The study was continued for three days.

A transpiration index was calculated by applying an estimated 24-hour transpiration rate on the LAI's for *A. zanzibarica, H. contortus* and *P. infestum* individually, and for the other grasses using the average transpiration rates of the two measured grasses. Those index data were extrapolated tentative estimates of transpiration (c.f. Cochard & Edwards 2004a).

At a site of very dense woodland north of site A, four 2 × 2 m^2 incision plots were created in May 2002 by digging a trench of about 30 cm depth around plots. By this depth most roots of *A. zanzibarica* seemed to be cut. Plots were surveyed in June 2002, February 2003 and June 2003.

FIRE EXPERIMENT

To investigate the effect of fire upon seed survival and germination, the plots of sites A and B were burnt at the end of February 2003. The ground temperature during a fire was measured by painting 48 thin stone plates with each of the 10 Thermax® colour markers. Each colour changes at a specified temperature, and from the array of changed colours a temperature range can be identified. The stones were placed on a wire frame so that they were held 15 cm above ground-level, and 50 acacia seeds were scattered beneath the stone within a circle of about 30 cm diameter. There were two replicates of this arrangement per plot. After the fire acacia seeds were collected and counted. Those which were obviously burnt were removed and the germinability of the remainder was tested. The seeds were placed in humid conditions in Petri dishes and kept in an incubator at 30° C for six days. Four Petri dishes of control seeds were also tested. The viability of seeds which did not germinate in this period was tested using 1% 2,3,5-triphenyl tetrazolium chloride (Yu & Wang 1996).

CALCULATIONS

MS Excel (Microsoft Inc.) was used for standard calculations of variables and Minitab 14 (Minitab Inc.) was used for graphics and for statistical analyses. Standard one-way analyses of variance (ANOVA) were used to test for site differences of treatment-independent variables such as pre-treatment tree structure and soil variables as summarised in Table 1. For the analyses of presumed treatment-dependent variables such as grass growth, transpiration index, soil water content, and tree recruitment by seedlings (Table 3), a general liner model (GLM) design including the factors 'site', 'F'-treatment and their interaction was used, and including any significant co-variables. Sets of possible co-variables for the GLM were pre-selected using best subsets regression analysis methods as outlined in Cochard & Edwards (2004a), and non-significant variables were subsequently excluded during GLM analyses. The 'P'-treatment was only relevant with regard to stump and root resprouting (Table 6), with two analyses being performed for the resprout data: one testing the 'F'-treatment including only NN and FN plots, and the other testing the 'P' treatment including only FN and FP plots. All other analyses only tested the 'F'-treatment, including all plots irrespective of 'P'-treatment. Plot values were used for all analyses except for the GLM analyses testing stump diameter depending on the factors 'site', 'P'-treatment and 'resprouting', and their respective interactions, as summarised in Table 5. In those analyses individual stump values were used. Before performing the analyses, all data were checked for equality of variances and normal distribution and if necessary were log-transformed. Outliers and leverage points were identified using residual plots, Cook's distance and Welsch Kuh's distance (DFITS). When necessary, points were deleted.

Results

PHYSICAL SITE CONDITIONS

There were some important differences among the sites in soil conditions. Sites A and B had a higher sand and lower clay content than sites C and D (vars 1 and 2; variables 1-16 refer to Table 1). Soil organic matter content was also lower in sites A and B (var. 3). Total nitrogen and ammonium content were higher in soils at sites C and D compared to A and B (vars 5 and 6), but there was no difference between sites in total phosphorus content (var. 4). Analyses including felling (F) treatment were also performed on soil nutrients, but the treatment was not significant. Sand and clay content of soils were highly correlated with most other soil variables except phosphorus content (Table 2).

Table 1. Summary of one-way ANOVA results for various plot variables. The tested factor was 'site', and the *df* were 3. For tree foliage variables (13-16) only control (NN) plots were measured.

plot variables	ANOVA		mean plot values (± standard deviation)			
	F	*p*	site A	site B	site C	site D
1. soil sand content (%)	11.36	<0.001	79.5 (3.8)	78.6 (5.0)	74.1 (7.2)	65.7 (8.8)
2. soil clay content (%)	13.22	<0.001	13.5 (2.5)	15.6 (4.2)	21.4 (6.7)	26.5 (7.5)
3. soil organic matter cont. (%)	3.36	0.027	0.13 (0.03)	0.14 (0.03)	0.17 (0.07)	0.18 (0.05)
4. soil phosphorus content (‰)	1.34	0.273	0.21 (0.02)	0.21 (0.01)	0.21 (0.01)	0.22 (0.01)
5. soil nitrogen content (‰)	3.1	0.036	0.40 (0.07)	0.48 (0.10)	0.47 (0.12)	0.53 (0.12)
6. soil ammonium (mg/100g soil)	10.47	<0.001	0.26 (0.07)	0.16 (0.08)	0.40 (0.14)	0.33 (0.13)
7. fire (0=no/1=yes), 10. 2002	4.01	0.013	0.58 (0.51)	0.42 (0.51)	0.0 (0.0)	0.50 (0.52)
8. fire (0=no/1=yes), 2. 2003	11.0	<0.001	1.0 (0.0)	1.0 (0.0)	1.0 (0.0)	0.50 (0.52)
9. fire (0=no/1=yes), 5. 2003	7.86	<0.001	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.42 (0.51)
10. initial tree count per 100 m^2	0.24	0.871	41.8 (11.2)	39.4 (16.3)	41.8 (8.6)	43.5 (10.5)
11. initial woody biomass (kg/m^2)	0.59	0.628	4.89 (1.27)	4.39 (1.54)	4.46 (1.01)	4.26 (1.09)
12. initial mean bole diameter (mm)	3.73	0.018	62.7 (8.09)	61.2 (10.5)	58.4 (5.95)	52.8 (5.7)
13. tree foliage mass (g/m^2), 3. 2002	1.69	0.223	79.2 (17.8)	47.3 (32.1)	59.6 (14.2)	64.7 (10.3)
14. tree foliage mass (g/m^2), 6. 2002	2.8	0.085	93.0 (13.9)	68.1 (33.8)	92.4 (29.5)	128.2 (36.0)
15. tree foliage mass (g/m^2), 2. 2003	17.64	<0.001	18.2 (11.4)	22.7 (7.3)	68.8 (16.5)	23.5 (7.7)
16. tree foliage mass (g/m^2), 6. 2003	4.25	0.029	107.3 (21.0)	37.6 (27.8)	56.9 (34.2)	91.1 (37.5)

Most plots were affected by fire at some stage during the study. In October 2002 about half of the plots at sites A, B and D were burnt (var. 7); this appeared to have been a cold fire, since few trees showed any damage (c.f. Cochard & Edwards 2004b). From November 2002 to February 2003 very little rain fell, so that fires in January and February were nourished by almost completely dry grass. In January and 2003 all plots were burnt at site C, and in February 2003 all plots at sites A and B and about half at site D (var. 8). A fire in March 2003 hit 5 plots at site D (var. 9). In parts that were not affected by fire in October, the dry season fires were intense and killed many trees (c.f. Cochard & Edwards 2004b).

Table 2. Correlation matrix of various soil variables, showing Pearson correlation index (upper half) and p-values (lower half).

	sand	loam	clay	organic matter	phosphorus	nitrogen	ammonium	soil water*
sand	Pearson correl. ▶	-0.470	-0.946	-0.636	-0.135	-0.555	-0.333	-0.662
loam	0.001		0.160	0.238	0.032	0.304	0.090	0.231
clay	<0.001	0.278		0.624	0.139	0.509	0.339	0.656
organic matter	<0.001	0.103	<0.001		0.002	0.535	0.292	0.607
phosphorus	0.361	0.828	0.346	0.987		0.265	0.136	0.054
nitrogen	<0.001	0.036	<0.001	<0.001	0.069		0.311	0.492
ammonium	0.021	0.541	0.018	0.044	0.357	0.032		0.104
soil water*,	<0.001	0.114	<0.001	<0.001	0.713	<0.001	0.482	◀ p-value

*8 hours after rain

INITIAL TREE STANDS AND TREE LEAF PHENOLOGY ON CONTROL PLOTS

Before cutting, all plots had closed stands of *Acacia zanzibarica* with similar biomass (mean 450 kg 100 m^{-2}) and tree density (42 trees 100 m^{-2}). There were no differences between the four sites in these parameters (vars 10 and 11), and only the average bole diameter was slightly lower at site D compared to the other sites (var. 12).

Tree foliage biomass and LAI on control plots differed considerably between seasons (ANOVA: $F = 18.98, p < 0.001, df = 3$; Fig. 1). Tree foliage levels were not different between sites in March and June 2002 (vars. 13 and 14). In late February 2003, however, tree foliage at site C was significantly higher than at other sites after the grass layer had been burnt in late January or early February (Fig. 1; var. 15). In June 2003, foliage levels were significantly lower at site B compared to site A, mainly because many trees had been killed by the fire in February 2003 on three plots at site B (Fig. 1; var. 16).

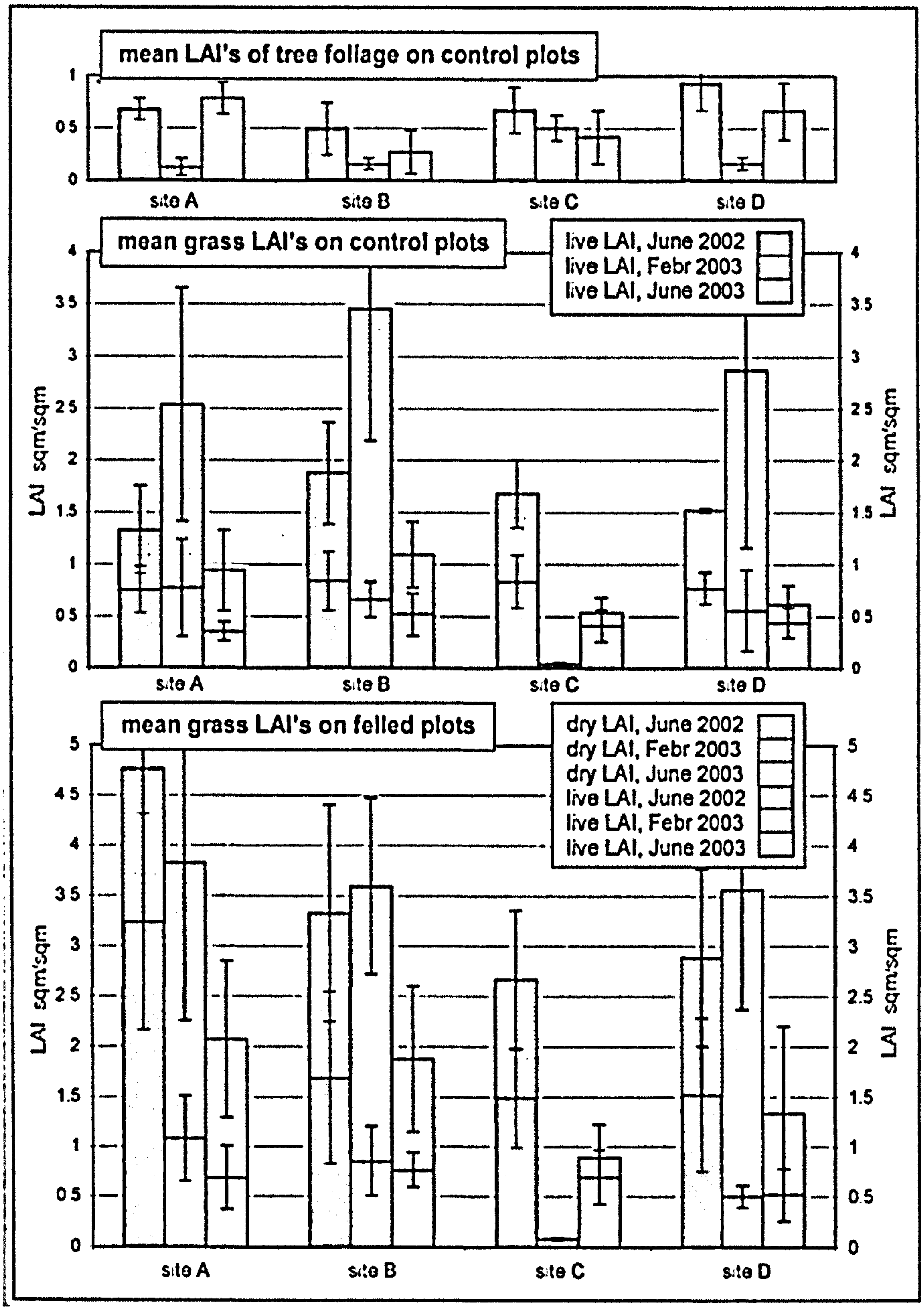

Fig. 1. Leaf area indices (LAI) of the tree and the grass layer (including total and live grass LAI ratios) on control plots and felled plots on the four study sites and at three sampling dates: June 2002, February 2003 and June 2003.

GRASS BIOMASS AND LAI

Following the cutting of trees in the F plots, the grass biomass developed very vigorously, and total grass biomass in June 2002 and 2003 was significantly higher in the F plots (612 ± 149, resp. 239 ± 114 g m^{-2}) than in the controls (290 ± 71, resp. 132 ± 49 g m^{-2}; vars 17 and 19; variables 17-36 refer to Table 3). There was no significant difference measured for treatments in February 2003, but soil clay and organic matter, and the October fire were significant co-variables in the equation (var. 18). Soil nutrients and fire were also significant co-variables determining grass biomass in June 2003 (var. 19).

The proportion of total grass biomass which was alive (live grass ratio) was not influenced by felling treatment, but in June 2002 ratios at site A (0.65 ± 0.10) were significantly higher than at sites B and D (0.48 ± 0.13, resp. 0.50 ± 0.11; site C: 0.54 ± 0.11; var. 20). Equally, in February 2003 live grass ratios at site A (0.30 ± 0.13) were significantly higher than at site D (0.17 ± 0.05; site B: 0.25 ± 0.14; var. 21). Live grass ratios at site C were close to 1 in February 2003, since the site had been recently burnt. In June 2003 only the site×F interaction was significant, but soil texture and soil ammonium were significant co-variables, which, as noted in the previous section, also differed between sites (var. 22). Pre-treatment woody biomass was also a significant co-variable determining live grass ratios in June 2002 and 2003 (vars 20 and 22).

Mean grass SLA increased slightly from June 2002 to June 2003, and was significantly higher at site A (64.5 ± 12.3, resp. 76.6 ± 11.56 cm^2/g) compared to the other sites (52.09 ± 7.8, resp. 57.9 ± 9 cm^2/g; vars 23 and 24). Closely correlated with grass biomass, the total grass LAI's were also significantly higher on the F plots at all three sampling dates (vars 25-27; Fig. 1). In June 2003 total grass LAI's were, furthermore, significantly higher at sites A and B compared to C and D (var. 27; Fig. 1). The only significant co-variable was the fire in October 2002 (vars 26 and 27). The LAI's of the woody and grass components were generally in the same range during the wet seasons in June 2002 and 2003 (Fig. 1). During the wet seasons the effective grass LAI's were significantly higher on the F plots than on controls (vars 28 and 30), whereas during the dry season there were significant differences between sites but not between treatments (excluding site C, which had been burnt in late January 2003; var. 29; Fig. 1).

Table 3. Summary of GLM results for various plot variables. The tested factors were 'site', felling treatment 'F' (irrespective of poisoning treatment 'P'), and the 'site×F' interaction. Significant plot co-variables included into the model are also listed, whereby the number before the bracket indicates the variable listed in Table 1. In the bracket the sign in regression analysis, and the *F* and *p* values in the GLM are given. For variables with a star (*) site C was not included as grass biomass was burnt in February 2003.

plot variables	plot mean (st. dev.)	GLM-Results	*F* / *p*			(sign, *F*, *p*)
		R^2 adj.	site (*df* = 3)	F treat. (*df* = 1)	site×F (*df* = 3)	co-variables (n°) (*df* = 1)
17. grass biomass (g/m^2), 6. 2002	504.2 (199.5)	65.4	0.51 0.681	80.37 <0.001	3.57 0.022	-
18. grass biomass (g/m^2), 2. 2003*	477.7 (347.6)	38.5	0.46 0.635	0.18 0.674	0.46 0.635	2 (+, 6.55, 0.016) 3 (-, 6.02, 0.021) 7 (+, 7.35, 0.012)
19. grass biomass (g/m^2), 6. 2003	203.0 (109.3)	51.8	1.43 0.249	14.3 0.001	0.24 0.871	4 (+, 4.38, 0.044) 5 (-, 4.32, 0.045) 6 (-, 5.23, 0.028) 7 (+, 8.44, 0.006) 8 (+, 4.94, 0.033)
20. grass living ratio (%), 6. 2002	0.54 (0.13)	29.4	3.56 0.023	2.04 0.161	0.15 0.927	11 (+, 5.55, 0.024)
21. grass living ratio (%), 2. 2003*	0.43 (0.35)	35.8	5.7 0.008	0.29 0.596	0.71 0.501	7 (-, 4.37, 0.045)
22. grass living ratio (%), 6. 2003	0.55 (0.25)	63.1	1.14 0.345	2.73 0.107	4.21 0.012	1 (+, 11.05, 0.002) 2 (+, 16.6, <0.001) 6 (+, 5.77, 0.02) 11 (-,10.45, 0.003)
23. mean grass SLA (cm^2/g), 6. 2002	55.3 (10.4)	17.6	4.65 0.007	0.28 0.602	0.08 0.968	-
24. mean grass SLA (cm^2/g), 6. 2003	63.1 (12.9)	48.8	14.8 <0.001	0.06 0.814	1.36 0.271	1 (-, 8.74, 0.005) 3 (-, 4.12, 0.05)
25. total grass LAI (m^2/m^2), 6. 2002	2.81 (1.42)	52.7	1.49 0.232	42.07 <0.001	2.87 0.048	-
26. total grass LAI (m^2/m^2), 2. 2003*	2.59 (1.83)	18.6	0.12 0.889	7.46 0.011	1.1 0.348	7 (+, 9.31, 0.005)
27. total grass LAI (m^2/m^2), 6. 2003	1.29 (0.78)	60.3	7.5 0.001	18.55 <0.001	0.65 0.591	7 (+, 6.24, 0.017)
28. live grass LAI (m^2/m^2), 6. 2002	1.59 (1.05)	50.9	2.96 0.044	29.49 <0.001	3.45 0.026	-
29. live grass LAI (m^2/m^2), 2. 2003*	0.59 (0.45)	21.3	3.79 0.034	1.54 0.225	0.81 0.453	-
30. live grass LAI (m^2/m^2), 6. 2003	0.59 (0.26)	16.6	0.93 0.436	10.59 0.002	0.58 0.634	-

Table 3. continued.

plot variables	plot mean (st. dev.)	GLM-Results		F / p		(sign, F, p)
		R^2 adj.	site (df = 3)	F treat. (df = 1)	site×F (df = 3)	co-variables (n°) (df = 1)
31. transpiration index (~ l/d/m^2), 6. 2002	0.091 (0.043)	38.4	3.57 0.022	2.01 0.164	4.89 0.005	-
32. transpiration index, 6. 2003	0.044 (0.028)	75.9	4.11 0.013	110.29 <0.001	11.7 <0.001	7 (+, 6.61, 0.014); 10 (+, 4.1, 0.05)
33. soil water content (%), 8 h after rain	23.48 (4.01)	4.2	1.33 0.279	3.29 0.077	0.25 0.86	-
34. soil water (%), 14 d after rain	8.68 (2.71)	49.6	0.64 0.593	46.28 <0.001	1.54 0.218	-
35. pod count on trees m^{-2} ground, February 2003 (only NN plots)	0.76 (1.88)	61.9	2.82 0.093	-	-	1 (+, 8.42, 0.016) 14 (+, 7.3, 0.022)
36. LN of seedling count, 3. 2002	0.63 (0.88)	75.6	30.78 <0.001	8.12 0.007	0.21 0.888	12 (+,12.14, 0.001)
37. seedling count, 6. 2002	0.16 (0.22)	31.0	0.18 0.907	17.34 <0.001	0.46 0.714	3 (+, 4.73, 0.036) 12 (+, 6.61, 0.014)
38. seedling count, 6. 2003	0.13 (0.21)	67.7	28.26 <0.001	5.72 0.022	0.47 0.702	-

GRAZING

Only 25% of the control plots showed traces of grazing, while 44 % of cut plots were grazed (Fig. 2). Furthermore, although the intensity of grazing within plots was very variable it was significantly higher on average in plots where trees had been removed (Mood's median test: $\chi^2 = 9.96$, $df = 2$, $p = 0.007$). In several cut plots >20 % of the area showed signs of grazing, while none of the control plots received such a high level of damage. For both sets of plots the distribution of grazing damage could be described by the gamma distribution as depicted in Fig. 2. Very little grazing was observed on a further 60 randomly selected grassland plots and on 21 densely wooded plots (all summarised under "random"), surveyed in June 2003 in the Mariamu area around sites A and B (Cochard & Edwards 2004a; Fig. 2).

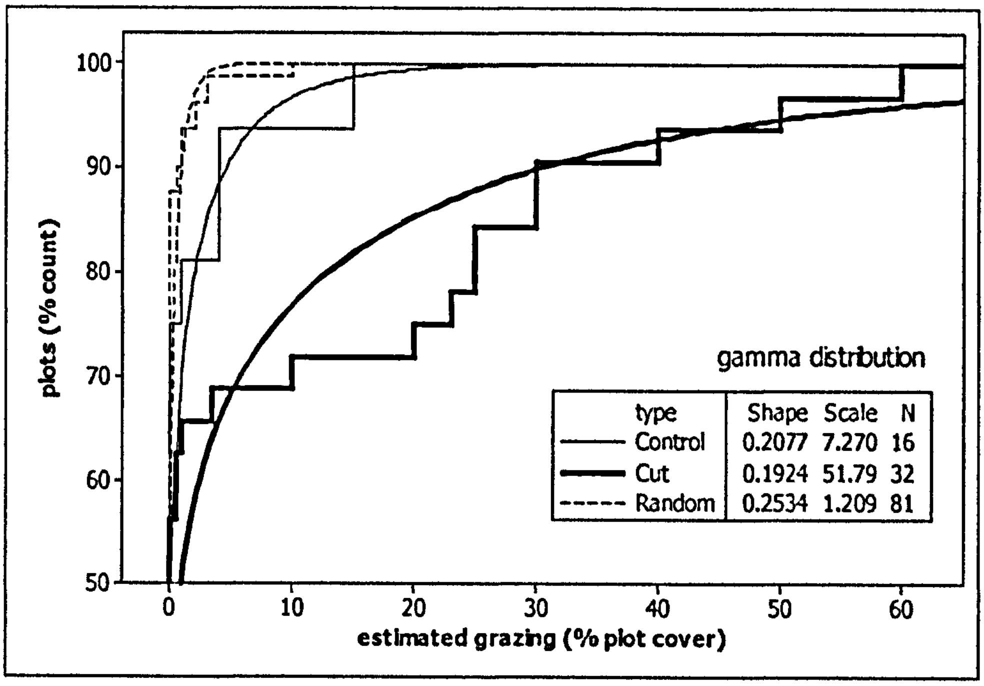

Fig. 2. Estimated percent grazing in June 2003 on control (NN) plots, cut (F) plots and on random plots surveyed in another study (Cochard & Edwards 2004a).

LEAF STOMATAL CONDUCTANCES

Grass biomass on the two plots where porometer measurements were performed was estimated to be 124 gm^{-2} for the control plot (woodland) and 890 gm^{-2} for the cut plot (woodland gap). *Panicum infestum* was the most abundant grass, accounting for 50.9 % of biomass on the control and 90.7 % on the cut plot. *Heteropogon contortus*, accounted for 23.2 % of biomass on the control and 3.8 % on the cut plot. The rest of the grass layer biomass was composed of the sedge *Fimbristylis triflora* (a detailed analysis of floristic patterns in the grass layer are given in Cochard & Edwards 2004c). Leaf biomass of *A. zanzibarica* was about 90.4 gm^{-2} on control and < 2 gm^{-2} on the cut plot.

The maximum mean stomatal conductance (g_{max}) of *Acacia zanzibarica* was 469 mmol s^{-1} m^{-2} for trees in the woodland gaps and 321 mmol s^{-1} m^{-2} for trees in the control plots. In both cases the highest values were recorded in the morning (at 11.00 in the gap and at 10.00 in the control plots), and thereafter g declined strongly to reach minimum mean values at 17.00 of 111 mmol s^{-1} m^{-2} in the gap plots and 134 mmol s^{-1} m^{-2} in the controls (Fig. 3). The mean values for the period 10.00-17.00 were 259 mmol s^{-1} m^{-2} in the woodland gap and 218 mmol s^{-1} m^{-2} in the dense woodland plot. The two grasses investigated, *H. contortus* and *P. infestum*, had much lower values of *g* than did *A. zanzibarica* (Fig. 3). Mean daily values of *g* were somewhat higher in the woodland gaps than in the control sites (63 and 55 mmol s^{-1} m^{-2}, respectively, for *Heteropogon contortus*, and 85 and 52 mmol s^{-1} m^{-2}, respectively, for *Panicum infestum*). In both species there was a decline in *g* from 10.00 until 18.00 but these declines were much less marked than for *A. zanzibarica*. A GLM analysis performed on the daily averages confirmed highly significant differences in *g* between the different species (F = 223.82, $p < 0.001$, df = 2) and between the gap and woodland plots (F = 12.46, $p < 0.001$, df = 1), whereas the plot×species interactions were not significant (F = 1.65, p = 0.195, df=2).

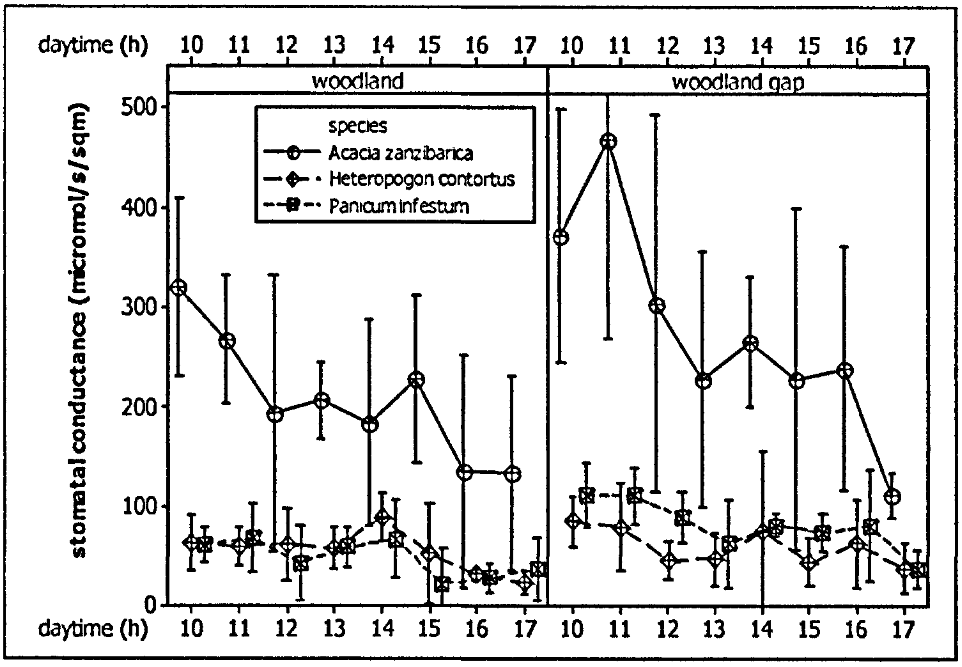

Fig. 3. Daily transpiration rates summarised over 3 days in mid June 2002, measured on an FN plot (woodland gap) and an adjacent control plot (woodland) at site A on *Acacia zanzibarica*, and the dominant grasses *Heteropogon contortus* and *Panicum infestum*. Day times indicate the beginning of the hours.

ESTIMATED TRANSPIRATION RATES, SOIL WATER CONTENT AND TRENCHING EFFECTS

Estimated total transpiration rates on plots were generally higher for control plots than in the gaps, except at site A where grass growth was prolific. In June 2002 there was therefore a significant 'site×F' interaction for transpiration index (var. 31). In June 2003 the two factors 'site' and 'F' and the interaction were significant, and initial tree count and the October fire were significant co-variables (var. 32).

That total transpiration during the wet season was higher on control plots than on felled plots was confirmed by the measurements of soil water content. Even though average soil moisture content about 6-10 hours after an intensive rainfall on 27th June 2002 was not significantly different between control (22.0 ± 2.9%) and cut plots (23.8 ± 5.1%; var. 33), about 14 days after heavy rain on 30th April 2002 mean soil moisture content on control plots (6.0 ± 1.2 %) was significantly lower than on cut plots (10.0 ± 2.2%; var. 32). Site differences were not significant on either occasion (vars 33 and 34).

The trenching experiment did not appear to show any effects, since grass biomass and greenness inside trenched plots was comparable to biomass and greenness outside of plots at all three sampling dates.

SEED PRODUCTION, SEEDBANKS AND EARLY WET SEASON SEEDLING ESTABLISHMENT

The production of pods and seeds was estimated on control plots in February 2003. Pod production averaged 2.3 ± 2.7 pods/m^2 and the average seed content of pods was 1.8 ± 1.5 (Fig. 6). Average seed weight was 23.2 ± 4.5 mg. Since pods are only produced once per year (out-of-season fruiting occurs but is negligible), the annual seed production in investigated stands of *A. zanzibarica* is estimated to be 409 ± 490 seeds 100 m^{-2} (Table 4). There was some variation in seed production between plots, which was related to difference in tree foliage density and soil texture (var. 35).

Table 4. Summary of reproductive variables at the four sites and the three treatments. Figures in bold indicate mean counts m^{-2}, figures below indicate standard deviation from mean. Control plots and overall totals are shaded in grey.

sites	plot treatment	mean seed count 100 m^{-2} ± st. dev.		mean seedling count 100 m^{-2} ± st. dev.			mean resprout count 100 m^{-2} ± st. dev.					
		seed bank	seed rain	March 2002	June 2002	June 2003	coppices		suckers		TOTAL	
		Nov. 2001	Feb. 2003				Feb. 2002	June 2003	Feb. 2002	June 2003	Feb. 2002	June 2003
A	NN	**25.0** 50.0	**225** 140	**88.7** 37.4	**3.1** 2.2	**0** 0	**0** 0	**2.0** 4.0	**1.6** 1.3	**4.7** 3.8	**1.6** 1.3	**6.7** 2.4
	FN	**25.0** 50.0	-	**218** 160	**39.8** 31.8	**0.4** 0.8	**21.9** 5.3	**4.7** 4.2	**1.9** 2.3	**0.4** 0.8	**23.8** 5.2	**5.1** 5.0
	FP	**75.0** 95.7	-	**164** 72	**24.6** 25.1	**2.3** 2.7	**4.3** 2.0	**1.2** 1.5	**1.2** 1.5	**0.4** 0.8	**5.5** 2.7	**1.6** 1.3
B	NN	**50** 100	**347** 288	**35.5** 30.2	**2.7** 3.2	**1.9** 3.0	**0** 0	**8.0** 6.7	**2.0** 2.0	**2.2** 5.7	**2.0** 2.0	**10.2** 5.2
	FN	**25.0** 50.0	-	**89.5** 110	**21.5** 24.3	**6.2** 4.0	**25.4** 5.0	**7.8** 3.4	**5.1** 5.2	**3.1** 3.8	**30.5** 6.6	**10.9** 4.0
	FP	**75.0** 95.7	-	**75.0** 83.4	**22.7** 24.5	**4.3** 5.9	**2.7** 0.8	**1.6** 1.3	**5.1** 4.1	**5.5** 3.7	**7.8** 4.9	**7.0** 4.9
C	NN	**25.0** 50.0	**159** 112	**5.9** 4.5	**3.1** 4.2	**16.0** 2.3	**0** 0	**0** 0	**0.7** 0.9	**8.2** 5.0	**0.8** 0.9	**8.2** 5.0
	FN	**75** 150	-	**9.4** 3.4	**28.5** 28.6	**46.1** 35.9	**22.3** 11.1	**3.1** 4.2	**1.6** 2.2	**5.9** 8.7	**23.8** 12.5	**9.0** 13.0
	FP	**25** 50	-	**9.0** 3.0	**12.5** 6.6	**41.4** 33.5	**5.5** 1.6	**1.2** 0.8	**3.1** 5.3	**5.5** 0.9	**8.6** 6.8	**6.6** 0.8
D	NN	**0**	**906** 788	**16.4** 4.7	**3.1** 4.2	**17.6** 28.0	**0** 0	**0** 0	**2.7** 1.5	**20.3** 10.4	**2.7** 1.5	**20.3** 10.4
	FN	**100** 115	-	**20.3** 7.8	**30.9** 34.2	**12.1** 12.6	**34.0** 5.0	**12.5** 10.5	**1.6** 3.1	**10.2** 7.1	**35.5** 6.5	**22.6** 17.2
	FP	**75** 96	-	**21.5** 13.1	**4.7** 7.4	**7.8** 8.7	**8.2** 4.0	**1.9** 2.3	**21.1** 16.1	**8.2** 5.6	**29.3** 15.3	**10.1** 6.8
Total	NN	**25** 58	**409** 490	**36.6** 39.4	**3.0** 3.2	**8.9** 15.1	**0** 0	**2.5** 4.8	**1.8** 1.5	**8.8** 9.4	**1.8** 1.5	**11.3** 8.0
	FN	**56** 96	-	**84.3** 122	**30.2** 27.6	**16.2** 25.1	**25.8** 8.1	**7.0** 6.7	**2.5** 3.4	**4.9** 6.5	**28.4** 8.9	**11.9** 12.1
	FP	**63** 81	-	**67.3** 80.1	**16.1** 18.3	**14.0** 22.8	**5.2** 3.0	**1.5** 1.5	**7.6** 11.3	**4.9** 4.2	**12.8** 12.6	**6.4** 5.0
Overall total		47.9 79.9	137 338	62.7 87.8	16.4 21.9	13.0 21.2	10.4 12.3	3.7 5.3	4.0 7.2	6.2 7.1	14.3 14.1	9.9 9.0

The mean density of seeds on the soil surface in November 2001 was only 48 ± 80 seeds 100 m^{-2} (Table 4). However, seeds showed a highly aggregated distribution, with most quadrats having no seeds while a few had many.

Seedling emergence was recorded in March 2002 after a period of heavy rainfall. The mean seedling numbers at the Mariamu sites (A and B) were 62 ± 42 seedlings 100 m^{-2} in the control plots and 137 ± 116 seedlings 100 m^{-2} in the felled plots. The difference between the treatments was highly significant (var. 36). However, at the Kichangani sites (C and D) relatively few seedlings (mean of 14 ± 9 per 100 m^2) were recorded in any of the plots, and there were no significant treatment effects (Table 4). The difference in seedling establishment between the two pairs of sites may be explained by fire impact. Low grass biomass at the Mariamu sites in February 2002 indicated that it had apparently been burnt at some time during October/November 2001, whereas sites C and D were unburnt. As illustrated in the next section, seeds in the soil seedbank may have been scarified by fire.

EFFECTS OF FIRE ON SEED DORMANCY AND VIABILITY

The deliberate burn of sites A and B in February 2003 was successful. At that time the grass was mainly dry and the fire swept through all plots removing almost all above-ground herbaceous vegetation. There was considerable variation in the temperatures recorded by indicator strips painted on slates held 15 cm above the soil surface. The mean temperature recorded in 12 plots burnt already in October 2002 was 168° C, in the other 12 plots only burnt in February it was 272° C, but individual values ranged from below 120° C to more than 600° C. A large part of this variation could be explained by the aboveground biomass of grass and its water content (adj. $R^2 = 54.4$ %, ANOVA: $df = 2$, $F = 27.81$, $p < 0.001$). The following regression equation for fire temperature against grass variables was obtained: *temperature (°C)* = exp (3.46 + 0.487 * ln *grass biomass (g)* – 0.839 * *grass water/biomass weight ratio*)

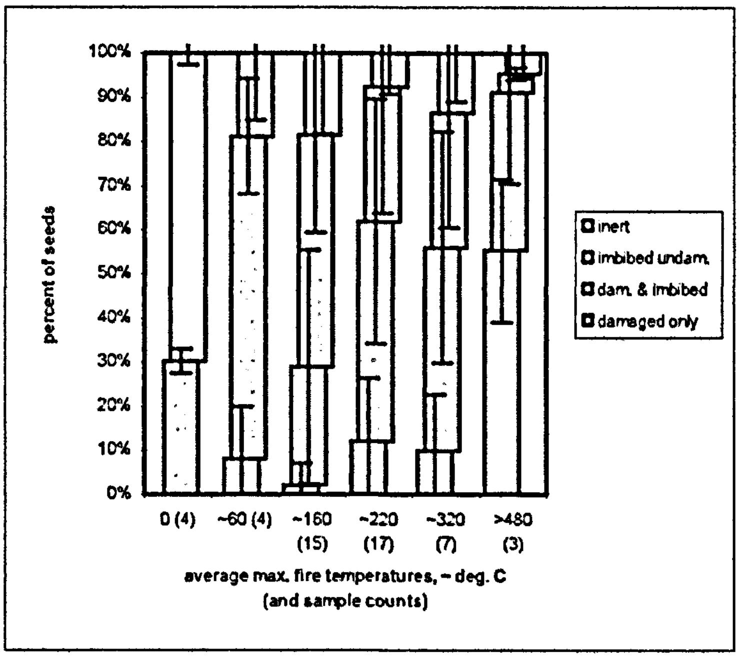

Fig. 4: Percentage seed loss (at ground level) owing to maximum fire temperature (measured 15 cm above ground). 'Damaged' seeds had been visibly affected by the fire. Many of the damaged seeds that did not imbibe water were completely charred, whereas damaged seeds that did imbibe may or may not have subsequently germinated. Overall only about 10 % of all imbibed seeds germinated after water imbibiton.

The temperature of the fire had a considerable effect upon the viability of seeds placed on the ground beneath the temperature slates. At higher temperatures (above 480° C) most seeds were visibly damaged by the fire and many were charred (Fig. 4). Over 40 % of the seeds exposed to temperatures over 200° C were killed. In contrast, exposure to lower temperatures actually increased the proportion of seeds which imbibed water compared to control seeds not affected by fire; thus 75-80 % of seeds exposed to temperatures in the approximate range 60 to 200° C imbibed water compared to 35% for controls seeds (Fig. 4). Very few of imbibed seeds (less than 1 %) subsequently germinated, however, and tetrazolium tests were mostly negative on ungerminated seeds. Germination levels were equally low for control seeds as for seeds exposed to fire.

SEEDLING PRESENCE IN THE LATE WET SEASON AND IN THE LATE DRY SEASON

In June 2002 rather few seedlings were present (mean of 16.4 ± 21.9 per 100 m^2; 8 plots with no seedlings), and there were no longer any differences between sites (var. 37; Table 4). Some plots at the Kichangani sites had more seedlings in June than in March 2002, indicating subsequent recruitment probably during the plentiful rainfalls in April 2002 (Table 4). At the Mariamu sites, on the other hand, most of the seedlings counted in March had apparently died by June 2002 (Table 4). In June 2003, the mean seedling numbers were equally low (13.0 ± 21.2 per 100 m^2; 13 plots with no seedlings), but compared to June 2002 there were significantly more seedlings at sites C and D, and significantly fewer at sites A and B, somewhat contrary to the pattern in March 2002 (Table 4; var. 36). On both occasions, there were significantly more seedlings in gaps than in control plots (vars 37 and 38; Table 4). In June 2002 initial tree bole diameter and soil organic matter content were significant co-variables (var. 38).

Most seedlings were small and we found no evidence of any long-term recruitment; no seedlings were observed on any plot in mid February 2003, and we assume that most of those recorded seven months earlier had died during the dry season. In June 2003 the mean height of seedlings was 3.0 ± 2.6 cm and the largest seedlings were 18 cm high; there were no size differences between sites (ANOVA: $F = 1.83, p = 0.142, df = 3$).

STUMP AND ROOT RESPROUTING

Overall, resprout density (including both coppicing and suckering) decreased from 14.3 ± 14.1 in February 2002 (4 control plots with no resprouts) to 9.9 ± 9.0 in June 2003 (2 FN and 2 FP plots with no resprouts). These numbers are similar to those for seedling densities in June 2002 and 2003 (Table 4). In the FN plots 71 % of all trees cut in November 2001 were coppicing from stumps in February 2002 (Table 5); mean stump coppicing density in these plots was 25.8 ± 8.1 per

100 m^2 (Table 4). Coppicing stumps were on average smaller than those stumps that were killed (Table 5). In the FP plots the poisoning of tree stumps was only partially effective, and 11 % of trees were coppicing (Table 5). Tree poisoning worked better on larger stumps, as the size difference between killed and coppicing tree stumps was even more significant on FP plots than on FN plots in February 2002 (Table 5).

Table 5. Summary of the effects of tree cutting and poisoning treatments on stump coppicing and survival. T-test comparisons and GLM analyses were performed on log-transformed data.

category			coppice lengths (cm)		stump bole diameters (cm)		stump bole comparisons	
		n	mean	st. dev.	mean	st. dev.	*t*	*p*
not poisoned	total tree stumps	392			5.73	2.47		
February 2002	stumps killed	127			6.27	2.47	2.99	0.003
	stumps coppice.	265	42.8	22.0	5.47	2.44		
June 2003	coppices killed	201			5.62	2.35	2.44	0.016
	coppices alive	72	41.2	30.8	4.87	2.50		
poisoned	total tree stumps	443			5.56	2.72		
February 2002	stumps killed	394			5.91	3.12	6.38	<0.001
	stumps coppice.	50	30.8	17.1	3.53	2.25		
June 2003	coppices killed	35			3.77	2.50		
	coppices alive	15	34.3	23.1	2.97	1.47	0.85	0.403

GLM factor results for comparisons of LN stump bole *F/p*

	site ($df = 3$)	P(F) treat. ($df = 1$)	coppices ($df = 1$)	site×P(F) ($df = 3$)	site×cop. ($df = 3$)	P(F)×cop ($df = 1$)	site×P(F)×cop. ($df = 3$)
February	0.19	38.94	55.5	2.99	0.65	16.19	0.4
2002	0.901	<0.001	<0.001	0.03	0.585	<0.001	0.754
June	1.04	20.89	5.66	1.37	1.08	0.3	0.39
2003	0.375	<0.001	0.018	0.252	0.357	0.585	0.758

Table 6. Summary of GLM results for resprout plot variables. A first analysis was performed including 'site' and 'F' (felling treatment) factors, not including the poisoned (NP) plots. A second analysis tested 'site' and 'P' (poisoning treatment) factors, only including felled (F) plots but excluding the control (NN) plots. Significant plot co-variables included into the model are also listed, whereby the number before the bracket indicates the variable listed in Table 1 or Table 2. In the bracket the sign in regression analysis, and the F and p values in the GLM are given

plot variables	GLM with site and F treatment				GLM with site and P treatment			
		F / *p*				*F* / *p*		
	R^2 adj.	site *df* = 3	F(N) treat. *df* = 1	Site ×F(N) *df* = 3	R^2 adj.	site *df* = 3	P(F) treat. *df* = 1	site ×P(F) *df* = 3
39. coppice count, 2. 2002	90.8	4.16	272.9	3.5	90.0	12.13	176.51	7.02
		0.017	<0.001	0.032		<0.001	<0.001	0.002
		co-vars: 6 (+, 9.05, 0.006)				co-vars: -		
40. coppice count, 6. 2003	68.3	4.64	5.47	2.67	49.7	3.68	25.37	2.57
		0.013	0.03	0.075		0.027	<0.001	0.08
		co-vars: 5 (+, 12.51, 0.002); 6 (+, 5.21, 0.034); 19 (+, 14.92, 0.001); 25 (-, 12.53, 0.002)				co-vars: -		
41. sucker count, 2. 2002	0.0	1.15	0.71	0.91	85.9	19.04	40.04	33.44
		0.35	0.409	0.45		<0.001	<0.001	<0.001
		co-vars: -				co-vars: 12 (-, 6.44, 0.019)		
42. sucker count, 6. 2003	65.3	10.84	0.24	1.43	77.1	31.09	1.1	2.46
		<0.001	0.627	0.261		<0.001	0.306	0.091
		co-vars: 11 (-, 5.46, 0.03); 22 (+, 8.17, 0.009)				co-vars: -		

The number of coppice shoots present in June 2003 was about a quarter of initial counts (mean shoot density of 7.0 ± 6.7 per 100 m^2; Table 4). Survival of shoots was highest amongst smaller trees with the result that average bole diameter of stumps with coppices was significantly smaller in June 2003 than in February 2002, at least in the FN plots (Table 5). Coppice length, in contrast, was not dependent on bole size (ANOVA: $F = 0.41$, $p = 0.523$, $df = 1$), and the surviving shoots in June 2003 were not longer than they had been in February 2002 (Table 5). In February 2002, 19 of the 315 shoots were inhabited by the tree ant *Crematogaster sjoestedtii*, and > 70 were visited or inhabited by predominantly ground-dwelling ants. The shoots visited by ants were significantly larger than average (mean length 55 cm). There was no sign of any ants on shoots in June 2003.

Overall, the density of resprouts decreased from 10.4 ± 3.7 in February 2002 to 3.7 ± 5.3 per 100 m^{-2} in June 2003. In February 2002 only stumps on felled plots were coppicing, but in June 2003 additionally some coppicing was present in control plots affected by hot fire (Table 4; c.f. Cochard & Edwards 2004b). As already indicated, poisoning of stumps was largely effective, as this is confirmed by the significant effect of the F and P treatments, both in February 2002 and June 2003 (vars 39 and 40; variables 39-42 refer to Table 6). Soil ammonium was an important co-variable of coppicing in February 2002 (var. 39). In June 2003 significant co-variables were soil ammonium and nitrogen, and total grass biomass and LAI (var. 40). Coppicing in February 2002 was particularly high at site D, and in all analyses there was a significant site effect and a site×treatment effect, except for the F analysis for June 2003 (vars 39 and 40; Table 4).

In contrast to coppice resprouts, overall counts of root suckers slightly increased from 4.0 ± 7.2 in February 2002 to 6.2 ± 7.1 per 100 m^{-2} in June 2003 (Table 4). There was no effect of the felling treatment on root suckering (vars 41 and 42). Suckering was, however, very high in February 2002 on three poisoned plots at site D, which largely explains the significant site, P treatment and site×P interaction effects (var. 41, Table 4). Also at site D, particularly on control plots, suckering was much increased in June 2003 compared to the other sites (Table 4). In contrast, suckering on felled plots at site A was very low compared to the other sites (Table 4). This explains the significant site effects in June 2003 (var. 42). Initial mean bole diameter was a significant co-variable in February 2002 (var. 41). In June 2003 initial woody biomass and grass living ratio were significant co-variables (var. 42).

Discussion

REGENERATION BY RESPROUTING

Most if not all of the African acacia species can resprout, though the importance of resprouting in acacia demography seems to have often gone unnoticed (Midgley & Bond 2001). Other authors have noted that resprouting acacias exhibit various characteristics including relatively low investment in the production of mainly small seeds (c.f. Vesk & Westoby 2004); in these respects *A. zanzibarica* appears to be a typical resprouter (c.f. Cochard & Edwards 2004b).

A tradeoff between sprouting and reproductive effort by seed has often been observed, whereby species with vegetative reproduction may be favoured under unpredictable and frequent disturbances such as fire or herbivory (Bond & Midgley 2003, Hoffmann 1998). Sprouting may, furthermore, be selected under conditions where recruitment events are rare and episodic (Bond & Midgley 2003). In *A. zanzibarica* such a tradeoff is evident, with the relative importance of the two modes of reproduction changing with increasing tree size (Cochard & Edwards 2004b): young trees have a strong resprouting capacity which is increasingly lost with age as the tree produces increasingly more seeds, and may become an obligate seeder at old age. The results of stump coppicing clearly seem to confirm this statement: smaller trees generally had a higher probability than large trees to survive both felling and felling-plus-poisoning, and to be still alive 20 months after felling. Similar patterns have also been observed in other acacias (Huang 1990, Huang, Zheng & Weng 1994) and savanna or miombo trees (Shackleton 2000, 2001, Luoga, Witkowski & Balkwill 2004). According to Bond & Midgley (2003) divergence in sprouting behaviour with size may be expected where disturbances kill juvenile stems but not adults, such as is the case in fire-prone savannas. They suggested that sprouting may be ubiquitous in woody plants caught in the flame zone (i.e. smaller than 3 m) of savanna fires (c.f. Cochard & Edwards 2004b), but taller adults vary in sprouting behaviour.

Despite its well developed ability to resprout, cut secondary *A. zanzibarica* woodlands did not regenerate effectively by sprouting under the prevailing post-ranching conditions, characterised by vigorous grass growth, very low grazing, and frequent hot fires. Coppicing was initially strong on felled, non-poisoned (FN) plots, but 18 months later differences in woody sprouts were, in fact, not much higher than on poisoned (FP) plots. None of the resprouts actually escaped the grass layer during the study period, and coppice shoots measured in June 2003 were on average no longer than in February 2002. Totral counts of resprouts on FN plots in February 2002, represented about ⅔ of initial tree counts, in June 2003 it was only about ¼. These data suggest that the numbers of persisting resprouts would have been insufficient to maintain tree density even if conditions for growth became more favourable, e.g. due to a renewed increase in grazing pressure. Additional root suckering or seedling establishment would therefore be necessary to fill the gaps.

While coppice numbers decreased during the study period, numbers of suckers overall remained about constant, and there were only 4 felled plots with no resprouts in June 2003. Root suckering was not influenced by tree felling, but it was particularly common at site D (most clayey soils) and sparse at site A (sandy soils), and it also appeared to be more common in younger stands (with lower biomass and/or mean bole diameters). There was apparently no effect of stump poisoning on sucker persistence and development, indicating that suckers were not affected by death and poisoning of mother trees. Since tree roots of *A. zanzibarica* can reach more than 15 m in lateral extension, it is also possible that some suckers originated from roots of trees outside the plots (Cochard & Edwards 2004a).

According to Bond & Midgley (2003) root suckering is common in some mesic savanna woodlands, but it is comparatively rare in fire-prone shrublands where resprouting from stumps and propagation by seed are more common. In *A. zanzibarica* root suckering did not appear to be promoted by fire, but root suckers seemed to be produced spontaneously as part of normal development

(Cochard & Edwards 2004b). Root suckering as a means of vegetative propagation in sprouting plants is common in many shrub species (Bond & Midgley 2003, Del Tredici 2001). While the ranch was in use much of the bush regeneration by resprouting was probably from root suckering (c.f. Klötzli 1980, Ford & Blaser 1971). Suckering in acacias and other savanna trees is often promoted under mechanical impact such as field ploughing (e.g. Strang 1974, Batty & Parsons 1992). In view of the heavy rollers with blades used during brush-cutting operations (initially weighing 1 ton and later 5 tons; That 2004) the soil must have been highly disturbed, and the superficial, lateral roots of acacias would have been heavily affected. Root suckering may also have been promoted by cattle trampling. It is equally possible that the higher levels of suckering we observed on clay soils resulted from root injury due to seasonal soil tensions in cracking clays.

SEEDBANK DENSITIES AND DYNAMICS

Propagation by seeds is advantageous for colonisation of gaps that might appear between sprouters (Bond & Midgley 2003). Cochard & Edwards (2004b) noted the very low levels of seed production in *A. zanzibarica*, with very large trees producing many more seed pods than trees of average height. Even though levels of seed production on control plots in February 2003 were higher than levels of early wet season seedling establishment in March 2002, the number of seeds found on the soil surface in November 2001 was lower than both the number produced and the number of seedlings. We presume that this partly reflected our sampling regime in November 2001: seeds in the soil were apparently distributed in a highly clumped pattern. Nonetheless, the low levels of seeds found in the soil seedbank in the present study, as well as the low germinability of seeds one year after collection, indicate that the seedbank is transient. There are still very few studies of soil seedbanks of African acacias, but the few data available suggest that the behaviour of acacias is very variable and may depend upon site history.

In a survey by Tybirk, Schmidt & Hauser (1992) no seeds were found in the soil beneath *Acacia senegal* (dehiscent pods) and *A. albida* (producing vast amounts of indehiscent pods). For *A. tortilis* (indehiscent pods) and the pseudo-gall bearing *A. seyal* (dehiscent pods), large soil seedbanks were found in Kenya, but no seeds were found at a site in Senegal. Beneath other acacias soil seed numbers of 14-2439 m^{-2} were counted (Tybirk, Schmidt & Hauser 1992, Argaw, Teketay & Olsson 1999).

Seed predation by bruchid beetles has often been reported to have a high impact on the seed budget of African acacias (Midgley & Bond 2001), but this predation appeared not to be very important in the seed budget of *A. zanzibarica.* In the seed sample collected from *A. zanzibarica* for the fire experiment, less than 5 % of seeds were preyed on by one bruchid species, and in the woodland where there were few seeds, this level is probably considerably lower. Predation by bruchids is probably low, because of efficient ant patrolling and bruchid egg predation (c.f. Willmer & Stone 1997, Traveset 1991), but there appeared also to be a high level of bruchid parasitism by several braconid and chalcid wasp species (bruchid/parasitoid ratio of about 1:1).

Savanna fires had probably the greatest impact on the soil seedbanks of *A. zanzibarica.* More than 80 % of seeds exposed to fire on the ground surface, compared to about 30% of controls, were either killed or germinated after wetting. These results are comparable to those of other studies, e.g. 65 % germination rates after fire were recorded compared to 10 % in controls for *Acacia sieberiana* (Sabitii & Wein 1987), up to 95% of seeds germinated or died after fire in the seedbanks of the invasive exotic *A. saligna* (Holmes 1988), and over 70% in the seedbanks of *A. longifolia* (Pieterse & Cairns 1986). Many of the seeds, particularly those exposed to higher temperatures, were killed by the fire. This is consistent with the results of Danthu *et al.* (2003), who tested germination and scarification of seeds of ten acacia species exposed to three fire intensities at various heights above ground and at two soil depths. Most seeds of all species exposed to medium and high fire temperatures on the ground surface were killed, while seeds exposed to low temperatures had lower viability levels compared to controls, but higher germination rates due to fire scarification.

SEEDLING ESTABLISHMENT AND PERSISTENCE

High seedling establishment at sites A and B in March 2002 seems to indicate that seed germination was, in fact, aided by scarification during a fire in November 2001 at those sites. Seedling establishment in March 2002 was much lower at sites C and D which were only burnt by later fires in October 2002, and February and May 2003. Seedling numbers in June 2002 were, nevertheless, similar for all sites, but in June 2003 seedling numbers were high at sites C and D, and low at sites A and B. The overall pattern suggests the following scenario: most of the seed in the seedbanks at the burnt sites A and B germinated after the first prolific rains in March 2002. Since there was little rain until late April, many of the established seedlings died, however, especially on the more sandy soils at sites A and B. In late April, when there was an exceptional rain event, some additional seeds at sites C and D germinated and managed to establish into seedlings, while the seedbank at site A and B was already largely exhausted. Thus, in June 2002 seedling counts between sites were about equal. Before June 2003 many seedlings could, however, only establish at sites C and D, since seeds in the soil were only scarified by fires after June 2002. Nevertheless, there were still some seedlings establishing on felled plots at sites A and B, even though very few seeds were apparently dispersed onto felled plots. This may indicate that ground-dwelling ants are important in secondary seed dispersal. Auld (1996), for example, observed that ants dispersed seeds to distances up to 10 m in Australian acacias. We observed that ants were abundant on the soil surface in the acacia woodlands at Mkwaja Ranch.

An additional explanation for high seedling establishment at sites A and B in March 2002 may be competition for water. In March 2002 grass biomass was still very low at the burnt sites (probably less than ⅛ of the biomass in June

2002), and therefore soil water content after rain was probably decreasing at a lower rate than at sites C and D (possibly ~ ¼ of June biomass). Wilson & Witkovski (1998), for example, suggested that constant moisture levels were needed for about 16 days for seeds of the three acacia species tested to germinate. The effects of competition are even more clearly demonstrated in our study, with higher seedling establishment and persistence on felled plots compared to controls.

GRASS BIOMASS CHANGES IN GAPS COMPARED TO WOODLAND

Grass growth on felled plots was prolific during the copious wet season in March-May 2002: mean biomass measurements in June 2002 (612 gm^{-2}) were even higher than the maximum measured (567 gm^{-2}) on the 81 'random' plots at Mariamu in the parallel study by Cochard & Edwards (2004a). In contrast, mean grass biomass on control plots (290 gm^{-2}) was similar to the mean of the 'random' plots (302 gm^{-2}). In June 2003, after below-average rainfall, the felled plots still had a relatively higher biomass (239 gm^{-2}) than the 'random' plots (191 gm^{-2}; Cochard & Edwards 2004a) but the difference was less marked. In contrast to other studies (e.g. Ludwig *et al.* 2004, Vitousek & Walker 1987), we detected no increase in soil nutrient concentrations or rate of nitrification on felled plots compared to controls, though there was an increase in soil water availability. Nevertheless, soil nutrients were generally significantly elevated in dense stands of woodland compared to more sparsely wooded vegetation (Cochard & Edwards 2004a). Therefore, after release from tree competition, high nutrient availability probably further stimulated grass growth compared to background savanna, particularly after the extreme rains in late April 2002.

There was no notable difference in grass wilting between cut and control plots, even though, as was demonstrated, water availability in the upper soil levels decreased at faster rates on control plots. Live grass ratios on plots were probably determined by previous fires and the plant species composition on individual plots, which also differed between sites and according to edaphic variables (Cochard & Edwards 2004c). Mean grass SLA, was highest at site A. As in the study by Cochard & Edwards (2004a, c.f. also 2004c) it seemed to be mainly influenced by soil texture, but felling treatment had no significant effect. As a consequence, total grass LAI in June 2003 was not only different between felling treatments, but also between the Mariamu and Kichangani sites.

Grass biomass in early June 2002 was seven times higher on the cut test plot compared to the control, while measured values of stomatal conductance (g) were on average only about 1.4 times higher on the cut plot. Measurements were made only during a 3-day period in the late wet season, and it is likely that rates of transpiration and photosynthetic efficiency were higher during the early growing season when water was abundant and intra-specific competition between grasses for water as well as for light was low. Overall, measurements of g for the grasses were comparable to other studies (g_{max} of ~ 80 mmol s^{-1} m^{-2}; Körner 1994; for daily curves see Kinyamario, Trlica & Njoka 1995). Measurements of g_{max} of 321, resp. 469 mmol s^{-1} m^{-2} for *A. zanzibarica* were generally above g_{max} measured for trees in most ecosystems (Körner 1994), and above measurements on acacias in very dry savannas (Ullmann *et al.* 1985, Ullmann 1985). Midgley *et al.* (2004), however, reported comparable g_{max} of 340 mmol s^{-1} m^{-2} for *A. mellifera* and 283 mmol s^{-1} m^{-2} for *A. erioloba*, and Pathre *et al.* (1998) measured a g_{max} of up to ~ 520 mmol s^{-1} m^{-2} in *A. auriculiformis*. All studies including ours showed a similar time-course of transpiration, with a peak at around 10-11 h in the morning and a slight depression in the early afternoon.

Overall, it is clear that *A. zanzibarica* trees strongly restricted growth of the grass layer, with this effect being due mainly to a high rate of water use by the trees rather than to shading (c.f. Cochard & Edwards 2004a). The effective grass LAI was significantly lower in woodland plots than on cut plots after both rainy seasons. Interestingly, however, there was a difference between treatments in the late dry season for all grass parameters, except total grass LAI (which was only slightly significant). To some degree, the random effect of the 2002 October fire may have blurred treatment and edaphic effects on the grass layer, but this is not sufficient as an explanation. It seems that, on parts which had remained unburnt, continued grass growth on cut plots was eventually limited at a certain high level of biomass after the wet season 2002, probably due to intra-specific competition for light. In contrast, on woodland plots the less crowded grass layer continued to grow and make efficient use of intermittent rainfalls. Particularly at site B, which was mainly dominated by *Heteropogon contortus*, levels of grass fuel eventually reached similar levels on control plots as in cut plots until January 2003. It then appears that the grass layer increasingly had an effect on the tree layer (c.f. Cochard & Edwards 2004a). In this regard the effect of grass removal by a fire in late January 2003 at site C is striking: levels of foliage biomass were about threefold the levels of the other sites by late February before the experimental fire. This post-fire foliage flush may, however, not just be due to release from grass competition but could be an adaptive response of the trees to burning, since loss of tree foliage would have a deleterious effect on symbiotic ant populations (c.f. Cochard and Edwards 2004a, 2004b).

WOODY REGENERATION POTENTIAL IN GAPS AND WOODLAND

Regeneration by sprouting has the advantage that a deep root system is already developed and contains carbon reserves which can be used for growth. In environments where successful seedling recruitment events are rare and episodic, populations of sprouters therefore have the capacity to "store" successful recruitment events (Bond & Midgley 2003). In contrast, obligate seeders are subjected to all uncertainties inherent of regeneration from seeds, such as success of pollination, seed maturation, dispersal, and seedling establishment and survival. Efficient seeders may, however, be more successful in colonising gaps (Bond & Midgley 2003). Under ranching, *A. zanzibarica* clearly seemed to be successful in a dual strategy of colonisation by seed and persistence by resprouting, and this encroachment success was particularly high within a certain soil texture range (Cochard & Edwards 2004a, 2004b).

As has been shown, root suckering was not influenced by any of the felling or poisoning treatments, and over ¼ of coppices persisted in the grass layer until June 2003. It appears, however, that during the study period resprouts were unable to grow out of the grass layer, especially during and after the extremely prolific grass growth in the 2002 wet season. Resprouts on the cut test plot showed elevated levels of stomatal conductance compared to the trees on the control plot. As mentioned, resprouts may have also had access to water resources deeper in the soil, but water levels on cut plots were in any case elevated. The main factor limiting their ability to compete with grasses was probably light, since by June 2002 most resprouts were completely immersed within the grass canopy.

Another problem of resprouting shoots may have been insect herbivory (pers. obs.). *Acacia drepanolobium*, a swollen thorn acacia similar to *A. zanzibarica*, is only weakly defended by symbiotic ants at the sapling stage (Palmer 2003, Stapley 1999), and chemical defences are comparatively low compared to acacias lacking ant symbionts (Ward & Young 2002). Shaw, Keesing & Ostfeld (2002) showed that seedlings of *A. drepanolobium* experienced high levels of insect and rodent herbivory at the seedling stage. In the acacia woodlands at Mkwaja Ranch, ground-dwelling ants may have played a significant role in the protection of acacia saplings from insects and other herbivores. However, although significant numbers of ants were observed on saplings in February 2002, there were very few in June 2003, perhaps because the leaves of the by then heavily shaded plants were unable to produce sufficient nectar.

The balance for successful seedling recruitment is typically delicate under natural conditions (Midgley & Bond 2001). Seedlings initially rely on carbon reserves stored within the seed. With an average weight of 23.2 mg seeds of *A. zanzibarica* are considerably smaller than those of most other acacias or invasive leguminous trees: e.g. 89-96 mg for various *Faidherbia* and *Acacia* spp.

(Bukhari 2004), 65-190 mg for 8 species of African *Acacia* (Teketay 1996), 73.1-90.9 mg for *Parkinsonia aculeata* (Cochard & Jackes 2004). Provided seed germination and seedling establishment are successful after a period of rainfall, most seedlings face high competition with grasses not only for light, but primarily for water in the grass rooting zone. There is a trend for tree seedlings in savannas to invest more in root growth under drier conditions in order to reach water stores in deeper soil layers (Otieno, Kinyamario & Omenda 2001, Barbosa & Prado 1991). Nevertheless, mortality at the seedling stage is probably one of the main bottlenecks in acacia demography, and successful recruitment is often highly episodic (e.g. O'Connor 1995, Kennenni & van der Maarel 1990, Mwalyosi 1988, Radford *et al.* 2002). Several studies have found higher seedling survival in dense grass, or in the shade of trees (e.g. O'Connor 1995, Jurena & van Auken 1998, Smith & Shackleton 1988), while others have reported high grass competition and higher seedling emergence and survival when grass is removed by cutting or grazing (e.g. Fetene 2001, Skarpe 1990, Chirara, Frost & Gwarazimba 1998). These studies illustrate that grass-seedling interactions are frequently complex and, as stressed by Davis, Wrage & Reich (1998), competition intensity may best be described by net resource supply rather than simply the biomass of plant neighbours. In our study higher seedling emergence and survival can probably be best explained by higher soil water levels on cut plots than on controls. On cut plots water transpiration rates were generally lower than on controls, particularly in March 2002, when grass biomass was still low. Direct evaporation from the soil was probably also lower on cut plots, since the grass cover was much denser than on controls, and *A. zanzibarica* trees provided little shade (Cochard & Edwards 2004a). As the dry season progressed, the differences in soil water between treatments probably declined, while seedlings could not accumulate sufficient storage reserves in the shade of grasses. Hence, recruitment did not occur as all seedlings were killed by the end of the dry season as a result of fire or competition with re-growing grasses.

Grass fuel on cut plots was higher, but until the late dry season in February 2003 fuel loads were also high on control plots, particularly at site B where most tree mortality occurred following a hot fire. Without grazing, fire intensities were sufficient to prevent regeneration and reduce survival of sprouts and seedlings. Whether the remaining resprouts and new seedlings stand a chance to grow into adult trees depends ultimately on fire frequencies and grazing intensity. There was rather little grazing in June 2003, but it is striking how wild herbivores preferred cut gaps over other plots. We suppose that this was due to the higher biomass and nutritional quality of grasses on cut plots (c.f. Cochard & Edwards 2004c); anti-predator strategy may have also been a factor (Young, Patridge & Macrae 1995), though visibility in woodland gaps was not greatly increased. Grazing patches were obviously greater in gaps than in woodland, and scale of patchiness is often important for grazing selectivity of larger ungulates (e.g. Wallis de Vries, Laca & Demment 1999). Grazing in June 2003 was probably mainly by warthog, *Phacochoerus africanus*, but also increasing numbers of other larger animals, such as waterbuck, *Kobus ellipsiprymnus*, and even wildebeest, *Connochaetes taurinus*, were observed in the area. Especially wildebeest and hartebeest, *Alcephalus buselaphus*, occur in large herds south in the area of former Saadani Game Reserve (Treydte 2004, Tobler, Cochard & Edwards 2003). Whether herds will immigrate north to the former ranching area, now also under protection within Saadani National Park, remains to be seen. It is clear that herbivory and fire regime could again alter the tree grass-balance in the future. If conditions remain as they were during this study, regeneration seems unlikely, and whether accelerated by elephant or not, woodlands will ultimately disappear (c.f. Cochard & Edwards 2004b). As has been proposed by several modelling studies (Jeltsch *et al.* 1998, Higgins, Bond & Trollope 2000, van Langevelde *et al.* 2003), regeneration may only be possible in safe sites (e.g. near termite mounds), and/or during periods of high environmental variability.

CONCLUSIONS

Our results have shown that in the absence of large numbers of grazers (or disturbance due to brushcutters), the regeneration potential of *A. zanzibarica* is low. This leads us to conclude that, under the prevailing ecological conditions, the extensive *A. zanzibarica* woodlands on the former Mkwaja ranch will gradually return to typical fire-maintained savanna. Two lessons concerning savanna management, whether for cattle grazing or for improving wildlife viewing for tourism (since Mkwaja Ranch is now part of a National Park), may be learned from these results: firstly, savanna regeneration is possible in secondary woodlands relieved from ranching impact and secondly, regeneration can be accelerated by wood cutting which does not disturb the soil and affect tree roots. Nevertheless, the dynamic nature of the system needs to be stressed, and savanna regeneration may be faster or slower or even be halted under varying rainfall conditions, fire frequencies and intensities, and regimes of herbivory.

Savanna regeneration will probably be retarded or even halted by controlled early fires, as formerly practiced in Saadani Game Reserve for wildlife management. Early dry season fires are much less effective than late season fires which are nourished by completely dry grass matter. Furthermore, green flushes of grass after early dry season fires often attract herds of animals which may prevent renewed grass biomass accumulation. Planned fires aimed at opening up woodlands in the new National Park may be best laid in the late dry season, when grass biomass is highest and driest. We advise, however, to leave fire impacts up to chance. The rate of fires emanating from closeby villages probably exceeds historic fire frequencies, and those fires are probably sufficient to have the desired impact.

With regard to former ranching practices, we conclude that the problem of bush encroachment does not inevitably make ranching impossible. If ranch management is not dictated by short-term productivity goals (That 2004), it should be possible to develop a long-term rotation system that is both profitable and sustainable. If cattle numbers were reduced to half the maximum present on

Mkwaja Ranch in the 1970's, one part of the ranching area could have been left for cattle grazing, while the other part would have been left for pasture regeneration after bush encroachment. Such a rotational system may compare to old traditional large-scale nomadic systems in drier savannas which also frequently account for bush encroachment, such as, for example, the Borana herding system in Northern Kenya (Coppock 1993; see also Reid & Ellis 1995). In this humid coastal ecosystem, we could even imagine a management system that takes account of bush encroachment in a profitable way. Large cities in Tanzania, such as Dar es Salaam or Zanzibar Town still largely depend on wood for energy. Until now, the main resource exploited to that end is Miombo woodland, which is increasingly replaced by cultivated land and secondary bushland. It is only a question of time until it may be profitable to exploit lower grade wood from acacias for charcoal production to supply nearby growing cities. The related *A. drepanolobium*, for example, is already used in Kenya for charcoal production (Okello, O'Connor & Young 2001).

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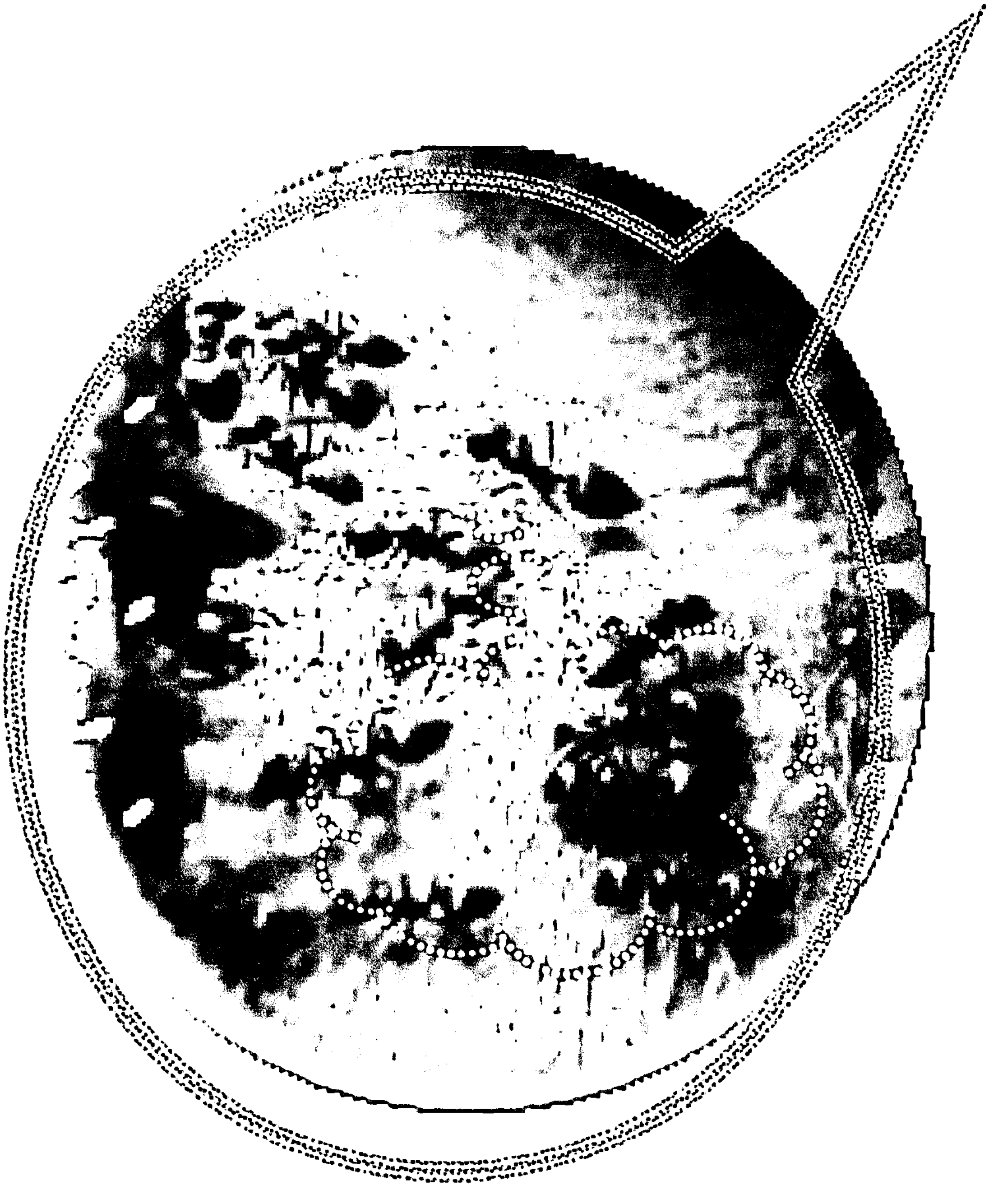
The limits of the soul you could not discover,
though traversing every path.

Heraclitus



Epilogue: some myrmecophilic thoughts

Over thousands of years generations of philosophers have marvelled about the meaning of time and space... The work presented in this thesis presents just a dust particle of advancement in the discipline of present-day science. It presents an exploration into spatial patterns of vegetation cover in one area of this planet at some narrowly-scattered points in time. What can we learn from it? We may learn some things about the ecosystem with which the work is concerned, and about how the environment has responded to the actions of human beings. We may learn a few things about why humans were doing what they were doing; more can be read about this aspect in the work by That (2004). But maybe the most important thing is to realise just how much our knowledge is still constrained and limited and that many of our actions are still guided by beliefs and projections.

Like most ecological field studies, this study is limited in its time aspect. I tried to concentrate more on spatial patterns, which can also provide some indirect informations about processes and changes over time. There have only been very few studies about the ecology of *Acacia zanzibarica,* all being of univariate nature. I tried, therefore, to cover a large array of variables which, at the beginning of these studies, I assumed to have some importance. Observations and final results typically differ from the initial 'educated guesses', and now, in retrospect, I think I should also have put more attention to some details which did not appear to be of great importance in the beginning.

One of those "details" is the fact that *Acacia zanzibarica* is a myrmecophyte tree, i.e. one of the species which is mainly defended against herbivores by symbiotic ants living on the tree. There are several important ecological differences between these trees and acacia trees that lack symbiotic ants, as listed by Ross (1981). Myrmecophytism may be regarded as functionally analogous to the possession of chemical defences. The main ecological distinction of myrmecophytes compared to other acacias may, therefore, lie in ant-plant interaction dynamics: variation in symbiotic ant populations may have an important influence on tree phenology and survival of myrmecophytes; *vice versa,* all myrmecophytes need to produce leaves throughout the year so as to maintain continuous protection from ant colonies by supplying them with food from foliar nectaries (or indirectly by making it possible for them to tend scale insects) (Ross 1981, Hocking 1970; c.f. Cochard 2004a, 2004b). Here I would like to draw attention to some thoughts and observations in this field and ask some possibly important questions which may be investigated in future.

How important are insects for acacia demography? Even in the absence of browsing by large mammalian herbivores, acacia trees may be vulnerable to attack by insect herbivores. Hocking (1970) made some valuable observations of insects on *A. drepanolobium* near Nairobi and Arusha. He observed a total 169 species of insects of eleven orders, including many insects which showed morphological and behavioural ant mimicry or specially sclerotised carapaces. Unfortunately we made very few observations of insects during this study, but we also observed some sap-sucking hemipterans and one orthopteran species displaying remarkable ant mimicry. To my knowledge the role and importance of insect herbivory on acacias in East Africa has not yet been assessed quantitatively, although Stanton & Young (1999) noted increased insect herbivory on *A. drepanolobium* abandoned by ants, and Shaw, Keesing & Ostfeld (2002) reported high mortality of seedlings due to insects. The fact, that Midgley & Bond (2001) only mention the role of bruchid beetles in their review of acacia demography in African savannas rather reflects the current state of research. The lack of emphasis on insect herbivory in savanna and acacia research does, however, hardly match its likely importance (c.f. also Lewinsohn & Price 1995).

What is the importance of tended scale insects for ant population dynamics and plant health? Hocking (1970) often found homopterans on young leaf shoots being tended by *Crematogaster mimosae*, and he estimated that 65 % of sugar production for ant populations was contributed by aphids and scales, while only 35 % came from extrafloral nectaries. Young, Stubblefield & Isbell (1997) observed tended scale insects on 28 % of *A. drepanolobium* trees occupied by *C. sjöstedti* and on 45 % of trees occupied by *C. mimosae.* At Mkomazi Krüger & McGavin (1998) also observed a positive relationship between ant biomass and phytophagous sap-suckers on six acacia species without pseudo-galls.

What are the ant species on *Acacia zanzibarica*? Unfortunately, it has not yet been possible to determine with certainty the ant species on *Acacia zanzibarica* at Mkwaja Ranch. According to our observations there were two species which, by comparison with the literature, we believe to be *Crematogaster sjöstedti* Mayr and *Crematogaster nigriceps* Emery. While I am still fairly sure that our red-abdomen cocktail ants were indeed *C. nigriceps*, I am no longer so confident whether the most common black cocktail ants were *C. sjoestedti* since there exists one difference: both, Linsey Stapley and Todd Palmer (personal communication), did not observe *C. sjoestedti* to build carton nests on trees at their study sites (Mkomazi, northern Tanzania and Laikipia, central Kenya), whereas such nests were frequent at our study site. Apart from this, the descriptions, however, seem to match those of this species, in particular that it nests inside of hollow stems. Furthermore, at Mkomazi *C. nigriceps* was commonly encountered on *Acacia drepanolobium* and *C. sjoestedti* on *A. zanzibarica* (Stapley 1999).

In upland Kenya a clear linear dominance hierarchy was demonstrated between colonies of the four obligate acacia ant species on *A. drepanolobium*, with *C. sjoestedti* being the most abundant species (Palmer *et al.* 2000). Nevertheless, *C. sjoestedti* was only the third most common species (about 20 % of trees; Young, Stubblefield & Isbell 1997). The second most common species was *C. nigriceps* which only ranked third in colony dominance (Young, Stubblefield & Isbell 1997, Palmer *et al.* 2000). Dominance ranking for the four species was reversed for fights between foundress queens colonising pseudo-galls on new tree saplings and resprouts, with foundress queens of *C. sjoestedti* rarely attempting to start new colonies (Stanton, Palmer & Young 2002). There was therefore a clear niche gradient in space (position of trees with respect to other trees and to termite mounds) and time (age of trees) of ant species colonizing trees (Palmer 2003). If our species identifications are indeed true, the complete dominance of *C. sjoestedti* at Mkwaja could therefore be explained in two ways: 1. biogeographical distribution with a dominance in coastal savannas, and 2. age and history of the *A. zanzibarica* stands at Mariamu.

Is the black cocktail ant a predominantly coastal species? *C. sjoestedti* is probably the dominant species of *A. zanzibarica* and may therefore have its centre of origin in humid coastal areas of Tanzania, with decreasing dominance at higher elevations. There are two characteristic observations which may support this assumption. Firstly, compared to other *Crematogaster* spp., *C. sjoestedti* is more competitive in more productive environments; secondly, *C. sjoestedti* may reveal some adaptations to the fact that productive humid coastal savannas are more fire dominated than the upland savanna, with the latter being more influenced by mammalian herbivory (c.f. below).

Do age and history of the *A. zanzibarica* stands at Mariamu explain dominance of *C. sjoestedti*? The overwhelming dominance of *C. sjoestedti* at Mariamu in 2002 may also reflect stand structure and regeneration history of *A. zanzibarica*, since *C. nigriceps* was much more common at Mkomazi (Stapley, personal communication). While it appears likely that *C. nigriceps* was the more successful coloniser during the first years of stand regeneration after brush-cutting (along the lines presented by Stanton, Palmer & Young (2002)), *C. sjoestedti* could probably easily take over young trees under the favourable conditions that also promoted tree growth under ranching. With increasing tree sizes, colonies of *C. sjoestedti* probably expanded exponentially, also expanding in foraging territory, and ultimately completely displacing *C. nigriceps* to a very few marginal trees away from the woodland core. Within woodlands, we sporadically observed trees with high spine densities and high branching. Those trees possibly had been pruned by their former *C. nigriceps* inhabitants in order to avoid branch contact with neighbouring trees occupied by *C. sjoestedti* as was described by Stanton *et al.* (1999) for *A. drepanolobium*. In 2002 all those trees were, however, occupied by *C. sjoestedti*.

Does the dominance of *C. sjoestedti* have an influence on tree demography? The almost complete displacement of *C. nigriceps* inside woodlands may have some important ecological consequences for woodland maintenance and regeneration. *C. sjoestedti* is more competitive in more productive environments, but it normally only occupies trees of high productivity, such as near termite mounds in central Kenya (Palmer 2003). Colonies often expand to neighbouring trees during productive wet seasons, but during times of environmental stress marginal trees are often abandoned again and may be recolonised by other ants (Palmer 2003). If other ant species are, however, completely lacking in the vicinity of abandoned trees, such trees may then remain unprotected against herbivory, and ultimately die due to cascading stress effects, particularly after fire (c.f. Cochard & Edwards 2004b).

Is tree mortality lower in dense stands because of ant population dynamics? *C. sjoestedti* is a polygynous species i.e. a large ant colony can have several queens which are found in the trunks of one large tree. Large colonies are often polydomous, i.e. expand to other satellite trees. Satellite trees which had been colonised from other, larger trees with resident queens, may, therefore, be more easily recolonised after abandonment, e.g. after fire, in dense tree stands.

What is the importance of wood boring beetles for ant population dynamics and plant health? *C. sjöstedti* is the only species producing colonies that regularly extend inside tree branches and stems within tunnels dug by long-horned (cerambycid) wood beetles (Stanton & Young 1999, Stapley 1999, Palmer, personal communication). Those beetles are apparently only tolerated by *C. sjoestedti*, but not by other *Crematogaster* ants, and it has been suggested that *C. sjoestedti* may, for that reason, be of less benefit to acacias than, for example, *C. mimosae* (Stanton & Young 1999). According to Palmer (personal communication), both cerambycid beetles as well as *C. sjöstedti* ants may tunnel within the stems. It is also my impression from observations of tunnels that ants may actually enlarge the tunnels. Nevertheless, many, mostly younger trees seem not to be penetrated by tunnelling. It is, therefore, possible that cerambycid beetles are crucial for providing access to the wood by digging the first entrance holes through the hard bark. If that is indeed the case, how do these beetles get to the stems without being attacked? What protects them against ants: sugar rewards, chemical repulsion, or simply chance, such as absence of ants, for example, after fires? It appeared to me that trees with dead branches had a higher chance to be penetrated by tunnels, but again I made no systematic survey (as yet).

Is there an explanation for wood boring and polygyny from fire ecology in humid savannas? Stanton & Young (1999) suggested that *C. sjoestedti* may increase its breeding space by using tunnels in branches and stems. However, the presence of both cerambycid beetles and wood-boring behaviour of ants could have an evolutionary explanation due to the fact that productive humid coastal savannas are more fire dominated than the upland savannas which are more influenced by mammalian herbivory. During strong fires, ant queens and brood may not be sufficiently protected in swollen thorns in the tree canopy, whereas they are safe in tree trunks or even underground. Also polygyny of *C. sjoestedti* colonies may be an adaptation to fire impact and also higher tree sizes in humid savannas: monogynous colonies would be too slow to regenerate and defend resident trees and recolonise satellite trees after catastrophic decline. On large trees, *C. sjoestedti* may therefore be well protected from fire, with the consequence that tree foliage can regenerate under protection and trees thus remain healthy. However, under environmental stress smaller satellite trees may be abandoned by ant colonies, which are established on neighbouring trees, and those satellite trees may face increased pressure from herbivores and wood borers (c.f. Palmer 2003). The ants on *A. zanzibarica* may therefore use wood tunnels as a safe fortress where they can retreat and from where they can recolonise the tree outposts that had to be abandoned. In contrast to African *Crematogaster*, *Pseudomyrmex* colonies on acacias in Central America follow a fairly different strategy of fire evasion: these ants often maintain an area of bare ground underneath resident trees, presumably to protect them from fire (Janzen 1967). Trees, especially smaller ones, are nevertheless often defoliated and get ultimately killed by strong fires. During Janzen's (1967) survey many trees affected by fire, ultimately died because of insect herbivory or competition with other plants.

Is there a long-term net benefit of wood boring to *A. zanzibarica*? Stanton & Young (1999) suggested that increased wood boring by beetles may be detrimental for trees of *A. drepanolobium*; they considered that *C. sjoestedti* ants may manifest a kind of selfishness, particularly since in central Kenya they apparently did not defend trees as aggressively against herbivores (including wood borers) as other ant species (Palmer, personal communication). This does not quite match my own experience, namely that the ants never miss a chance to attack and bite! Are the ants on the coast more aggressive defenders than those in the highlands, possibly because of different nutrient provision? Or what kind of defenders must be the other ant species there up in the highlands...? Wood boring could theoretically also be beneficial to the plant, provided it is a factor in saving the ant colonies, and provided that *C. sjoestedti* is an efficient defender against...., against what? Could it be that aggressiveness has been defined by observations of ant's reaction to mammalian herbivores only? What about the cleaning of insect herbivores...?

In these concluding remarks I have ventured into the realms of speculation. My purpose has been to put down these thoughts as an inspiration for further investigations for anybody interested in ants. I would not be surprised, if many of my wild suggestions were proven wrong. I would, however, be even less surprised if much would be found to have a true ecological bearing. It's fascinating...!

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Appendices

Appendix 1. Description of plot variables (physical and grass variables) used in regression calculations (Paper 2 and 3). Each variable counted 97 data points. All variables were used as predictors; variables in bold were, furthermore, analysed as dependent variable. Variables with one star (*) are calculated or modelled based on regression calculations (Appendix, p. 114), the ones with two stars (**) are furthermore based on some informed assumptions. For all other variables simple field data was available.

var. name	plot variable description	mean	stdev.	median	max.	min.
1.	**physical and grass variables**					
sand	soil sand content (% soil mass)	78.1	9.084	78.15	95.35	58.2
clay	soil clay content (% soil mass)	15.84	7.664	15.3	34.2	0.1
som	soil organic matter (% soil mass)	0.184	0.085	0.177	0.478	0.047
H2Oc	soil water content (% soil mass) at 10 cm depth, after rain ≈ soil water field capacity	25.43	5.752	25.76	38.86	14.86
P	soil Phosphorus content (% soil mass)	0.021	0.002	0.021	0.024	0.016
N	soil Nitrogen content (% soil mass)	0.022	0.006	0.021	0.066	0.016
fire1	plot hit by fire (1 = yes; 0 = no), October 2002	0.536	-	1	1	0
fire2	plot hit by fire (1 = yes; 0 = no), Feb. 2003	0.557	-	1	1	0
*fireint1***	estimated fire intensity (maximum temperature (°C) at 15 cm above ground), October 2002	192.5	184.1	283.3	488.0	0
*fireint2***	estimated fire intensity (°C), February 2003	250.2	245.2	228.1	631.9	0
grmass1	grass biomass (g/m²), June 2002	299.2	89.7	286.5	567.0	121.4
grmass2**	estimated grass biomass, February 2003	361.5	166.9	333.0	742.2	138.2
grmass3	grass biomass, June 2003	190.8	85.81	176.0	522.0	52.5
*grlife2***	estimated living grass biomass (g/m²), February 2003	39.41	6.914	39.04	57.6	25.08
grlife3*	living grass biomass, June 2003	83.4	46.97	73.33	306.0	0.908
grSLA*	mean grass specific leaf area index (leaf transpiration area (cm²)/leaf weight (g)), June 2003	60.14	8.159	60.76	77.32	38.33
*grH2O2***	water/grass ratio ((wet grass (g) – dry grass (g))/dry grass (g)), February 2003	0.839	0.513	0.69	2.118	0.006
grH2O3	water/grass ratio ((wet grass (g) – dry grass (g))/dry grass (g)), June 2003	0.839	0.513	0.69	2.118	0.006
grLAI1*	total grass leaf area index, LAI (leaf transpiration area (m²)/ground area (m²)), June 2002	1.793	0.6	1.712	4.086	0.644
grLAI2**	estimated total grass LAI, February 2003	1.362	0.613	1.272	3.033	0.383
grLAI3*	total grass LAI, June 2003	1.154	0.578	1.058	3.862	0.318
*grLeff2***	estimated live (effective) grass LAI (transpiration area (m²) of living leaves/ground area (m²)), February 2003	0.238	0.058	0.237	0.385	0.133
grLeff3*	live grass LAI, June 2003	0.497	0.287	0.467	1.92	0.006

Appendix 2. Description of plot variables (tree variables) used in regression calculations (Paper 2 and 3). Each variable counted 97 data points. All variables were used as predictors; variables in bold were, furthermore, analysed as dependent variable. Variables with one star (*) are calculated or modelled based on regression calculations (Appendix, p. 114), the ones with two stars (**) are furthermore based on some informed assumptions. For all other variables simple field data was available.

var. name	plot variable description	mean	stdev.	median	max.	min.
2.	**tree variables**					
trden1	tree density (tree count/100 m^2), June 2002	16.08	12.43	11.94	49.74	1.99
trden2	tree density, June 2003	14.25	12.09	9.95	47.75	0
trmass1*	tree life woody biomass (g/m^2), June 2002	1851	1056	1776	5018	121
trmass2*	tree life woody biomass, June 2003	1738	1041	1685	4819	2.86
avdiam	average tree diameter (mm) on plots, June 2002	75.53	19.07	73.0	145.3	44.02
maxdiam	maximum tree diameter (mm), June 2002	111.4	29.88	105.7	220.0	46.4
avtrhgt	average tree height (m), June 2002	9.91	2.534	9.611	17.6	3.71
trsurv	relative tree survival on plots June 2002 - June 2003 ((*trden1* – *trden2*)/*trden1*)	0.876	0.221	1	1	0
wdtsurv*	living wood June 2003/living wood June 2002	0.917	0.2	1	1	0
trkill	absolute tree death on plots June 2002 – June 2003	1.47	2.95	0	13.9	0
trkillF	absolute tree death on plots burnt by hot fire only June 2002 – June 2003	2.64	4.25	0	13.9	0
wdlifert	living wood/total wood ratio, June 2002	0.853	0.14	0.9	1	0.2
folmass1*	tree foliage biomass (g/m^2), June 2002	47.61	30.96	45.05	148.7	0.537
folmass2*	tree foliage biomass, February 2003	10.37	6.51	9.63	36.89	0.498
folmass3*	tree foliage biomass, June 2003	32.99	24.01	28.44	111.4	0
poddrop	pod count on trees per m^2 ground area, February 2003	4.135	5.172	2.268	31.97	0
seedl1	seedling count per m^2, June 2002	0.037	0.075	0.02	0.617	0
seedl2	seedling count per m^2, June 2003	0.04	0.096	0	0.796	0
resp	resprout count per m^2, June 2003	0.052	0.063	0.02	0.259	0
coppice	coppice count per m^2, June 2003	1.62	4.09	0	29.8	0
sucker	root sucker count per m^2, June 2003	3.84	5.8	0.02	25.9	0

Appendix 3. Description of tree (on plots) and branch (random samples) variables used in regression calculations (Paper 2 and 3). Each tree variable counted 781, branch variables 119 data points. The numbers of equations (Appendices 4 and 6) are indicated where the variable was used as predictor and either entered in the final equation or deleted during analysis. Variables with one star (*) are calculated or modelled based on regression calculations (Appendix, p. 62), the ones with two stars (**) are furthermore based on some informed assumptions. For all other variables simple field data was available.

var. Name	**tree variable description**	**mean**	**stdev.**	**median**	**max.**	**min.**
compet1	tree competition index, June 2002 (Σ (*trdiam* of neighbouring trees / distances (m) to respective trees))	0.357	0.173	0.358	1.012	0.002
compet2	tree competition index, June 2003	0.336	0.179	0.331	0.964	0
trdiam	tree diameter (mm), June 2002	64.54	28.9	59.6	220	13
trhgt	tree height (m), June 2002	9.024	4.561	8.25	23.1	0.825
width	approximate crown width / tree height ratio, June 2002	0.299	0.216	0.21	1	0.058
brcat	branching category (from low to high: 1-4), June 2002	2.397	0.783	2.5	5	1
trlifert	approximate ratio of life wood / total (incl. dead) wood, June 2002	0.881	0.175	0.95	1	0.2
survive	tree alive in June 2003 (1 = yes / 0 = no)	0.89	0.313	1	1	0
folcat1	foliage category (from low to high: 0-4), June 2002	2.259	0.793	2.5	4	0
folcat2	foliage category, February 2003	0.836	0.521	1	3.5	0
folcat3	foliage category, June 2003	1.645	0.9	2	4	0
antnest	ant nest count per tree, June 2002	3.697	5.35	2	60	0
swcat	swollen thorn category (from low to high: 0-4), June 2002	2.112	0.8	2	4	0.5
spcat	spine category (from low to high: 0-4), June 2002	2.239	0.787	2.5	4	0.5
swsprt	approximate swollen thorn / spine ratio, June 2002	0.318	0.131	0.333	1	0.05
flocat	flower category (from low to high: 0-4), November 2002	1.08	1.304	0.5	0	4
podcnt	pod count per tree, February 2003	13.53	50.44	0	560	0
trcop	presence of coppices at stem base (yes/no)	0.101	0.482	0	11	0
	branch variable description					
brdiam	branch base diameter (cm)	1.486	0.663	1.38	3.75	0.48
brcnt	branching count	9.236	11.03	7	76	2
spwgt*	Actual spine weight (g)	6.733	6.387	4.971	39.52	0.308
potspwt**	Potential spine weight (including broken spines calculated on *spwgt* average for the branch)	10.38	22.27	6.285	223.0	0.707
swwgt*	actual swollen thorn weight (g)	27.13	41.42	12.91	221..0	1.128
potswwt**	potential swollen thorn weight (including broken thorns calculated on the *swwgt* average for the branch)	29.64	43.01	14.3	220.0	0.128
folwgt	foliage weight (g)	28.29	34.59	18.9	195.0	1.0

Appendix 4. Regression equations for woodland structure plot variables (as summarised in Table 3, Paper 2, p. 114; c.f. variable numbers on the right side). All equations were highly significant ($p < 0.001$). With regard to the final printed equation, the stepwise inclusion of the predictor variables is indicated by order from left to right and by the *adjusted* R^2 (in brackets) at the step of inclusion. The first R^2 is therefore the one of the equation, where only the first predictor is included, the second R^2 belongs to an equation with the first and second predictor, and the last and highest R^2 belongs to the final equation. Variable descriptions are listed in Appendices 1 and 2.

1		$\mathit{sand} = 96.2 - 1.14 * \mathit{clay}$
	1	**incl. *clay* (92.9)**
2		$\mathit{clay} = 79.6 - 0.816 * \mathit{sand}$
	2	**incl. *sand* (92.9)**
3		$\mathit{som} = 0.671 - 0.00634 * \mathit{sand}$
	3a	**incl. *sand* (62.6)**
4		$\mathit{som} = -0.427 + 0.000017 * \mathit{trden1} + 0.0406 * \ln \mathit{grmass3} - 0.0062 * \mathit{sand}$
	3b	**incl. *sand* (56.8), *grmass3* (60.6), *trden1* (64.3)**
5		$\mathit{H2O} = 87.6 + 14.9 * \mathit{som} - 0.758 * \mathit{sand} - 0.351 * \mathit{clay}$
	4	**incl. *sand* (76.9), *som* (78.6), *clay* (80.3)**
6		$P = 0.0193 + 0.0077 * \mathit{som}$
	5a	**incl. *som* (15.1)**
7		$P = 0.0193 + 0.000325 * \ln \mathit{trden2} - 0.000476 * \mathit{fire2} + 0.00478 * \mathit{som}$
	5b	**incl. *som* (12.0), *trden2* (15.9), *fire2* (17.1)**
8		$N = 0.0904 + 0.133 * \mathit{som} - 0.000969 * \mathit{sand}$
	6a	**incl. *som* (69.9), *sand* (77.3)**
9		$N = -0.0199 + 0.00315 * \ln \mathit{trden1} - 0.000005 * \mathit{trmass1} + 0.00024 * \mathit{folmass1} - 0.00002 * \mathit{grmass1}$
		$+ 0.000014 * \mathit{fireint2} + 0.132 * \mathit{som} + 0.000979 * \mathit{H2O}$
	6b	**incl. *som* (67.5), *H2O* (77.1), *folmass1* (81.6), *fireint2* (83.6), *trden1* (84.3), *trmass1* (85.4),**
		***grmass1* (86.0)**
10		$\mathit{trmass1} = 795 + 26988 * N$
	7a	**incl. *N* (29.4)**
11		$\mathit{trmass1} = 854 + 59.5 * \mathit{clay}$
	7b	**incl. *clay* (24.1)**
12		$\mathit{folmass1} = 180 + 0.0213 * \mathit{trmass1} - 1.9 * \mathit{sand} - 2.02 * \mathit{clay} + 198 * N$
	8	**incl. *trmass1* (75.3), *N* (78.9), *sand* (79.0), *clay* (82.4)**
13		$\mathit{folmass2} = 96.1 + 1.68 * \ln \mathit{trden1} + 0.00236 * \mathit{trmass1} + 0.565 * \mathit{grlife2} - 0.0241 * \mathit{fireint1}$
		$- 0.998 * \mathit{sand} - 0.902 * \mathit{clay} - 0.414 * \mathit{H2O} - 465 * P$
	9	**incl. *trmass1* (32.5), *fireint1* (37.6), *grlife2* (48.7), *trden1* (52.9), *clay* (52.8), *sand* (61.0),**
		***H2O* (65.5), *P* (66.9)**
14		$\mathit{folmass3} = 162 + 0.0179 * \mathit{trmass2} - 0.0501 * \mathit{grlife3} - 1.64 * \mathit{sand} - 2.38 * \mathit{clay} + 308 * N$
	10	**incl. *trmass2* (69.3), *N* (71.3), *clay* (73.0), *sand* (76.3), *grlife3* (76.9)**
15		$\mathit{grmass1} = \exp(4.14 + 0.0175 * \mathit{sand} + 3.48 * N)$
	11	**incl. *sand* (15.0), *N* (17.1)**
16		$\mathit{grmass3} = \exp(5.65 - 0.000079 * \mathit{trmass2} - 0.618 * \mathit{fire2} - 0.00933 * \mathit{clay} + 3.13 * N)$
	12a	**incl. *fire2* (57.7), *trmass2* (60.0), *clay* (60.4), *N* (61.0)**
17		$\mathit{grmass3} = \exp(4.58 + 0.0656 * \mathit{trden2} - 0.00575 * \mathit{folmass3} + 1.97 * \mathit{som} - 0.022 * \mathit{H2O} + 38.3 * P)$
	12b	**incl. *som* (4.2), *folmass3* (9.6), *H2O* (14.0), *P* (17.3), *trden2* (18.6)**
18		$\mathit{grH2O} = -1.89 - 0.00501 * \mathit{folmass3} - 0.25 * \mathit{fire1} + 0.497 * \mathit{fire2} + 0.027 * \mathit{sand} + 0.0393 * \mathit{clay}$
	13	**incl. *fire2* (45.5), *folmass3* (51.6), *fire1* (55.7), *clay* (57.3), *sand* (58.4)**
19		$\mathit{grlife3} = 163 - 10.4 * \ln \mathit{trden2} - 10.6 * \ln \mathit{folmass3} - 35.3 * \mathit{fire1} + 231 * \mathit{som} - 1.95 * \mathit{H2O}$
	14	**incl. *trden2* (20.3), *fire1* (37.5), *som* (42.7), *H2O* (46.4), *folmass3* (49.4)**
20		$\mathit{grSLA} = 53.9 + 2.39 * \ln \mathit{trden2} - 0.507 * \mathit{clay} + 243 * N$
	15	**incl. *N* (15.4), *clay* (26.6), *trden2* (32.7)**
21		$\mathit{grLAI3} = \exp(0.472 - 0.00208 * \mathit{folmass2} - 0.645 * \mathit{fire2} - 0.0235 * \mathit{clay} + 10.3 * N)$
	16	**incl. *fire2* (54.7), *N* (55.3), *clay* (61.7), *folmass2* (62.3)**
22		$\mathit{grLeff3} = -0.134 - 0.00354 * \mathit{folmass3} + 0.180 * \mathit{fire2} + 1.66 * \mathit{som} + 0.00733 * \mathit{sand}$
		$- 0.0106 * \mathit{H2O}$
	17	**incl. *folmass3* (12.3), *fire2* (19.6), *som* (21.8), *sand* (32.3), *H2O* (33.3)**
23		$\mathit{transp3} = -4.37 - 0.0543 * \mathit{trden1} + 0.000299 * \mathit{trmass1} + 0.000233 * \mathit{fireint2} - 0.0236 * \mathit{sand}$
	18	$- 0.0442 * \mathit{clay} + 7.27 * N$
		incl. *trmass2* (49.7), *clay* (50.8), *N* (59.2), *fireint2* (60.8), *sand* (62.4), *trden2* (63.2)

Appendix 5. Regression equations and stepwise R^2 values for woodland structure tree variables (as summarised in Table 4, Paper 2, p. 61; c.f. variable numbers on the right side). All equations were highly significant ($p < 0.001$). Variable descriptions are listed in Appendices 1, 2 and 3.

24 $\mathit{trhgt} = -12.6 + 8.99 * \ln \mathit{trdiam} + 4.52 * \mathit{compet1} - 0.162 * \mathit{sand} - 0.193 * \mathit{clay} - 0.088 * \mathit{H2Oc} + 32.9 * N$

1 incl. ***trdiam*** (68.0), ***compet1*** (72.3), ***N*** (72.7), ***clay*** (73.4), ***sand*** (73.8), ***H2Oc*** (74.1)

25 $\mathit{trdiam} = \exp(4.59 - 1.09 * \mathit{compet1} - 0.0165 * \mathit{H2Oc} + 0.718 * \mathit{som} + 3.85 * N)$

2 incl. ***compet1*** (13.8), ***N*** (14.8), ***H2Oc*** (16.5), ***som*** (17.1)

26 $\mathit{width} = \exp(-2.7 - 0.245 * \ln \mathit{trdiam} - 0.966 * \mathit{compet1} + 0.0222 * \mathit{sand} + 0.0173 * \mathit{clay} + 0.0105 * \mathit{H2Oc}$

$+ 27.0 * P - 4.14 * N)$

3 incl. ***compet1*** (7.7), ***trdiam*** (11.6), ***N*** (13.0), ***P*** (13.5), ***sand*** (13.5), ***clay*** (13.9), ***H2Oc*** (14.1)

27 $\mathit{brcat} = -2.6 + 1.25 * \ln \mathit{trdiam} - 0.0417 * \mathit{trhgt} - 1.33 * \mathit{som} + 13.2 * N$

4 incl. ***trdiam*** (24.5), ***N*** (26.5), ***trhgt*** (28.1), ***som*** (28.8)

28 $\mathit{spcat} = 2.67 - 0.218 * \ln \mathit{trdiam} - 1.48 * \mathit{compet1} + 0.141 * \ln \mathit{width} + 0.124 * \mathit{brcat} + 0.349 * \mathit{swcat}$

$- 0.0983 * \mathit{clay} + 1.49 * \mathit{som}$

5a incl. ***swcat*** (15.9), ***compet1*** (25.1), ***width*** (26.1), ***som*** (27.0), ***brcat*** (27.3), ***trdiam*** (28.0), ***clay*** (28.5)

29 $\mathit{spcat} = 4.33 - 1.35\ \mathit{compet1} - 0.0158\ \mathit{trhgt} + 0.0996\ \mathit{brhgt} + 0.193\ \mathit{brcat} - 0.0190\ \mathit{sand} - 0.0344\ \mathit{clay} + 1.17\ \mathit{som}$

5b incl. ***compet1*** (10.2), ***brcat*** (12.5), ***trhgt*** (13.2), ***clay*** (13.6), ***som*** (14.6), ***sand*** (14.9), ***brhgt*** (15.2)

30 $\mathit{swcat} = 1.03 + 0.583 * \ln \mathit{trdiam} - 0.0251 * \mathit{trhgt} + 0.113 * \mathit{brcat} + 0.349 * \mathit{spcat} - 0.031 * \mathit{sand}$

$- 0.0456 * \mathit{clay} - 2.31 * \mathit{som} + 39.8 * P + 15.0 * N$

6a incl. ***spcat*** (14.3), ***trdiam*** (18.8), ***brcat*** (20.4), ***N*** (21.2), ***som*** (23.8), ***clay*** (24.6), ***sand*** (25.5), ***trhgt*** (26.0), ***P*** (26.3)

31 $\mathit{swcat} = 3.53 + 0.578 * \ln \mathit{trdiam} - 0.031 * \mathit{trhgt} + 0.185 * \mathit{brcat} - 0.0402 * \mathit{sand} - 0.0593 * \mathit{clay} - 1.98 * \mathit{som}$

$+ 12.5 * N$

6b incl. ***brcat*** (7.3), ***trdiam*** (8.8), ***clay*** (9.7), ***sand*** (12.1), ***N*** (12.7), ***som*** (14.0), ***trhgt*** (14.8)

32 $\mathit{antnest} = -1 + \exp(-7.8 + 0.702 * \ln \mathit{trdiam} - 0.46 * \mathit{compet1} + 0.0283 * \mathit{trhgt} + 0.113 * \mathit{brcat} + 0.0765 * \mathit{swcat}$

$- 0.23 * \ln \mathit{swsprt} + 0.447 * \mathit{folcat1} + 0.2 * \ln \mathit{folcat2} + 0.105 * \mathit{folcat3} - 0.244 * \ln \mathit{grLAI1}$

$+ 0.0423 * \mathit{sand} + 0.0172 * \mathit{clay} + 0.0383 * \mathit{H2Oc} - 36.4 * P + 6.39 * N)$

7 incl. ***trdiam*** (42.5), ***folcat1*** (56.6), ***brcat*** (57.7), ***swsprt*** (58.6), ***folcat3*** (59.5), ***P*** (60.1), ***swcat*** (60.4), ***H2Oc*** (60.8), ***sand*** (61.4), ***trhgt*** (61.7), ***grLAI1*** (61.9), ***compet1*** (62.0), ***N*** (62.3), ***folcat2*** (62.5), ***clay*** (62.6)

33 $\mathit{folcat1} = 6.08 - 0.0241 * \mathit{trhgt} + 0.442 * \ln \mathit{antnest} - 0.0994 * \mathit{swcat} + 0.22 * \ln \mathit{swsprt} + 1.47 * \mathit{trlifert}$

$+ 0.415 * \ln \mathit{grLAI1} - 0.0632 * \mathit{sand} - 0.054 * \mathit{clay} - 0.0351 * \mathit{H2Oc} + 76.5 * P$

8a incl. ***antnest*** (22.8), ***trlifert*** (29.4), ***P*** (31.8), ***grLAI1*** (33.0), ***swsprt*** (33.5), ***trhgt*** (34.0), ***H2Oc*** (34.2), ***sand*** (34.7), ***clay*** (35.6), ***swcat*** (36.0)

34 $\mathit{folcat1} = -3.72 + 0.879 * \ln \mathit{trdiam} - 0.0508 * \mathit{trhgt} + 0.172 * \ln \mathit{swsprt} + 2.38 * \mathit{trlifert} + 0.367 * \ln \mathit{grLAI1}$

$- 0.0268 * \mathit{H2Oc} + 58.2 * P + 7.06 * N$

8b incl. ***trlifert*** (22.7), ***trdiam*** (26.0), ***P*** (28.4), ***grLAI1*** (29.8), ***trhgt*** (30.6), ***H2Oc*** (31.3), ***N*** (32.2), ***swsprt*** (32.7)

35 $\mathit{folcat2} = -1 + \exp(1.56 - 0.00521 * \mathit{trden1} - 0.00924 * \mathit{trhgt} + 0.0685 * \ln \mathit{antnest} + 0.0315 * \mathit{swcat}$

$- 0.0838 * \ln \mathit{swsprt} + 0.285 * \mathit{trlifert} + 0.248 * \ln \mathit{grmass2} - 0.0253 * \mathit{sand} - 0.0272 * \mathit{clay}$

$- 0.0114 * \mathit{H2Oc}$

9a incl. ***grmass2*** (19.9), ***antnest*** (25.0), ***trlifert*** (26.3), ***trden1*** (27.5), ***clay*** (28.1), ***sand*** (29.8), ***trhgt*** (30.7), ***H2Oc*** (32.0), ***swsprt*** (32.4), ***swcat*** (32.7)

36 $\mathit{folcat2} = -1 + \exp(0.507 - 0.193 * \mathit{compet1} + 0.0436 * \ln \mathit{width} + 0.0443 * \mathit{swcat} - 0.0951 * \ln \mathit{swsprt}$

$+ 0.306 * \mathit{trlifert} + 0.396 * \ln \mathit{grmass2} + 0.213 * \mathit{grH2O2} - 0.0209 * \mathit{sand} - 0.0219 * \mathit{clay}$

$- 0.00776 * \mathit{H2Oc} - 11.0 * P)$

9b incl. ***grmass2*** (18.7), ***trlifert*** (21.9), ***compet1*** (23.7), ***swcat*** (24.1), ***swsprt*** (25.6), ***grH2O2*** (26.0), ***clay*** (25.9), ***sand*** (27.4), ***H2Oc*** (27.7), ***width*** (28.0), ***P*** (28.2)

37 $\mathit{folcat2} = 2.58 - 0.00573 * \mathit{trden2} + 0.0401 * \mathit{brhgt} + 0.0507 * \mathit{swcat} - 0.108 * \ln \mathit{swsprt} + 0.365 * \mathit{trlifert}$

$- 0.195 * \mathit{fire1} - 0.0214 * \mathit{sand} - 0.0259 * \mathit{clay} - 0.00803 * \mathit{H2O}$

9c incl. ***fire1*** (12.1), ***trlifert*** (16.4), ***trden1*** (19.1), ***clay*** (19.6), ***sand*** (21.9), ***H2Oc*** (22.4), ***swcat*** (22.8), ***swsprt*** (24.2), ***brhgt*** (24.6)

38 $\mathit{folcat3} = 4.52 + 0.45 * \ln \mathit{trdiam} + 0.0134 * \mathit{trden2} - 0.0368 * \mathit{trhgt} + 0.258 * \ln \mathit{antnest} - 0.0731 * \mathit{swcat}$

$+ 0.0661 * \mathit{spcat} + 1.68 * \mathit{trlifert} - 0.00391 * \mathit{grlife3} + 0.33 * \ln \mathit{grLAI3} - 0.166 * \mathit{fire1}$

$- 0.0566 * \mathit{sand} - 0.0947 * \mathit{clay}$

10a incl. ***trlifert*** (21.7), ***antnest*** (29.9), ***grlife3*** (35.2), ***clay*** (41.1), ***sand*** (43.0), ***grLAI3*** (44.3), ***trden2*** (44.8), ***trhgt*** (44.9), ***trdiam*** (45.7), ***fire1*** (46.0), ***swcat*** (46.1), ***spcat*** (46.3)

39 $\mathit{folcat3} = 3.25 + 0.68 * \ln \mathit{trdiam} + 0.012 * \mathit{trden2} - 0.0374 * \mathit{trhgt} + 0.105 * \mathit{brcat} - 0.0654 * \mathit{swcat}$

$+ 0.0877 * \mathit{spcat} + 2.16 * \mathit{trlifert} - 0.00429 * \mathit{grlife} + 0.453 * \ln \mathit{grLAI} - 0.258 * \mathit{fire1}$

$- 0.0561 * \mathit{sand} - 0.0971 * \mathit{clay}$

10b incl. ***trlifert*** (21.9), ***clay*** (28.8), ***grlife3*** (32.8), ***brcat*** (35.2), ***grLAI3*** (37.0), ***sand*** (39.2), ***trdiam*** (40.2), ***fire1*** (40.9), ***trhgt*** (41.7), ***trden2*** (42.3), ***spcat*** (42.6), ***swcat*** (42.8)

40 $\mathit{folcat3} = 6.46 + 0.63 * \ln \mathit{trdiam} + 0.0117 * \mathit{trden2} - 0.037 * \mathit{trhgt} + 0.111 * \mathit{brcat} - 0.0824 * \mathit{swcat}$

$+ 0.0827 * \mathit{spcat} + 2.05 * \mathit{trlifert} - 0.000218 * \mathit{fireint2} - 0.0855 * \mathit{sand} - 0.119 * \mathit{clay} - 0.024 * \mathit{H2Oc}$

10c incl. ***trlifert*** (17.6), ***clay*** (23.3), ***sand*** (26.4), ***trdiam*** (28.1), ***trden2*** (29.7), ***trhgt*** (30.9), ***H2Oc*** (31.5), ***brcat*** (32.1), ***fireint2*** (32.3), ***swcat*** (32.5), ***spcat*** (32.8)

Appendix 6. Regression equations and stepwise R^2 values for tree density, survival and recruitment plot variables (as summarised in Table 1, Paper 3, p. 90; c.f. variable numbers on the right side). All equations were highly significant ($p < 0.001$). Variable descriptions are listed in Appendix 1 and 2.

41		$\mathit{trden1} = \exp(-0.089 + 71.4 * P + 30.0 * N)$
	1	incl. ***N*** (43.7), ***P*** (44.7)
42		$\mathit{trden2} = \exp(1.63 - 0.00073 * \mathit{fireint2} - 3.71 * \mathit{som} + 0.0194 * \mathit{clay} + 34.1 * N)$
	2	incl. ***N*** (35.2), ***fireint2*** (36.4), ***som*** (38.2), ***clay*** (39.0)
43		$\mathit{trmass1} = 795 + 26988 * N$
	3	incl. ***N*** (29.4)
44		$\mathit{trmass1} = 854 + 59.5 * \mathit{clay}$
	4	incl. ***clay*** (24.1)
45		$\mathit{avdiam} = \exp(5.12 - 0.275 * \ln \mathit{trden1} + 0.000126 * \mathit{trmass1} - 18.7 * P)$
	5	incl. ***trden1*** (56.0), ***trmass1*** (73.9), ***P*** (75.4)
46		$\mathit{maxdiam} = \exp(4.28 - 0.176 * \ln \mathit{trden1} + 0.000198 * \mathit{trmass1} + 22.2 * P)$
	6	incl. ***trmass1*** (30.2), ***trden1*** (59.0), ***P*** (61.2)
47		$\mathit{avtrhgt} = \exp(3.14 - 0.229 * \ln \mathit{trden1} + 0.000136 * \mathit{trmass1} - 0.00609 * \mathit{clay} - 28.8 * P + 3.98 * N)$
	7	incl. ***trden1*** (18.8), ***trmass1*** (41.6), ***P*** (44.6), ***N*** (46.9), ***clay*** (48.8)
48		$\mathit{trsurv} = \exp(2.18 + 0.221 * \ln \mathit{avdiam} - 0.147 * \mathit{maxdiam} - 0.154 * \ln \mathit{grmass3} - 0.000495 * \mathit{fireint2} - 0.417 * \mathit{som} - 0.00618 * \mathit{sand} - 0.017 * \mathit{H2Oc} + 18.4 * P)$
	8a	incl. ***H2Oc*** (14.4), ***fireint2*** (32.6), ***grmass3*** (43.3), ***avdiam*** (44.3), ***maxdiam*** (45.3), ***P*** (46.7), ***sand*** (47.8), ***som*** (49.3)
49		$\mathit{trsurv} = \exp(0.08 + 0.102 * \ln \mathit{trden1} + 0.507 * \ln \mathit{avdiam} - 0.285 * \mathit{maxdiam} - 0.000459 * \mathit{fireint2} - 1.01 * \mathit{som} - 0.0102 * \mathit{sand} - 0.0232 * \mathit{H2Oc} + 19.4 * P)$
	8b	incl. ***H2Oc*** (15.8), ***fireint2*** (33.4), ***som*** (37.1), ***sand*** (39.1), ***trden1*** (39.0), ***avdiam*** (40.6), ***maxdiam*** (43.7), ***P*** (44.5)
50		$\mathit{wdsurv} = 1.46 + 0.115 * \ln \mathit{avdiam} - 0.115 * \ln \mathit{grmass3} - 0.000344 * \mathit{fireint2} - 0.00497 * \mathit{sand} - 0.0187 * \mathit{H2Oc} + 25.9 * P$
	9	incl. ***H2Oc*** (11.7), ***fireint2*** (26,2), ***grmass3*** (32.4), ***P*** (37.8), ***avdiam*** (39.4), ***sand*** (41.0)
51		$\mathit{trkill} = -14.6 + 0.845 * \ln \mathit{trden1} + 1.7 * \ln \mathit{grmass3} + 0.00672 * \mathit{fireint2} + 0.141 * \mathit{H2Oc}$
	10a	incl. ***fireint2*** (10.1), ***H2Oc*** (21.2), ***trden1*** (23.3), ***grmass3*** (25.9)
52		$\mathit{trkillF} = 2.67 + 1.54 * \ln \mathit{trden1} + 16.3 * \mathit{som} - 0.276 * \mathit{clay} + 0.474 * \mathit{H2Oc} - 673 * P$
	10b	incl. ***H2Oc*** (26.5), ***clay*** (33.2), ***trden1*** (37.2), ***P*** (39.3), ***som*** (42.7)
53		$\mathit{wdlifert} = 0.827 + 0.000043 * \mathit{trmass1} - 0.00407 * \mathit{clay} - 0.00449 * \mathit{H2Oc} - 2.14 * N$
	11	incl. ***clay*** (3.7), ***trmass1*** (8.2), ***N*** (15.6), ***H2Oc*** (17.2)
54		$\mathit{poddrop} = \exp(-5.65 + 1.81 * \ln \mathit{avdiam} + 0.008 * \mathit{folmass1} + 0.0182 * \mathit{folmass2} + 0.0237 * \mathit{clay} - 56.1 * P - 16.6 * N)$
	12a	incl. ***avdiam*** (31.1), ***folmass1*** (36.0), ***N*** (40.8), ***clay*** (42.9), ***folmass2*** (44.3), ***P*** (45.5)
55		$\mathit{poddrop} = \exp(3.42 - 0.42 * \ln \mathit{trden1} + 0.000361 * \mathit{trmass1} + 0.00568 * \mathit{folmass1} - 81.3 * P - 8.76 * N)$
	12b	incl. ***trmass1*** (3.0), ***trden1*** (21.3), ***P*** (24.2), ***N*** (25.6), ***folmass2*** (26.1)
56		$\mathrm{nscor}\ \mathit{seedl1} = -0.53 - 1.11 * \ln \mathit{avtrhgt} - 0.00271 * \mathit{grmass1} - 2.73 * \mathit{som} + 0.0688 * \mathit{sand} + 0.0694 * \mathit{clay} - 152 * P + 26.2 * N$
	13a	incl. ***grmass1*** (6.4), ***avtrhgt*** (12.0), ***P*** (17.0), ***N*** (25.8), ***som*** (28.0), ***clay*** (27.1), ***sand*** (31.2)
57		$\mathrm{nscor}\ \mathit{seedl1} = -5.7 + 0.259 \ln \mathrm{trden1} - 0.000219 * \mathrm{trmass1} - 0.00277 * \mathrm{grmass1} - 2.56 * \mathrm{som} + 0.086 * \mathrm{sand} + 0.0932 * \mathrm{clay} - 113 * \mathrm{P} + 23.5 * \mathrm{N}$
	13b	incl. ***grmass1*** (7.0), ***N*** (11.4), ***P*** (15.0), ***som*** (16.8), ***trden1*** (17.2), ***trmass1*** (19.7), ***clay*** (20.4), ***sand*** (25.0)
58		$\mathrm{nscor}\ \mathit{seedl2} = 2.66 - 1.35 * \ln \mathit{avtrhgt} + 0.00253 * \mathit{grlife3} - 0.41 * \mathit{fire1} + 12.8 * N$
	14a	incl. ***avtrhgt*** (12.5), ***fire1*** (18.9), ***N*** (27.4), ***grlife*** (28.7)
59		$\mathrm{nscor}\ \mathit{seedl2} = -25.4 + 0.189 * \ln \mathit{trden2} - 0.000198 * \mathit{trmass2} + 4.8 * \ln \mathit{grmass3} - 0.0421 * \mathit{grlife3} - 4.14 * \ln \mathit{grLAI3} + 5.85 * \mathit{grLeff3} + 1.1 * \mathit{grH2O3} - 2.17 * \mathit{som} + 23.6 * N$
	14b	incl. ***N*** (8.3), ***grH2O3*** (14.8), ***som*** (16.4), ***trmass2*** (17.3), ***trden1*** (19.3), ***grmass*** (19.1), ***grLAI3*** (22.2), ***grlife*** (22.6), ***grLeff3*** (28.1)
60		$\mathrm{nscor}\ \mathit{seedl2} = -9.69 - 0.404 * \mathrm{fire1} + 0.0705 * \mathrm{sand} + 0.123 * \mathrm{clay} + 123 * \mathrm{P}$
	14c	incl. ***clay*** (13.3), ***fire1*** (17.7), ***P*** (22.2), ***sand*** (25.9)
61		$\mathrm{nscor}\ \mathit{resp} = 7.36 - 1.84 * \ln \mathit{avdiam} + 0.000103 * \ln \mathit{trmass2} - 0.615 * \mathit{fire1} + 0.0217 * \mathit{clay} - 82.8 * P + 11.8 * N$
	15a	incl. ***avdiam*** (29.3), ***N*** (42.3), ***fire1*** (55.9), ***P*** (57.5), ***clay*** (59.7), ***trmass*** (60.5)
62		$\mathrm{nscor}\ \mathit{resp} = -4.75 + 0.393 * \ln \mathit{trden2} - 0.000398 * \mathit{trmass2} + 0.349 * \mathrm{nscor}\ \mathit{trsurv(abs)} + 0.0123 * \mathit{folmass3} - 0.274 * \mathit{fire1} + 0.0529 * \mathit{sand} + 0.0918 * \mathit{clay} - 66.5 * P$
	15b	incl. ***trsurv(abs)*** (18.3), ***trden2*** (34.4), ***clay*** (37.5), ***fire1*** (41.9), ***P*** (43.5), ***trmass2*** (45.0), ***folmass3*** (46.0), ***sand*** (47.9)
63		$\mathrm{nscor}\ \mathit{coppice} = -0.632 + 0.507 * \mathrm{nscor}\ \mathit{trsurv(abs)} + 0.376 * \ln \mathit{grLAI3} + 0.00118 * \mathit{fireint2} + 0.0228 * \mathit{clay}$
	16	incl. ***trsurv(abs)*** (45.6), ***fireint2*** (49.5), ***clay*** (52.4), ***grLAI3*** (55.3)
64		$\mathrm{nscor}\ \mathit{sucker} = -6.56 - 1.75 * \ln \mathit{avdiam} + 0.00642 * \mathit{folmass3} - 0.406 * \mathit{fire1} + 2.7 * \mathit{som} + 0.14 * \mathit{sand} + 0.162 * \mathit{clay}$
	17a	incl. ***avdiam*** (29.8), ***clay*** (33.3), ***sand*** (41.2), ***folmass3*** (43.8), ***fire1*** (46.7), ***som*** (49.6)
65		$\mathrm{nscor}\ \mathit{sucker} = -7.29 + 0.51 * \ln \mathit{trden2} - 0.000634 * \mathit{trmass2} + 0.014 * \mathit{folmass3} + 0.0654 * \mathit{sand} + 0.101 * \mathit{clay}$
	17b	incl. ***trden2*** (11.4), ***trmass2*** (20.7), ***clay*** (24.2), ***folmass*** (24.9), ***sand*** (27.6)

Appendix 7. Regression equations and stepwise R^2 values for tree density, survival and recruitment tree variables (as summarised in Table 2, Paper 3, p. 91; c.f. variable numbers on the right side). All equations were highly significant ($p < 0.001$). Variable descriptions are listed in Appendices 1, 2 and 3.

66		$\mathit{compet1} = 0.389 - 0.121 * \ln \mathit{trdiam} + 0.00169 * \mathit{sand} - 0.00395 * \mathit{H2Oc} - 0.499 * \mathit{som} + 9.53 * P + 7.68 * N$
	1	incl. ***N*** (20.2), ***trdiam*** (31.1), ***som*** (35.1), ***H2Oc*** (36.9), ***P*** (37.6), ***sand*** (37.7)
67		$\mathit{compet2} = 0.269 - 0.112 * \ln \mathit{trdiam} + 0.263 * \mathit{fire2} - 0.00056 * \mathit{fireint1} - 0.000825 * \mathit{fireint2} - 0.00889 * \mathit{sand} + 0.00764 * \mathit{clay} - 0.00431 * \mathit{H2Oc} + 13.1 * P + 5.76 * N$
	2	incl. ***N*** (15.9), ***trdiam*** (27.9), ***fireint1*** (31.6), ***fireint2*** (35.1), ***fire2*** (40.3), ***H2Oc*** (43.7), ***P*** (45.1), ***sand*** (45.2), ***clay*** (46.1)
68		$\mathit{trdiam} = \exp(4.59 - 1.09 * \mathit{compet1} - 0.0165 * \mathit{H2Oc} + 0.718 * \mathit{som} + 3.85 * N)$
	3	incl. ***compet1*** (13.8), ***N*** (14.8), ***H2Oc*** (16.5), ***som*** (17.1)
69		$\mathit{survive} = 0.565 + 0.128 * \ln \mathit{trdiam} + 0.0034 * \mathit{trden1} - 0.0113 * \mathit{trhgt} + 0.0406 * \mathit{brcat} - 0.0406 * \mathit{swcat} + 0.0521 * \ln \mathit{swsprt} + 0.583 * \mathit{trlifert} - 0.122 * \ln \mathit{grmass1} + 0.000154 * \mathit{fireint1} - 0.000268 * \mathit{fireint2} + 10.8 * P - 3.2 * N$
	4a	incl. ***fireint2*** (9.6), ***trlifert*** (16.9), ***N*** (18.6), ***grmass1*** (20.2), ***brcat*** (20.8), ***trden1*** (21.7), ***swcat*** (22.0), ***swsprt*** (22.5), ***P*** (22.7), ***trdiam*** (22.7), ***trhgt*** (23.3), ***fireint1*** (23.5)
70		$\mathit{survive}\ (\mathit{Febfire.0}) = 0.504 + 0.528 * \mathit{trlifert}$
	4b	incl. ***trlifert*** (26.1)
71		$\mathit{survive}\ (\mathit{Febfire.hot}) = -6.21 + 0.316 * \ln \mathit{trdiam} + 0.00919 * \mathit{trden1} - 0.0225 * \mathit{trhgt} + 0.56 * \mathit{trlifert} + 0.0463 * \mathit{sand} + 0.0318 * \mathit{clay} + 0.023 * \mathit{H2Oc} + 44.1 * P - 10.5 * N$
	4c	incl. ***N*** (9.4), ***trden1*** (15.5), ***trdiam*** (19.1), ***trhgt*** (22.1), ***trlifert*** (24.1), ***P*** (26.0), ***sand*** (25.9), ***clay*** (28.2), ***H2Oc*** (29.9)
72		$\mathit{trlifert} = 1.05 + 0.00245 * \mathit{trden1} + 0.0143 * \mathit{trhgt} + 0.0188 * \ln \mathit{width} - 0.0259 * \mathit{brcat} + 0.00257 * \mathit{sand} - 0.00426 * \mathit{clay}$
	5	incl. ***trhgt*** (10.7), ***trden1*** (14.5), ***brcat*** (15.7), ***clay*** (16.0), ***width*** (16.2), ***sand*** (16.4)
73		$\mathit{flocat} = -1 + \exp(-1.79 + 0.366 * \ln \mathit{trdiam} + 0.334 * \mathit{trlifert} + 0.00822 * \mathit{trden1} - 0.52 * \mathit{compet1} + 0.0508 * \mathit{trhgt} + 0.0639 * \mathit{brcat} + 0.184 * \ln \mathit{grLAI1} + 0.0123 * \mathit{clay} - 0.00929 * \mathit{H2Oc} - 0.671 * \mathit{som})$
	6	incl. ***trhgt*** (49.3), ***trdiam*** (52.6), ***trlifert*** (53.3), ***grLAI1*** (53.9), ***brcat*** (54.3), ***clay*** (54.4), ***som*** (55.5), ***H2Oc*** (55.9), ***compet1*** (55.9), ***trden1*** (56.2)
74		$\mathit{podcnt} = -1 + \exp(-1.5 - 1.47 * \mathit{compet1} + 0.17 * \mathit{trhgt} + 0.217 * \ln \mathit{width} + 0.292 * \ln \mathit{antnest} - 0.155 * \mathit{spcat} + 0.442 * \mathit{grLAI1} - 1.23 * \mathit{grLeff1} + 1.86 * \mathit{som} - 15.9 * N)$
	7	incl. ***trhgt*** (37.4), ***compet1*** (43.4), ***antnest*** (45.8), ***grLeff2*** (47.8), ***N*** (48.6), ***spcat*** (49.2), ***width*** (49.7), ***som*** (50.0), ***grLAI1*** (50.5)
75		$\mathit{trcop} = 0.704 - 0.366 * \mathit{survive} - 0.00261 * \mathit{trden2} - 0.00519 * \mathit{trhgt} - 0.0261 * \ln \mathit{brhgt} + 0.000359 * \mathit{grlife3} + 0.0382 * \ln \mathit{grLAI3} - 0.000132 * \mathit{fireint1} + 0.000156 * \mathit{fireint2} - 0.0034 * \mathit{sand}$
	8	incl. ***survive*** (27.4), ***fireint2*** (29.7), ***trden2*** (30.7), ***sand*** (31.1), ***grlife3*** (31.5), ***trhgt*** (31.7), ***brhgt*** (31.9), ***fireint2*** (32.0), ***grLAI3*** (32.1)

Appendix 8. Regression equations and stepwise R^2 values for branch variables (as summarised in Table 5, Paper 2, p. 62; c.f. variable numbers on the right side). All equations were highly significant ($p < 0.001$). Variable descriptions are listed in Appendix 3.

76		$\mathit{spwgt} = \exp(-0.204 + 0.345 * \ln \mathit{brcnt} + 0.172 * \ln \mathit{folwgt} + 0.225 * \ln \mathit{swwgt}$
	1	incl. ***brcnt*** (39.9), ***swwgt*** (46.7), ***folwgt*** (49.0)
77		$\mathit{potspwt} = \exp(0.456 + 0.763 * \ln \mathit{brdiam} + 0.332 * \ln \mathit{brcnt} + 0.18 * \ln \mathit{folwgt}$
	2	incl. ***brdiam*** (57.1), ***brcnt*** (60.9), ***folwgt*** (63.5)
78		$\mathit{swwgt} = \exp(1.23 + 1.18 * \ln \mathit{brdiam} + 0.268 * \ln \mathit{brcnt} + 0.326 * \mathit{spwgt})$
	3	incl. ***brdiam*** (57.1), ***spwgt*** (62.4), ***brcnt*** (63.8)
79		$\mathit{potswwt} = \exp(1.49 + 2.2 * \ln \mathit{brdiam} + 0.187 * \ln \mathit{folwgt})$
	4	incl. ***brdiam*** (73.4), ***folwgt*** (74.3)
80		$\mathit{folwgt} = \exp(2.18 + 1.29 * \ln \mathit{brdiam} + 0.206 * \ln \mathit{spwgt})$
	5	incl. ***brdiam*** (49.4), ***spwgt*** (51.3)

Mwanzo kokochi mwisho nazi!

The beginning is bud the end is coconut!

Swahili Proverb

Kidole kimoja hakivunji chawa!

One finger cannot crush a louse!

Swahili Proverb

Kupotea njia ndiyo kujua njia!

To get lost is to know the way!

Swahili Proverb

Acknowledgements

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The whole Mkwaja research project has evolved over the past years from an adventurous, exploratory engagement to a handsome, still developing institution, which I hope will continue to be upheld for many years to come. Many persons have been working with enthusiasm, spirit and foresight, helping the young plant in the African savanna survive and eventually develop the roots to keep on going. We passed through many vivacious occasions of pleasure, also some cumbersome moments of turmoil. I look back on a chapter that is filled with the dynamics of life and interactions with others that have shared my views or have mystified me with their unique way of looking at things differently. It was an enriching experience not to be missed, and I am grateful for everything and everybody that was there and helped to bring matters forward.

First I want to thank my supervisor Professor Dr. Peter Edwards for his continuing support during those last four years, for his stewardship and for his manifold scientific inspirations, but in particular for having the courage and the will to engage in an initially uncertain, but finally rewarding venture. With his various connections in Tanzania and Switzerland, and his assertive ideas on the scientific front, Professor Dr. Frank Klötzli was vital in planting the seeds of this project. In particular I want to thank Frank as well as Dr. Urs Blösch for their introduction to the vegetation and their enthusiastic help and advice regarding species identification. PD Dr. Ewald Weber was accompanying this project at various crucial stages, both logistically and scientifically. His fine sense of assistance and navigation skills through some coral reefs are highly regarded.

PD Dr. Sabine Güsewell was involved with logistics at the beginning of the project. In particular I want to thank her for scientific advice regarding statistical and related 'arithmetic' problems. Katharina Rentsch kept a close eye on the project finances and various correspondences. While matters were sometimes tangled and heated, she always managed to keep an admirable calm and common sense. Rose Trachsler and Marilyn Gaschen were responsible for careful laboratory nutrient analyses of many soil samples. Dieter Ramseyer made some very useful suggestions with regard to study designs. I also want to thank other persons from the Geobotanical Institute and elsewhere: Markus Hofbauer for his technical and field assistance, Jürg Leuenberger (from ITÖ) for help with soil texture analyses, René Graf for ready logistics support, Professor Dr. Andreas Gigon for letting us have his porometer for several weeks, Hans-Heini Vogel, Hans-Jörg Dietz, Georg von Arx, Karsten Rohweder and Erika Aeschbach for help with computer, bureau and other matters. At the end of my student life, I was pleased to get to know my two co-examiners Dr. Jean-Pierre Sorg and Dr. Werner Suter who have been scanning through my final paperwork.

In Tanzania we received kind support from Dr. Samwel L.S. Maganga, Professor L.L.L. Lulandala and Mr. David Muyenjwa of Sokoine University of Morogoro (SUA) for importing our first cars and obtaining the donated Nissan Patrol car at low tax costs. Our research partnership with SUA facilitated connections and dealings with other Tanzanian organizations such as the Wildlife Department, TAWIRI (Tanzanian Wildlife Research Institute), COSTECH (Commission for Science and Technology) and TANAPA (Tanzanian National Parks Authority). I want to thank Dr. Alex Sanga, Mr. Bruce Fox, Mr. E. Kikotta and Mr. Muawi from Amboni Ltd. for their hospitality during the last days of Ranch operation in 2000 and later. Dr. Jürgen Göbel and Mr. Janett in Switzerland helped us with contacts and with securing the remaining ranch reports. Mr. Minja from the Wildlife Department gave access authorization and provided support when we were visiting Saadani Game Reserve, and Mr. Ndauka and other game scouts were accompanying us on many walks through the bush.

I was excited when I heard that our study area would become a national park, and even more so when the TANAPA staff finally moved in the houses on the ranch. I thereby want to thank Domician Njao, George Koroso as well as the other TANAPA staff for their unreserved backing of our research venture, their logistic support, and, in particular, their very amicable neighborhood. I hope the present work and other pieces of research by our team will ultimately be of benefit for understanding of the Saadani ecosystem and future management by TANAPA.

I shall not forget to mention the terrific help we received from our cook Benjamin sr., his son Benjamin jr. and from Makarena. Kila siku wamepika chakula kizuri kabisa kwa watu wote nyumbani, na bila shaka wametusaidia vilevile kwa vitu vingi vingine... Ahsante sana! ...na ninataraji mtakuwa na wakati kizuri pamoja na wazungu wataofika kwenda pollini mara ingine na vilevile kufanya hovyohovyo nyumbani...!

Some *wazungu* and locals in Dar es Salaam also provided generous logistic, technical and other personal support. Without the great help and advice of our car mechanic Jakob Dopple many of our problems would hardly have been resolved so easily (if at all...): he not only repaired and maintained our cars at an expedient rate, but also provided patient advice on administrative, political and logistical matters from getting the best deal for car taxes and insurances to buying a solar drying oven or constructing the earthing of our generator... Claire-Lise Reift and Peter Arnold of the Swiss Development Co-operation in Tanzania (SDC) as well as Titiano Bassi from the Swiss Embassy were assisting with other logistic support like helping to get shipments of research material to Tanzania, offering a safe parking space in Dar es Salaam, and helping with official dealings with Tanzanian agencies. In particular I want to thank Marianne Wyss from the Swiss Embassy for her kindhearted hospitality, providing a safe heaven in Dar es Salaam for all of us during our first visits in Tanzania, and during my 10 days of Swahili course in Dar es Salaam. Dr. Rolf Baldus and Kirsten Roettcher from the GTZ were of great assistance for getting access to Saadani Game Reserve, the Saadani guesthouse and for hiring game scouts. Furthermore, I shall mention

Heinz Rieben from Unicef Tanzania who supported us with our submission for a second-hand car donation, and James Lyamba who created an electronic plant database.

In our vicinity at the Tides Beach resort near Mwera, Stephanie and Uli Kürzinger were wonderful, convivial neighbors on whom we always could rely for help if needed: I particularly want to thank them for bringing me to hospital and looking after me during my malaria dropdown in December 2002. Given my befuddled, psychedelic state I guess this has been a rather awkward situation for them as well...! During more serene times the Tides Beach Resort was also a welcome palm oasis were we all could stretch our legs after some days of bush-data-bashing...

In 2000 this Africa venture started off on a pilot project with a team of enthusiastic ETH students. Diving head-on into Mkwaja realities I think we did a decent job of getting research on track, even if we lost the overview in between. For that phase of the project I want to particularly express thanks to André Wehrli and his wife Loes for their considerable efforts with first logistics, public relations, field work and scientific assistance. Mathias Tobler was writing his diploma thesis at that time. With him I had a vivid, rewarding scientific interaction in the field as well as at the computer that culminated in the publication of our first paper (in this thesis); and his 'expert' contribution is still continuing to this day. I also want to thank Christoph von Känel for his companionship and assistance as a practical trainee.

After the SNF provided a grant for two PhD students Anna Treydte joined the project in April 2001, and I want to express my appreciation for her support on logistic and administrative (especially finance) matters. From 2001-2003 many other students helped with field research and logistics. Ari Stucki joined us in mid 2001 for a practical placement. I hope that, in retrospect, he can be philosophical about the fact that we finally spent more days in Dar es Salaam than in the field repairing cars, looking to buy a new car and waiting for other things... In any case, his technical expertise and help (he was the constructor of our generator light system...!), as well as his settled nature are very well remembered. Robin Riedmann and Natascha Eisenhut helped with field work in February 2002. We had to mend a car tyre about every second day because of acacia thorn impact, yet it was a considerably better working atmosphere which indicated that we're about over the hill... During the next wet season Chris Bohr made a marvelous Diploma study on grasshopper communities on paddocks and in the savanna, while Stephanie Halsdorf made a study on warthogs with Anna. In February 2003 Pueng That visited the ranch as an initial step for his Diploma thesis about the former Mkwaja Ranch management history. With him I had many enriching philosophical exchanges, and I hope that the work with the "real experiment" study group around Dr. Holger Hoffmann-Riem may continue for a while. During 2002 and 2003 we were also visited again two times by Frank Klötzli and Urs Blösch, who made some valuable vegetation surveys in savanna thicket clumps and coastal forests. Peter Edwards, Ewald Weber and Markus Hofbauer joined us in 2001 and 2002 for field instruction and help; and I got to know many students and friends of Anna's acquaintance.

I am most thrilled about the fact that we can now hand over our little research station to our successors; this is probably the best evidence of success for which all the above-listed persons have made their amazing contributions! Our house will be filled with student life for at least another 3 years, and I wish the future PhD students Stephanie Halsdorf and Patrick Cech and all other ranch visitors all the best for their stay and research! I hope that the plant we all have planted will grow very old under subsequent watering regimes...!

Curriculum Vitae

Roland Cochard
born 5.10.1974, Zurich, Switzerland

Educational Background

04.2001 – 12.2004	PhD student at the Geobotanical Institute, ETH, Zurich, Switzerland; 20 months of field work at Mkwaja Ranch, including supervision of Diploma studies
06.2000 – 06.2001	Setting up of research facility at Mkwaja Ranch, Tanzania; writing of research proposal for two PhD projects; preliminary scientific surveys and evaluation; Swahili language course
10.1999 – 05.2001	Postgraduate Studies at the University of Neuchâtel, Switzerland *Degree: Postgraduate Certificate in Applied Statistics
07.1999 - 10.1999	Practical Placement at the Cantonal Office for Land and Nature, Section Agriculture, Zurich, Switzerland (dealing with issues of agricultural law)
08.1998 - 03.1999	Diploma (Honours) Thesis: „A seed ecology study of *Parkinsonia aculeata*"
02.1998 - 07.1998	Semester at the University of Costa Rica, San José, Costa Rica (courses in tropical flora) and practical placement in Palo Verde National Park, Costa Rica: research on the invasive pest plant *Parkinsonia aculeata*
03.1995 - 03.1999	James Cook University of North Queensland, Townsville, Australia *Degree: Bachelor of Applied Science with Honours in Environmental Science
03.1987 - 09.1993	Kantonsschule Hohe Promenade (High School) in Zurich, Switzerland *Degree: Swiss Matura Type B (with English and Latin)

Skills

Languages	German (first language); English (fluently spoken and written); French and Spanish (good knowledge, spoken and written); Indonesian and Swahili (intermediate spoken fluency); Latin (written)
Computer	Office and design software, statistical software (Minitab, SPSS, Systat, S-Plus), some knowledge of GIS software (ARC-View, ENVI, Ozi-Explorer)
Social & logistic	Supervision of Swiss students in Tanzania; logistic organization of research station at Mkwaja Ranch; upholding connections with Tanzanian stakeholders, including various research, government and development aid institutions; social occasions for college

Personal interests

Ecology and conservation of biodiversity; issues in development aid and policy; entomology, philosophy, ethnology, economics, history & literature...; extensive nature & culture travels in Australia and Malaysia (1994 and later), Ecuador (1996), Indonesia (1997), Southern Africa (1998), Central America (1998), New Zealand and Fiji (1999), and East Africa (2000-2002); hiking; scuba diving; photography

Publications

Tobler, M.W., Cochard, R. & Edwards, P.J. (2003) The impact of cattle ranching on large-scale vegetation patterns in a coastal savanna in Tanzania. *Journal of Applied Ecology*, 40, 430-444.

Cochard, R. & Jackes, B.R. (2004) Seed ecology of the invasive tropical tree *Parkinsonia aculeata. Plant Ecology* (accepted).

And like seeds dreaming beneath the
snow your heart dreams of spring.
Trust the dreams, for in them
is hidden the gate
to eternity.

Khalil Gibran,
The Prophet