INFLUENCE OF LAND USE ON STRUCTURE AND DYNAMICS OF POPULATIONS OF WOODY PLANTS IN SAVANNAS, WEST AFRICA

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Dekanin: .... Prof. Dr. Anna Starzinski-Powitz

Erster Gutachter: ....Prof. Dr. Rüdiger Wittig

Zweiter Gutachter: ....Prof. Dr. Oliver Tackenberg

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Chapter 1

General Introduction and Scope

1.1 General Introduction

Savannas cover about one third of the world's land surface and are defined as tropical or near-tropical seasonal vegetation with a continuous, often grass-dominated herbaceous layer and a significant but, discontinuous layer of trees and shrubs (Huntley & Walker 1982, Skarpe 1991, Shorrocks 2007). An important trait in savanna ecosystems is the high degree of spatial and temporal dynamics driven by a complex web of environmental factors, modifying the structure and functioning of these ecosystems (Skarpe 1991, Scholes & Archer 1997, Higgins et al. 1999). The ratio between grasses and woody plants varies between savanna types and is the consequence of several interacting factors including climate (mean annual precipitation), soil properties, fire and herbivory (Huntley & Walker 1982, Scholes & Archer 1997, Bond 2008, Sankaran et al. 2008). The importance of different processes in regulating woody cover may vary in different savanna regions; however, mean annual precipitation is the primary determinant of woody cover controlling grass production (Higgins et al. 2000, Sankaran et al. 2004, Midgley et al. 2010). Mean annual rainfall determines the variation in the frequency of recruitment events (seedling to adult transition), the ratio of non-reproductive to adult stems and the stem densities (Burgman & Lamont 1992, Wiegand et al. 1995); these differences are best explained by examining the mean and variance in rates of establishment seed to seedling transition), recruitment and mortality (Higgins et al. 2000). While different types of savannas are determined by the above-mentioned interacting factors, many savannas are also continuously modified by human land use practices over the millennia (Bourliere & Hadley 1983, Skarpe 1991, Higgins et al. 1999, Wittig et al. 2007).

1.2 Human land use in West-African savannas

Savanna regions in West Africa are valuable cultural landscapes and provide a wide range of ecosystem services for human benefit. Human land use involves the management and modification of natural environment with the intention to obtain products and benefits through using land resources, such as crop production, animal husbandry and harvesting of natural resources (plants and game) (Mücher et al. 1993, Turner & Meyer 1994, Mvawu & Witkowski 2008). Land use changes the structure and functioning of savannas, leading to changes in land cover, which is the ecological state and physical appearance of the land surface reflecting interactions between the natural environment (especially vegetation) and its use (Skarpe 1991, Turner & Meyer 1994, Higgins et al. 1999, Gong et al. 2009).

In West Africa, the most common agricultural system is shifting cultivation in which a patch of land is cleared, followed by several years of crop production until the soil loses fertility (Ruthenberg 1980, FAO 1983, Okigbo 1985, Alexandre & Kaïré 2001). Once the land becomes inadequate for crop production, it is abandoned for several years until the soil regains its fertility and is often reclaimed by natural vegetation. By shifting cultivation, a typical example of a savanna landscape in West Africa represents an alternating mosaic of croplands, fallows and non-arable land. Aside from agricultural activities, harvesting of timber and non-timber forest products (NTFP) is crucial for household income, alimentation and medicinal purposes (Kéré 1998, Krohmer et al. 2006, Heubach et al. 2011, Sieglstetter et al. 2011). NTFPs include any products other than timber (e.g., fruits, seeds, bark and leaves) derived from savannas, woodlands or agroforestry systems (Chandrasekharan 1995, FAO 1999). To maintain these important ecosystem services, some frequently used tree species are protected when land is cleared for agriculture (Nye & Greenland 1960, Boffa 1999, Petit 2003, Augusseau et al. 2006). These species are of high local and regional value for the human population. The most important are the shea tree (*Vitellaria paradoxa* C.F.Gaertn.), the baobab (*Adansonia digitata* L.), and the locust bean tree (*Parkia biglobosa* (Jacq.) R.Br. ex G.Don) and the tamarind (*Tamarindus indica* L.).

An integral part of land use is extensive livestock breeding of both cattle and small ruminants such as goats and sheep. Mixed livestock, in herds of different size, rotationally graze during the day, affecting all land-cover types by grazing and trampling. Intense and repeated livestock grazing may cause a decrease in perennial palatable species, in total production of ground cover and the replacement of relatively palatable perennial species by less palatable and annual species (Skarpe 1991). During the dry season, trees are pruned to provide additional forage for the livestock. Throughout West Africa, fire is a major determinant of vegetation cover and is widely applied in the tropics as a land management tool (Gillon 1983, Laris 2002, Goldammer & de Ronde 2004). Rural people set fires for many purposes associated with daily life. The most common reasons for fires in West Africa are related to livestock grazing and crop production. Livestock farmers often set fires at the beginning of the dry season, November and December, to initiate off-season re-growth of herbs and grasses. In the shifting cultivation system, fire plays an important role for land clearing and preparation by clearing fields of residuals at the end of the dry season in March and protecting animals through destruction of potential disease causing organisms. In the communal area, the traditional fire management creates a mosaic of burned and unburned sites (Sheuyange et al. 2005, Butz 2009); this provides safe-sites where fire and drought sensitive seedlings may persist (see Harper 1977, Zida et al. 2008, Gignoux et al. 2009). Fire increases the level of nutrients for crops by combustion of plant nutrients and prevents the replacement of the herbaceous strata by woody species (Menault 1983, Bond & van Wilgen 1996). In addition, prescribed fires are used to provide firebreaks against large-scale, extensive fires, to increase landscape and wildlife visibility or provoke tree mortality for fire wood extraction (Hough 1993, Mbow et al. 2000, Laris 2002).

Social and economic conditions in West Africa have changed dramatically during the last decades causing fragmentation and loss of habitats and biodiversity (see Descroix et al. 2009, Norris et al. 2010, Ouedraogo et al. 2010). Increasing population growth, coupled with migration, has contributed to agricultural expansion due to the growing need for arable land (Brink & Eva 2009, Norris et al. 2010). Concurrently, traditional management strategies are being replaced by a more intensive agriculture characterized by an increased use of chemical and mineral fertilizers and pesticides, the mechanization of cash crop cultivation methods (e.g., cotton and cashew) (Matson et al. 1997, Lambin et al. 2003, Baudron et al. 2009). In addition, traditional fallow periods of 15 to 20 years are shortened or omitted and hence, the time allowing vegetation and soil to naturally regenerate has decreased over the last decades (Giller et al. 1997, Hahn-Hadjali 1998, Wittig et al. 2007). The ongoing exploitation of natural resources such as wood extraction for firewood, charcoal production and construction has shown to be an important cause of savanna degradation (Kouami et al. 2009, Norris et al. 2010, FAO 2011). Aside from the negative environmental consequences, these changes also have a negative socio-economic impact. Human-induced changes in structure and functioning of savanna ecosystems, therefore, affect the type and quantity of ecosystem services produced (Higgins et al. 1999). From a socio-economic point of view, this means not only a loss of ecosystem services, but also the decline of livelihoods and of cultural values (Brink & Eva 2009, Heubach 2011).

1.3 Land use and population biology of woody plants

A population is a group of individuals belonging to the same species, living in the same geographic area at the same time. Populations have several kinds of structure: a genetic, a spatial, an age and a size structure. The size structure describes the proportion of juveniles (young, immature individuals), sub-adults and adults and is hereafter referred to as the population structure. Population biology, more specifically population dynamics, attempts to explain the origin of these different kinds of structure and understand how and why they change with time (Silvertown & Charlesworth 2007).

Human land use activities, as stated above, influence growth conditions for plants (Mwavu & Witkowski 2008) by altering various abiotic factors, such as light, nutrient availability and water supply. They are found to alter demographic parameters (e.g., germination, seedling and sapling growth, survival and mortality rates) of woody plant individuals and alter the structure and stability of populations (Guariguata & Pinard 1998, Kwit et al. 2004, Pulido & Dìaz 2005, Mendoza et al. 2009). The degree of anthropogenic disturbance varies between land-cover types, distance to settlements, and protection status.

Several studies from West Africa reported a strong influence of land use on population structures and a significant decrease in seedling population density as well as of specific reproductive tree species due to human pressure: compared to semi-natural savannas or protected areas, juveniles in communal areas such as croplands and fallows were less frequent (Kelly et al. 2004, Dhillon & Gustad 2004, Djossa et al. 2008, Fandohan et al. 2010, Schumann et al. 2010). *In situ* experimental studies from West Africa and semi-arid South Africa have revealed that seedling survival and growth are negatively affected by low soil moisture (Bognounou et al. 2010), shading (Veenendaal et al. 1995, Hood et al. 2004), temperature and nutrients (van Auken & Bush 1998, Kraaij et al. 2006, Staver et al. 2009, van der Waal et al. 2011), all of which affect population densities. In addition, due to the ongoing changes in both land usage and cultivation techniques, regeneration niches are reduced. Aside from the impact of land use on seedlings and saplings, the removal of medium-sized stems and of large reproductive trees may lead to a lack of sub-adults in the larger stem diameter classes, reducing seed availability leading to a decrease in tree regeneration resulting in a substantial decline in population numbers (Plumptre 1995, Makana & Thomas 2006, McLaren et al. 2005). However, some of these studies also report a partially higher density of juveniles and mature woody plants in communal areas (e.g., croplands and fallows) compared to semi-natural savannas or protected areas (e.g., Boffa 1999, Petit

2003, Augusseau et al. 2006, Ky-Dembele et al. 2007, Pare et al. 2009, Nacoulma et al. 2011, Schumann et al. 2011). Due to the immediate value of the NTFPs of woody plants, both immature and mature individuals of some species are protected while land is cleared or prepared for agricultural production. Some of these species are well adapted to the alternating cycle of cultivation and fallows and their populations are in a healthy state, showing a high number of juvenile individuals and a gradual decline with increasing stem diameter. All these studies corroborate the impact of human land use on woody plant population in West African savannas. However, the results of the studies mentioned above contradict, but also indicate apparent species-specific differences in their performance in relation to land use. Other studies addressing a large number of woody species are rather scarce, which highlights the need for further research on population structure for multiple species.

Livestock grazing and browsing may influence reproductive output by decreasing flowering or seed-set due to consumption or damage of juveniles by trampling (Milton 1995a, Todd & Hoffmann 1999, Goheen et al. 2007). However, after the seedling and sapling stage, where woody plants are sensitive to environmental conditions and natural and human-induced disturbances, browsing was reported to have a very low impact on individual tree mortality and thus, total density, unless other conditions such as drought and fire arose, or in cases where the livestock densities were very high (Milton 1994, 1995b, Midoko-Iponga et al. 2005, Zida et al. 2008). Repeated shoot dieback due to herbivory is a more common phenomenon reducing growth rates, and thus the development of a young plant into a reproductive adult (Ky-Dembele et al. 2007, Midgley et al. 2010). Whether a young plant will develop into a reproductive adult depends on its species-specific ability to persist in one stage and to re-develop after adverse environmental conditions or repeated disturbances either by resistant above-ground structures or the re-sprouting organs ("the persistence niche"; Bellingham & Sparrow 2000, Bond & Midgley 2001, 2003). Young savanna woody plants can persist in a quasi-permanent stage for several years without a notable increase in plant height, while still showing a distinct increase in stem diameter (Bond & van Wilgen 1996, Higgins et al. 2000, Nzunda et al. 2008). The escape of suppressed juveniles from the persistence stage to the adult population strongly depends on stem growth rates and the frequency and intensity of fire (Trollope 1984). Thus, studies of survival and diameter growth in relation to human impacts are required to evaluate the consequences of growing land-use pressures on the dynamics of the seedlings and saplings of savanna woody plants.

The negative impacts of human-induced disturbances on woody plant populations appear to have been counterbalanced by some positive effects increasing the probability of woody plant seedling establishment in numerous ways. Grazing of domestic livestock disperses woody plant seeds and increases seed processing (Reid & Ellis 1995, Brown & Archer 1989, 1999, Razanamandranto et al. 2004). By preferential utilization of grasses, livestock affects competitive interactions between young woody plants and grasses reducing intra- and inter-specific plant competition for light, water and nutrients, changing growth rates, morphology, and resource allocation (Bush & Van Auken 1995, Kelly et al. 2004, Dhillon & Gustad 2004, Djossa et al. 2008, Staver et al. 2009, van der Waal et al. 2011). Moreover, grazing reduces fire frequency and intensity by changing ground-level biomass, which then has an impact on tree growth and demography (e.g., Walker et al. 1981; van Langenvelde et al. 2003, Werner 2005; Werner et al. 2006, Goheen et al. 2007). The presence of a dense grass cover provides a high amount of flammable biomass, supporting more frequent and high intensity fires (e.g., Scholes & Archer 1997, Higgins et al. 2000, Sankaran et al. 2008,). Variation in fire intensity can be attributed to changes in standing crop biomass, plant moisture content (which varies with species and season), air temperature, humidity and wind speed. Spatial variation in fire intensity may be due to patchy biomass production and erratic herbivory patterns (Higgins et al. 2000). The death of the aerial biomass caused by fire (top kill) maintains woody plants in suppressed, non-reproductive size classes and can reduce the availability of seeds (Hoffmann 1998, 2003, Midgley et al. 2010). Some studies reported a strong influence of annual early fire on dynamics of sapling population; i.e., it significantly reduced species richness, density of saplings and slowed the growth rates of saplings down (Zida et al. 2007, Staver et al. 2009). However, a few studies have shown that fires tend to have only slightly negative effects and, in some cases, positive effects on the total seedling density by affecting the competitive interaction between young woody plants and grasses found in high moisture soil (see Zida et al. 2008). All these findings show that human activities (timber harvesting, fire and extensive livestock grazing) can have both negative and positive effects on woody plant populations. Compared to protected areas, some species tend to develop better in communal areas. The performance of each species must be determined on a case-by-case basis due to the large variability of the impact of human-induced disturbances on woody plant populations

1.4 Scope and outline of this thesis

In the context of land-use changes, studies from West Africa on the current state of woody plant populations have increased during the last years. Several studies showed a long-term change in population structure due to a combination of factors, such as drought-induced establishment failures (Teklehaimanot 2004, Djossa et al. 2008), insufficient management activities (Etejere et al. 1982, Boffa 1999, Byakagaba et al. 2011) and excessive land use change (Kelly et al. 2004, Brink & Eva 2009, Norris et al. 2010). Local knowledge indicates that many species have decreased in numbers, with some species becoming extinct over the last three decades (Wezel & Lykke 2006). Due to increasing habitat loss, the shortening of fallow periods, and over-grazing, diverse sites for woody plants are becoming diminished. The impact of human land use on woody plant populations in West African savannas is known only for a few species (e.g., *Vitellaria paradoxa*, *Adansonia digitata* and *Tamarindus indica*), whereas other studies addressed multiple species, but did not link the observed population structures with each other. In particular, the seedling and sapling stages represent a demographic bottleneck for plant populations as they are sensitive to land use and habitat conditions. Human land-use activities specifically modify demographic parameters such as seedling and sapling growth and mortality rates (Guariguata & Pinard 1998) and may limit the survival and growth of young plants, influencing the demographic structure and stability of a population (Fensham & Bowman 1992, Gurevitch et al. 2006, Silvertown & Charlesworth 2007). Thus, studies of population dynamics in relation to human impact are absolutely required to evaluate the consequences of increasing land-use pressures on the dynamics of the seedlings and saplings of savanna woody plants.

This study was carried out near Sampeto village, located in the northern part of Benin in the periphery of the trans-boundary W National Park (Fig. 1). The communal area of the village represents a typical savanna landscape in West Africa with an alternating mosaic of croplands, fallows and non-arable land. Because the location is at the periphery of a national park (W National Park), it was also possible to study the influence of reduced land use pressure in the buffer zone of the park. Thus, I was able to determine the population structure and population dynamics of woody species that were less altered by human impacts under semi-natural conditions in comparison to the patterns in communal areas. All single studies presented in this thesis were performed in three land-cover types: (1) tree and shrub savanna on shallow skeletal soils without prior cultivation (hereafter referred to as “non-arable”); (2) tree and shrub savanna on poor to moderately fertile previously cultivated soils (at least ten years prior to the study, different crops; hereafter referred to as “fallows”); and (3) semi-natural tree and shrub savanna on medium soils. This land-cover type can only be found in the buffer zone of the W National Park; thus, we will refer to it as the “buffer zone”. In contrast, non-arable and fallow sites were studied in the communal area.

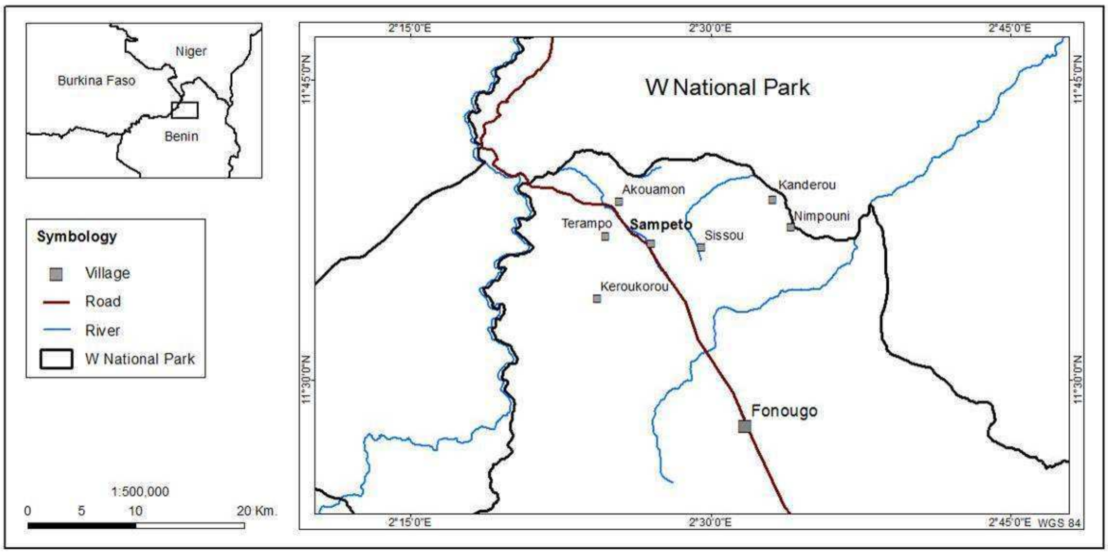

Fig. 1: Study area (UTM zone 31 North, WGS 84).

The first study (**chapter 2**) compares population structures by size-class distribution of 30 woody species common in West African savanna ecosystems across different land-cover types. By using generalized linear models, I separately analyzed the size-class distribution of the study species to reveal the influence of land use on population structures and to identify comparable population structures of species with similar ecological preferences. The results of this study help to understand population structures of common savanna woody species that are affected by human-induced disturbances.

The following two studies cover the impact of land use and habitat conditions on seedling and saplings in natural populations. In **chapter 3**, I estimated these effects on the survival and growth rates of a broad set of characteristic savanna species in natural populations using repeated measurements in permanent plots. I applied multistate capture-recapture models as this method allows a thorough analysis of the data. With this study, differences in population turnover and growth rates and the effects on size-class patterning was elaborated. In **chapter 4**, I investigated patterns of juvenile densities in relation to land use and environmental parameters such as soil properties and vegetation structure. The results describe how human land use affects the density of woody species seedlings and saplings by altering the state of the physical, chemical, and biological characteristics of the land.

Chapter 2

Population Structure of Woody Plants in Relation to Land Use in a semi-arid Savanna, West Africa

with Karen Hahn, Rüdiger Wittig and Markus Bernhardt-Römermann

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Indigenous woody species are important natural resources in West African savannas. Information about their population structures and response to human impact, particularly land use, however, is scarce. In this study we explored: (1) the effect of land use on the population structure of woody savanna species; and (2) searched for species with similar population structures related to comparable ecological preferences.

Using generalized linear models, we separately analyzed the size-class distribution (SCD) of 30 species to reveal the influence of three land-cover types (non-arable land, fallows, and protected areas) on population structures. Generalized linear models were applied to identify comparable population structures of species with similar ecological preferences.

We were able to identify five groups for shrub species and four groups for tree species with different population structures and comparable ecological preferences. In terms of human impact, we detected four groups of species responding similarly to land use. Especially for trees we found a strong influence of local land use on SCD and hence, population structures. The SCD of shrub species tend to be more related to species' ecological preferences. Some of the shrub species may be characterized as ubiquitous species as their SCD is neither related to land use nor ecological preferences, indicating a high tolerance to disturbance. The observed results have implications on local woody species composition in relation to land use. According to this, we propose focusing on trees when developing appropriate local land use management strategies.

* Population Structure of Woody Plants in Relation to Land Use in a semi-arid Savanna, West Africa. Katrin Jurisch, Karen Hahn, Rüdiger Wittig, and Markus Bernhardt-Römermann (2012). *Biotropica* 44(6): 744-751. Copyright© 2000-2012 by John Wiley & Sons, Inc., Wiley-Blackwell.

2.1 Introduction

Savanna regions in West Africa are valuable cultural landscapes and provide a wide range of ecosystem services for human well-being. Besides agricultural activities, harvesting of timber and non-timber forest products (NTFP) is crucial for household income, alimentation and medicinal purposes (Krohmer et al. 2006, Avocèvou-Ayisso et al. 2009, Vodouhe et al. 2009). To maintain these important ecosystem services, some frequently used tree species are protected when land is cleared for agriculture (Boffa 1999, Petit 2003, Augusseau et al. 2006). Most indigenous woody species, however, are affected by high anthropogenic pressure. Social and economic conditions have changed dramatically during the last decades (see Descroix et al. 2009, Norris et al. 2010, Ouedraogo et al. 2010, for detailed studies), causing habitat fragmentation and disturbance. The ongoing exploitation of natural resources affects the population structure, *i.e.* the proportions of juveniles (young, immature individuals), sub-adults, and adults, and effect that is more pronounced among woody plants that have long generation times (Grime 2002).

Woody cover in savannas is determined mainly by nutrient availability, water supply, frequency of fires and herbivory (Scholes & Archer 1997, Bond 2008). In settlement areas, agricultural land use and selective logging, along with harvesting of NTFPs, also affect the performance of plant species. The degree of anthropogenic disturbance varies between land-cover types, distance to settlements, and protection status.

The impact of human land use on population structures in West African savannas is known only for a few woody species. Most of these species are of high local and regional value for the human population, including the shea tree (*Vitellaria paradoxa*; Kelly et al. 2004, Djossa et al. 2008), the baobab (*Adansonia digitata*; Dhillon & Gustad 2004, Schumann et al. 2010) and the tamarind (*Tamarindus indica*; Fandohan et al. 2010). These studies reported a strong influence of land use on population structures: juveniles in communal areas (*e.g.*, croplands) were less frequent compared to semi-natural savannas or protected areas. Higher densities of large trees were, however, found in communal areas as many mature trees are maintained due to the immediate value of their NTFPs for the rural community. Other studies addressed multiple species, but did not relate the observed population structures to each other (*e.g.*, Sokpon & Biaou 2002, Kindt et al. 2008, Mwavu & Witkowski 2009). The present study seeks to compare population structures of a large number of woody savanna species across different land-cover types in northern Benin.

We described population structures by size-class distribution. We expected the extent to which species respond to frequent human-caused or natural disturbances is affected by environmental conditions (Bissels et al. 2004, Poschlod et al. 2011). The detected patterns are discussed in relation to the species' ecological preferences, which refer to the environmental conditions under which the species is most likely to occur. We aim to answer two questions: (1) How are the population structures of woody savanna species affected by land use? (2) Can we identify comparable population structures of species with similar ecological preferences?

2.2 Methods

Study site

The study was carried out around Sampeto village (11°40′–12°23′ N and 2°04′–3°05′ E) located in the northern part of Benin in the periphery of the trans-boundary W National Park, one of the largest protected areas in West Africa. Sampeto had 1500 inhabitants in 2002 (INSAE 2002), although this number has most likely increased since the last census. The area belongs to the North-Sudanian vegetation zone, characterized by a semi-arid climate with an average precipitation of 700–1000 mm and a six-month rainy season from May to October (Bonou 2008).

All field data were collected in the surroundings of Sampeto (in maximal distance of 10 km). The communal area of the village represents a typical example of a savanna landscape in West Africa with an alternating mosaic of croplands, fallows and non-arable land. Due to the location in the periphery of a national park (W National Park) we could also study the influence of reduced land use pressure in the buffer zone. Thus, we were able to determine population structures of woody species less altered by human impact under semi-natural conditions in comparison to the population structure in communal areas.

An integral part of land use is extensive livestock breeding of both cattle and small ruminants like goats and sheep. Mixed livestock in herds of different size is rotationally grazed during the day affecting all land-cover types by grazing and trampling. The buffer zone is mainly grazed by cattle, but generally less altered by livestock grazing activities compared to the communal area.

Harvesting of NTFPs for firewood (*e.g.*, *Detarium microcarpum, Crossopteryx febrifuga*), medical purposes (*e.g.*, *Annona senegalensis*) or livestock forage (*e.g.*, *Pterocarpus erinaceus, Philenoptera laxiflora*) is common in the settlement area. In the buffer zone, these activities are limited by law, but illegal timber extraction occurs, especially of *Isoberlinia doka*, *Afzelia africana* and *Khaya senegalensis*. Fires are set by the farmers once or twice during the dry season to support the re-growth of palatable forbs and grasses to protect against extensive fires. In the buffer zone, early fires are set for management purposes at the beginning of the dry season. The fire density (the number of fires per 1000 ha detected over a given period of time) is approximately the same in the buffer zone and the adjacent communal area (SUN 2010, unpubl. data).

Three land-cover types were studied: (1) tree and shrub savanna on shallow skeletal soils without prior cultivation, but with frequent use of NTFPs and as pasture (hereafter referred to as ‘non-arable’); (2) tree and shrub savanna on poor to medium, previously cultivated soils (at least 10 yr ago, with different crops), frequent use of NTFPs and as pasture (hereafter referred to as ‘fallow’); and (3) semi-natural tree and shrub savanna on medium soils where use of natural resources is limited by law (hereafter referred to as ‘buffer zone’). The latter is located in the buffer zone of the W National Park, while the first two land-cover types can be found in the communal area. Fallows and non-arable land are exposed to similar disturbance intensities (fire, grazing, harvesting) and are freely accessible.

Data collection

Plants were sampled from May to July in 2008 and from May to July in 2009. Each land-cover type was characterized by at least 20 randomly selected study plots (non-arable = 23, fallows = 20, buffer zone = 21). To examine the population structure of trees and shrubs, squared plots of two sizes were established at each study site. Adult individuals were sampled on 1800 m^2 plots, while juveniles were determined on four 6.25 m^2 nested sub-plots. Juveniles were recorded individually, so we were able to distinguish between established individuals and new recruits. For our analysis we only chose individuals that were present at the end of the dry season and at the end of the rainy season in 2009.

We analyzed trees and shrubs separately. Trees were defined as single-stemmed individuals branched above breast height (130 cm). Shrubs were shorter than 10 m in height and either with several straight stems, visibly connected at ground level or one single trunk with attached branches below breast height (Powell 2005, Nzunda *et al.* 2007).

Biometric data for sub-adults and adults with diameter at breast height (dbh) of more than 5 cm were collected, measuring dbh (cm) and height (m). For all juveniles with dbh of less than 5 cm, we measured basal diameter (cm) and height (cm). For multi-stemmed individuals all stems with dbh larger than 5 cm were measured. According to Pretzsch (2002) we used the equation $\sqrt{(\sum d_i^2)}$ to reduce multiple diameter of a multi-stemmed individual to a single composite measurement in order to be able to compare it with those of single-stemmed trees.

Data analysis

We characterized population structures by diameter size-class distribution separately for each land-cover type and species. For further analyses, only species occurring with more than ten individuals in total on all sampled plots were included. A list of species with less than ten individuals in total is available in Table S1.

For trees, we defined nine regular 5 cm-wide classes ranging from 0 to > 40 cm in width. Shrubs were grouped into five classes on a 4 cm scale from 0 to > 20 cm. We used the finer scale for shrubs because their mean stem diameter is generally lower in comparison to stem diameters of trees. To analyze if a population has good regeneration relative to the number of adult trees, we calculated the ratio between juveniles (trees: dbh < 5 cm, shrubs: < 4 cm) to sub-adults (trees: dbh 5- < 15 cm, shrubs: dbh 4- < 12 cm) and sub-adults to adults (trees: dbh > 15 cm. shrubs: dbh > 12 cm).

As a proxy for species' performance in relation to land use, we described population structures using their size-class distributions. A regenerating population should have a large number of juvenile individuals. We describe the population structures using untransformed data (numbers per size class) with generalized linear models (GLM). We used GLMs of the 'Gamma' family as this error best described the distribution of the residuals. The statistical analyses aimed (i) to identify species with similar size-class distributions, and (ii) to analyze the influence of land use on population structures for single species. For the first objective we divided trees and shrubs and fitted the maximal model with number of individuals as dependent variable, and size class (numerical) and species names (factor) as explanatory variables. This model was simplified by merging species showing no significant differences in the estimators for intercepts and slopes (tested by ANOVA; for details on this procedure compare Crawley 2007). Our minimal adequate model contained groups of species with similar behavior and size-class distribution. With this procedure, it was possible to identify which species do not significantly differ in size-class distribution (irrespective of land use). Only samples of those land-cover types were included where size classes of a given species were well distributed. For this purpose, we plotted the number of individuals per size class for each species.

We also sought to identify differences between land-cover types (second objective). A maximum GLM was fitted for each species using the number of individuals as dependent variable, and size class (numerical) and land-cover type (factor) as explanatory variables. The minimal adequate model was found by merging non different land-cover types (compare above). Based on their minimal adequate models, we assigned each tree and shrub species to a certain group. As an example, two species that showed no statistical differences in size-class distribution between all three land-cover types would be grouped together even though the size-class distribution of two species might differ. All statistical analyses were done in R 2.11.1 (R Development Core Team 2010).

2.3 Results

Differences in population structure between species

In total, we included 18 shrub and 12 tree species in our analysis. Using GLMs we searched for groups of species with comparable population structures. Irrespective of land-cover type we found five statistically different groups of shrub species (S1-S5), each containing members with similar size-class distribution (Table 1, Fig. S1). The GLM results are available in Table S2.

Detarium microcarpum was the only member of S1. This species had a high density of juveniles which was abruptly reduced in the sub-adult stage (juveniles: > 6500/ha, sub-adults: > 80/ha). In all diameter classes of the sub-adult stage (dbh 4- < 12 cm), similar numbers of individuals were present; with increasing diameter in the adult size classes, individual numbers declined gradually (dbh 12- > 20 cm). The second group (S2) contained the following six shrub species, having comparable size-class distributions: *Annona senegalensis*, *Combretum glutinosum*, *Crossopteryx febrifuga*, *Piliostigma thonningii*, and *Strychnos spinosa*. For this group, there was an obvious decrease in individuals’ density from the juvenile to the sub-adult stage, followed by a continuous decline in numbers of individuals with increasing size classes; these species had in general fewer juveniles and a smaller sub-adult to adult ratio compared to S1 (Table 1). Species of group S3 (*Combretum collinum*, *C. nigricans*, *Feretia apodanthera*, *Gardenia aqualla*, and *G. erubescens*) had a higher juveniles to sub-adult ratio compared to S2, but a smaller sub-adult to adult ratio (Table 1).

Table 1 Shrub species with similar size-class distribution. Also presented are the mean (± S.E.) of the density [ha] per affiliation group of shrubs, divided according to their development stage: juveniles, sub-adult and adult. The groups’ mean ratios of juveniles to sub-adults, and of sub-adults to adults, are shown.

Group	Species	Juveniles	Sub-adults	Adults	Juveniles : Sub-adults	Sub-adults : Adults
S1	*Detarium microcarpum*	6556.5 ± 0.0	83.7 ± 0.0	18.1 ± 0.0	135.1 ± 0.0	8.0 ± 0.0
S2	*Annona senegalensis, Combretum glutinosum, Combretum molle, Crossopteryx febrifuga, Piliostigma thonningii, Strychnos spinosa*	680.5 ± 109.8	18.9 ± 1.7	2.8 ± 0.6	53.3 ± 11.7	6.5 ± 0.9
S3	*Combretum collinum, Combretum nigricans, Feretia apodanthera, Gardenia aqualla, Gardenia erubescens*	826.2 ± 218.5	7.1 ± 1.8	0.8 ± 0.2	134.9 ± 40.0	4.9 ± 0.9
S4	*Dichrostachys cinerea, Diospyros mespiliformis, Hexalobus monopetalus, Pteleopsis suberosa*	1857.1 ± 783.3	2.2 ± 1.4	0.4 ± 0.2	633.6 ± 201.0	1.7 ± 1.0
S5	*Bridelia ferruginea, Gardenia ternifolia*	75.1 ± 66.1	1.3 ± 0.8	0.1 ± 0.1	28.5 ± 22.2	2.6 ± 1.1

For species of group S3, individuals in the largest diameter classes (dbh > 16 cm) were absent. A very high juveniles to sub-adult ratio, in combination with very low numbers of individuals in the sub-adult and adult diameter classes, was typical for species belonging to group S4 (*Dichrostachys cinerea*, *Diospyros mespiliformis*, *Hexalobus monopetalus*, and *Pteleopsis suberosa*). Aside from group S1, we found the highest number of juveniles in group S4 whose density was reduced in the sub-adult stage. For S4 the sub-adult to adult ratio was close to one, indicating approximately equal numbers of individuals in both stages. Group S5 contained two species only (*Bridelia ferruginea* and *Gardenia ternifolia*) with low density of juveniles per hectare and a lack of individuals in several size classes (Fig. S1).

For trees, we detected four groups of species (T1-T4), each containing species with similar size-class distributions (Table 2, Fig. S2). The GLM results are available in Table S3. *Anogeissus leiocarpa* and *Vitellaria paradoxa*, forming group T1, had large numbers of individuals in the juvenile stage compared to the groups T2, T3 and T4 (Table 2). The species' size-class distributions were characterized by an abrupt decrease from the juvenile to the sub-adult stage (juveniles: > 1200/ha, sub-adults: > 9/ha). This followed a slight decrease in individual numbers with increasing dbh expressed by a sub-adult to adult ratio greater than one, indicating more individuals in the adult stage compared to the sub-adult stage (Table 2). The species of group T2 (*Burkea africana*, *Isoberlinia doka*, *Lannea acida*, and *Pericopsis laxiflora*) had fewer individuals in the medium and large diameter classes compared to group T1 (dbh > 5 cm). The density of individuals per hectare was clearly reduced in the sub-adult stage compared to the juvenile stage; the sub-adult to adult ratio was close to one, indicating approximately equal numbers of individuals in the sub-adult and adult stage (Table 2).

Table 2 Tree species with similar size-class distribution. Also presented are the mean (± S.E.) of the density [ha] per affiliation group of trees, divided according to their development stage: juveniles, sub-adult and adult. The groups' mean ratios of juveniles to sub-adults, and of sub-adults to adults, are shown.

Group	Species	Juveniles	Sub-adults	Adults	Juveniles : Sub-adults	Sub-adults :Adults
T1	*Anogeissus leiocarpa, Vitellaria paradoxa*	1271.8 ± 340.4	9.4 ± 1.5	1.9 ± 0.5	150.6 ± 52.1	3.1 ± 0.4
T2	*Burkea africana, Isoberlinia doka, Lannea acida, Pericopsis laxiflora, Prosopis africana, Terminalia avicennioides, Xeroderris stuhlmannii*	429.3 ± 127.3	4.3 ± 1.3	1.2 ± 0.3	99.0 ± 22.3	2.7 ± 0.9
T3	*Pterocarpus erinaceus*	382.6 ± 0.0	0.2 ± 0.0	0.3 ± 0.0	216.7 ± 0.0	-
T4	*Philenoptera laxiflora, Stereospermum kunthianum*	824.8 ± 48.2	0.6 ± 0.1	0.1 ± 0.2	500.8 ± 48.2	0.4 ± 0.0

The species of group T3 (*Pterocarpus erinaceus*) and T4 (*Philenoptera laxiflora* and *Stereospermum kunthianum*) had high recruitment rates, while sub-adults and adults rarely occurred. Species of group T3 had more individuals in the adult stage in comparison to the sub-adults, whereas species of group T4 have slightly more individuals in the sub-adult size classes and lower numbers of adults (Table 2).

Differences in population structure between land-cover types

We detected four groups of species (A–D). All species of one group responded similarly to land use (Table S4; Fig. S3 A–D; size-class distributions of all species are available in Fig. S4). The largest group was group A (eight shrubs and six trees) containing species showing no influence of land use on size-class distributions. For species of group B no differences were found between non-arable land and fallows, but they differed from the buffer zone. Group C comprised shrub and tree species with similar size-class distributions on non-arable land and in the buffer zone, which differed from those on fallows. Species of group D (three shrubs) differed significantly in size-class distribution between all land-cover types.

2.4 Discussion

Differences in population structure between species

For trees and shrubs we detected groups of species with different size-class distributions. The populations of species assigned to group S1 and group T1 (*Detarium microcarpum*, *Vitellaria paradoxa,* and *Anogeissus leiocarpa*) are in a healthy state, showing well-shaped size-class distributions with high numbers of juveniles and a gradual decline with increasing stem diameter. The observed high juvenile numbers, however, might be explained by different factors according to species-specific properties. For the shrub *Detarium microcarpum* high numbers of juveniles are probably due to its good regeneration capacities by re-sprouting via root suckers (Rietkerk et al. 1998, Bationo et al. 2001, Bellefontaine 2005); the species is well adapted to shallow skeletal and sandy soils (Arbonnier 2002, Vautier et al. 2007b; Table 3), where its competitive strength is enhanced by its ability for vegetative reproduction. In contrast to our results, Ouedraogo (2006) described populations of *D. microcarpum* as disturbance-intolerant indicated by a lack of establishment in shrub savannas of the North-Sudanian zone of Burkina Faso, although he studied dryer conditions where *D. microcarpum* is at its northern distribution limit and may perform worse. *Vitellaria paradoxa,* the shea tree, is facilitated by traditionally managed agro-forestry systems. This tree has a high socioeconomic importance and is spared when woodland is cleared for agriculture (individuals of all diameter classes are often maintained on fallows and non-arable sites; Lovett & Haq 2000). Large numbers of seedlings result from a high production of fruits, assuming that seeds are not removed by humans or animals (Makana & Thomas 2006). Other studies, however, reported a long-term change of population structure of the shea tree due to establishment failures and insufficient management activities (Boffa 1999, Teklehaimanot 2004, Djossa et al. 2008, Byakagaba et al. 2011). Human land-use influences growing conditions for species (Mwavu & Witkowski 2008) and might facilitate or hinder the development of individuals. For example, a pioneer species like *Anogeissus leiocarpa*, whose seeds primarily germinate on bare soils, is favored on fallows (Sacande & Sanogo 2007, Bognounou et al. 2010) compared to sites with a dense vegetation cover.

Tree species of group T2 (*e.g.*, *Burkea africana*, *Isoberlinia doka,* and *Lannea acida*), T3 and T4 (*e.g.*, *Pterocarpus erinaceus* and *Philenoptera laxiflora*) had high juveniles to sub-adult ratios, but the ratio between sub-adults and adults indicates a lack of sub-adults in the larger diameter classes. Such pattern might be related to rural people's preference to use medium-sized stems' as construction material (see Obiri et al. 2002*,* Gwali et al. 2010). Thus, for frequently used species, gaps in medium and large diameter classes do not necessarily indicate recruitment failures (Condit et al.

1998, Pulido et al. 2001). In untouched populations, non-occupied diameter classes might be caused by strong environmental filtering resulting in longer-term fluctuations in population dynamics (McLaren *et al*. 2005). Such population responses might be triggered by periods of environmental conditions not allowing the establishment of juveniles, or repeated disturbances (*e.g.*, fire, browsing) damaging tree seedlings and saplings. If re-sprouting is possible, plant individuals may persist as juveniles for many years (Bond & van Wilgen 1996, Higgins et al. 2000, Bond & Midgley 2001). The escape of suppressed juveniles from the persistence stage to the adult population strongly depends on stem growth rates and the frequency and intensity of fire (Trollope 1984).

For shrub species of group S3, S4 and S5, such as *Combretum collinum* and *Diospyros mespiliformis*, we recorded very small numbers of individuals in large diameter classes. This is partly due to the exploitation of appropriate individuals for firewood (*e.g.*, *Combretum collinum*, *Gardenia erubescens,* both S3), and partly due to the species inherently limits to a maximum diameter size (*e.g.*, *Dichrostachys cinerea* (S4), *Gardenia aqualla* (S3), and *Pteleopsis suberosa* (S4)). Species like *Gardenia ternifolia* (S5), *Stereospermum kunthianum* (T4) and *Xeroderris stuhlmannii* (T2) have a scattered distribution by nature (Arbonnier 2002; Table 3), which might result in an under-representation of the larger diameter classes. Other species show explicit habitat preferences like, for example, *Feretia apodanthera* (S3) and *Diospyros mespiliformis* (S4), which are often found on termite mounds or in (gallery) forests (Lawesson 1990, Ellery et al. 1993, Hovestadt et al. 1999; Table 3).

Differences in population structure between land-cover types

Our results document that land-cover type influenced size-class distribution to some extent, but did not affect the population structure of a majority of the studied species. Some species, such as *Combretum molle*, *Piliostigma thonningii* and *Strychnos spinosa* showed a well-shaped size-class distribution with high recruitment rates, regardless of land-cover type (group A). The mentioned species are not site-specific, partly invasive and show wide ecological amplitudes (Arbonnier 2002; Table 3); they can be characterized as ubiquitous. The ability to tolerate coppicing and to reproduce vegetatively, as well as the presence of fire resistance traits, enhance the competitive strength of ubiquitous species and allow their persistence (see Lavorel et al. 1997, Bond & Midgley 2001, Devineau & Fournier 2005, Drobnik et al. 2011). In contrast to these species, the juvenile numbers of the other species of group A vary, and gaps of diameter classes in the sub-adult and adult stages occur. For *Pterocarpus erinaceus* and *Philenoptera laxiflora* we observed high recruitment and low numbers of individuals in the larger diameter classes. For *P. erinaceus* this corresponds to the findings of Lykke (1998), Ouedraogo (2006), and Glèlè Kakaï *et al.* (2009), where the small numbers of individuals in the sub-adult and adult diameter classes were clearly human-caused. Both *P. erinaceus* and *P. laxiflora* are two of the five most important fodder tree species in the study area (L. Houessou, pers. comm.). They are pruned to provide additional forage for the livestock during the dry season, and some small stems are even cut down. The wood of these species is also used as construction material (Arbonnier 2002) resulting in the removal of large reproductive trees. This can reduce the availability of seeds and might reduce regeneration potential. The affiliation to group A indicates similar overall harvesting pressure across the species, which is likely to increase in protected areas following further resource depletion and land use change in communal areas (Luoga et al. 2002, Mwavu & Witkowski 2008).

The size-class distribution of species assigned to group B (population structures in the buffer zone differing from non-arable land and fallows) is an expression both of protection efforts and ecological processes. Protection by law has noticeable effects on plant populations, especially when they are harvested for timber or firewood. The timber tree *Isoberlinia doka* had more individuals with large dbh in the buffer zone where cutting is prohibited. In contrast, large stems were missing on non-arable land and fallows. For all other species of group B, however, recruitment was lower in the buffer zone compared to the communal area. We explain this unexpected pattern by the composition of the herb layer in the buffer zone, which is composed of tall bunch grasses. These may shade out juvenile woody plants; the presence of plants growing in the surrounding of a young plant individual affect its survival and growth performance by limiting light and water supply (Harper 1977). In communal areas, palatable tall perennial grasses are widely absent due to intensive livestock grazing that reduces ground-level biomass (Midgley et al. 2010). Additionally, in the buffer zone seedlings and saplings are more affected by fire, as the presence of tall grasses provides a high amount of inflammable biomass. In the communal area the traditional fire management creates a mosaic of burned and unburned sites (Sheuyange et al. 2005, Butz 2009); this provides safe-sites where fire and drought sensitive seedlings may persist (see Harper 1977, Zida et al. 2008, Gignoux et al. 2009). The affiliation to group B indicates a similar overall impact of natural dynamic processes such as fire, especially in the first stage of the life cycle, which lowers the number of individuals to be able to grow up in the larger stages.

Some species, such as *Annona senegalensis*, *Crossopteryx febrifuga* and *Burkea africana*, showed different size-class distributions on fallows compared to non-arable and the buffer zone (group C). In fallows we found a discontinuous decrease in the frequency of juveniles to adults indicating a failure to develop healthy population structures. These species show habitat preferences to dry rocky and split soils or rubble (Arbonnier 2002, Wilson & Witkowski 2003; Table 3). In contrast, *Anogeissus leiocarpa* displayed very high recruitment rates and slightly more individuals in the larger diameter classes on fallows compared to the other land-cover types. This example shows that often, only certain stages of the life cycle are affected by land use practices.

The species of group D contained species with size-class distributions differing between all land-cover types. We detected high recruitment numbers for all species within this group (*Detarium microcarpum*, *Combretum glutinosum*, and *Pteleopsis suberosa*) on non-arable land. *D. microcarpum* and *C. glutinosum* had high individual numbers in the larger size classes. All species seem to be less competitive on fallows or in the buffer zone indicated by low recruitment and few individuals in medium and large diameter classes. For *P. suberosa*, the medium to large diameter classes might be under-represented, owing to this species' preference for heavy and temporarily inundated soils (Arbonnier 2002; Table 3). Although Arbonnier (2002) and Vautier et al. (2007a) did not indicate any soil preferences for *C. glutinosum* (Table 3), this species performed differently in all land-cover types; thus, we suppose that land use leads to the contrasting performance pattern.

Conclusion

In this study, we used size-class distributions to reveal the dependence of population structures on land-cover types for 30 woody species common in West African savanna ecosystems. We established groups of woody plants to test if species population structures differed between land use and environment. We stressed that the size-class distributions of trees were closely related to land use, while those of shrubs depend on species' ecological preferences. Some shrubs may be characterized as ubiquitous as their size-class distribution is neither related to land use nor environment. Based on the analyses presented in Table 3, we found that tree populations are strongly affected by local land use. Species-specific management strategies are needed to allow a sustainable use of trees. In addition, more demographic studies on survival and mortality rates of populations in their natural habitat and on species-specific fertility in relation to land use are required.

Table 3 Relation of size-class distribution (SCD) of the 30 analyzed species to ecological preferences and land use. Sensitiveness is marked by plus (+), insensitiveness by minus (-). Species where we assume a specific spatial distribution were separated and referred to as “scattered”. Growth form: S: shrub, T: tree. Information on habitat requirements and species specific comments are presented.

Species	**SCD related to ecological preferences**	**SCD related to land-use**	**Distribution**	**Habitat and species-specific comments (Arbonnier 2002)**
Annona senegalensis (S)	-			on gravel, fallows
Anogeissus leiocarpa (T)	+	+		usually on loamy compact soils; tolerates temporary inundation
Bridelia ferruginea (S)	+			divers soils, fallows
Burkea africana (T)	+	+		on soft, well drained soils, also rocky hills, laterite
Combretum collinum (S)	-	+		all soil types
Combretum glutinosum (S)	-	+		all soil types; drought resistant
Combretum molle (S)	-	-		all soil types
Combretum nigricans (S)	+			prefers clayey and loamy soils; also on rocky, arenaceous, sandy soils
Crossopteryx febrifuga (S)	-	-		on rubble and grit, small rifts
Detarium microcarpum (S)	+			arenaceous, laterite; esp. on laterite and fallows
Dichrostachys cinerea (S)		+		heavy profound soils; invasive on fallows and talus
Diospyros mespiliformis (S)	+			gallery forest, riverbank, termite mounds, rocky hills
Feretia apodanthera (S)	+			termite mounds, temporary water bodies, compact soils
Gardenia aqualla (S)			scattered	shady depressions, alluvial terraces
Gardenia erubescens (S)			scattered	diverse soils
Gardenia ternifolia (S)			scattered	divers soils, compact, loamy soils, arenaceous, temporary inundated
Hexalobus monopetalus (S)	+	-		gallery forest, medium soils
Isoberlinia doka (T)		+		loamy and well drained soils, medium soils
Lannea acida (T)		+		all soil types
Pericopsis laxiflora (T)		+		on rocky soils, or laterite, poor fallows
Philenoptera laxiflora (T)	-	+		all soil types
Piliostigma thonningii (T)	-	-		all soil types; invasive on fallows, savannas and degraded forests
Prosopis africana (T)		+		esp. on sandy, .loamy soils; on old fallows
Pteleopsis suberosa (T)	-	-		silt, close to temporary water bodies, medium soils
Pterocarpus erinaceus (T)		+		all soil types, incl. laterite
Stereospermum kunthianum (S)			scattered	all soil types
Strychnos spinosa (S)	-	-		all soil types, incl. laterite and gravel
Terminalia avicennioides (T)	-	+		arenaceous soils, fallows
Vitellaria paradoxa (T)	-	+		all soil types except, inundated soils
Xeroderris stuhlmannii (T)			scattered	rocky soils, fallows

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Chapter 3

Land Use Impact on the Growth and Survival of Seedlings and Saplings in West African Savannas

with Karen Hahn, Rüdiger Wittig and Markus Bernhardt-Römermann

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In frequently disturbed habitats such as savannas, the survival of seedlings and saplings depends on the species-specific ability to persist for a long time and to re-sprout following disturbances that are damaging to individuals. This physiological ability increases with increasing stem diameter, as re-sprouting requires sufficient nutrient reserves. In this study we ask if survival and growth of seedlings and saplings of woody savanna species are related to habitat conditions and land-cover type.

For individuals of 18 common woody species less than 1m in height, basal diameter and height were repeatedly measured in five censuses from 2008 to 2010. Measurements took place in the land-cover types non-arable sites, fallows and protected areas. We used multistate capture-recapture models to estimate survival and transition probabilities between diameter classes.

We detected six groups of species with similar survival and transition probabilities. For one of these groups we found no correlation to land use whereas the other groups comprise species with distinct preferences for different land-cover types. Most species developed better in the communal area compared to the protected areas. For five species (one shrub and four trees), we detected an extremely low transition probability for the latter land-cover type.

For some species groups, differences in plant performance were explained by a human caused opening of the canopy which is beneficial for the germination of seeds and enhances the survival of juveniles by reducing the competition for light, water and nutrients. Other species showed their best demographic performance in the communal area on non-arable sites with unfavorable environmental conditions and resulting small scale heterogeneity (mosaic of bare *ground and areas with low herbaceous cover), whereas five species are likely to decline in the protected area.*

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3.1 Introduction

The savanna regions in West Africa are frequently affected by human-induced disturbances. Aside from agricultural activities (crop production and animal husbandry), the harvesting of timber and non-timber forest products is crucial for household income, alimentation and medicinal purposes (Krohmer et al. 2006; Avocèvou-Ayisso et al. 2009; Vodouhe et al. 2009). Most indigenous woody species have undergone increasing anthropogenic pressure as social and economic conditions have changed dramatically during recent decades (for detailed studies see Descroix et al. 2009; Norris et al. 2010; Ouedraogo et al. 2010), resulting in further habitat fragmentation and increased disturbance severity.

Human land-use activities influence growing conditions for plants (Mwavu & Witkowski 2008) and particularly modify demographic parameters such as germination, seedling and sapling growth and mortality rates (Guariguata & Pinard 1998). The effects of human disturbances on plant species populations are often described by changes in demographic structures. In particular, the seedling and sapling stages represent a demographic bottleneck for plant populations, as plants at these stages are sensitive to drought, soil conditions (nutrients and water), natural and human-induced disturbances (fire and herbivore activity) and biological interactions, resulting in fluctuations in population size and age structure (Abrahamson 1980; Zida 2007; Bond 2008; Prior et al. 2010). All of these factors may limit the survival and growth of young plants, influencing the demographic structure and stability of a population (Fensham & Bowman 1992; Gurevitch et al. 2006; Silvertown & Charlesworth 2007).

Whether a young plant will develop into a reproductive adult depends on its species-specific ability to persist in one stage and to re-develop after adverse environmental conditions or repeated disturbances to seedlings and saplings (Bellingham & Sparrow 2000; Bond & Midgley 2001, 2003). Young savanna woody plants can persist in a quasi-permanent stage for several years without a notable increase in plant height, while still showing a distinct increase in stem diameter (Bond & van Wilgen 1996; Higgins et al. 2000; Nzunda et al. 2008). The importance of stem diameter for the survival of seedlings and saplings was shown by Hoffmann & Solbrig (2003), who found individuals with small stem diameters experience high mortality rates. Moreover, the ability to re-sprout (given the physiological capacity of an individual) increases with the stem diameter, because re-sprouting requires sufficient resource allocation, which increases with stem diameter (Gignoux et al. 1997; Hoffmann & Solbrig 2003; Wigley et al. 2009). Thus, studies of survival and diameter growth in relation to human impacts are required to evaluate the consequences of growing land-use pressures on the dynamics of the seedlings and saplings of savanna woody plants.

The impact of human land use on the development of seedlings and saplings in West African savannas has been determined for only a few woody species by analyzing their abundance at a particular time (e.g., Ky-Dembele et al. 2007; Pare et al. 2009; Schumann et al. 2011). Such studies generally report a significant decrease in seedling population density due to human pressure, but also report a partially higher density of juveniles in communal areas, such as croplands and fallows. However, only a few studies have estimated the effect of land use and habitat type on the survival and growth rates of seedlings in natural populations using repeated measurements in permanent plots. Ouedraogo (2006) found that the survival rates of some species were significantly higher in study sites at lower latitudes in the South-Sudanian zone compared to the Sahel, due to the prolonged dry season. *In-situ* experimental studies have revealed that seedling survival and growth are negatively affected by low soil moisture (Bognounou et al. 2010) and shading (Veenendaal et al. 1995; Hood et al. 2004). However, Biaou et al. (2011) found a positive relationship between seedling survival and shading, especially under low moisture conditions. Grazing and fire tend to have a slight negative effect on the total seedling density, as shown by Zida et al. (2008). Based on these findings, we also expect to observe a significant effect of habitat conditions altered by human land use on the survival and growth of seedlings and saplings in natural populations. To study this effect, we estimated the survival and transition probability of a broad set of characteristic savanna species to obtain a better understanding of the influence of land use on the population dynamics of woody species during their most sensitive stage of life.

3.2 Methods

Study site

This study was carried out near Sampeto village (11°40'-12°23' N and 2°04'-3°05' E), located in the northern part of Benin at the periphery of the trans-boundary W National Park, one of the largest protected areas in West Africa. The W National Park was established by decree in 1937, and since 2000, through the implementation of a regional management, including the establishment of a buffer and transition zone, has been supported through the EU-funded Project ECOPAS (French: Ecosystèmes Protégés en Afrique Soudano-Sahélienne). Before establishment of the W National Park, disturbance intensity was high due to illegal grazing, particularly by transhumant pastoralists. Since then, traditional land use changed to more intensive agricultural use (increased use of fertilizers and pesticides, mechanization and the cultivation of cash crops) in the communal area adjacent to the park, also leading to human-induced disturbances in the protected areas (Luoga et al. 2002, Mwavu & Witkowski 2008). However, disturbance intensity through livestock grazing in the buffer zone is low compared to that in the communal area. Sampeto had 1500 inhabitants in 2002 (INSAE 2002), and this number has most likely increased since the last census. The area belongs to the North-Sudanian vegetation zone, characterized by a semi-arid climate with an average precipitation of 700-1000 mm and a 6-mo rainy season from May to October (Bonou 2008).

All field data were collected in the surroundings of Sampeto (within a maximal distance of 10 km). The communal area of the village represents a typical savanna landscape in West Africa, with an alternating mosaic of croplands, fallows and non-arable land. Because the location is at the periphery of a national park (W National Park), we were also able to study the influence of reduced land use pressure in the buffer zone of the park. Thus, we were able to determine the population dynamics of woody species that were less altered by human impacts under semi-natural conditions in comparison to the population dynamics in communal areas.

An integral part of land use is extensive livestock breeding of both cattle and small ruminants such as goats and sheep. Mixed livestock in herds of different size is rotationally grazed during the day, affecting all land-cover types through grazing and trampling. The buffer zone is mainly grazed by cattle, but generally less altered by livestock grazing activities compared with the communal area. Harvesting of non-timber forest products (NTFPs) for firewood (e.g. *Detarium microcarpum*, *Crossopteryx febrifuga*), medical purposes (e.g. *Annona senegalensis*) or livestock forage (e.g. *Pterocarpus erinaceus*, *Philenoptera laxiflora*) is common in the settlement area. In the buffer zone, these activities are limited by law, but illegal timber extraction occurs, especially of *Isoberlinia doka*, *Afzelia africana* and *Khaya senegalensis*. Fires are irregularly set by farmers once or twice during the dry season to support the re-growth of palatable forbs and grasses and to protect against intense fires at the end of the dry season. In the buffer zone, early fires are set for management purposes at the beginning of the dry season. The mean fire density was three fires per 1000 ha between 2004 and 2009, and is approximately the same in the buffer zone and the adjacent communal area (Tools for Management and Sustainable Use of Natural Vegetation in West Africa [SUN], 2010, Periodic Activity Report, unpublished data).

Three land-cover types were studied. (1) Tree and shrub savanna on shallow skeletal soils without prior cultivation, but with frequent use of non-timber forest products (NTFPs) and as pasture. This habitat is dominated by the shrub species *Detarium microcarpum* whereas the herbaceous layer is sparsely developed (hereafter referred to as ‘non-arable’). (2) Tree and shrub savanna on poor to medium, previously cultivated soils (at least 10 yr ago, with different crops), frequent use of NTFPs and as pasture. The canopy layer is composed of different woody plants, such as *Piliostigma thonningii*, *Dichrostachys cinerea*, *Terminalia laxiflora* and *Flueggea virosa*. The herb layer is characterized by *Tephrosia pedicellata*, *Spermacoce ruelliae*; *Pennisetum polystachion*, *Desmodium velutinum* and *Chasmopodium caudatum* (hereafter referred to as ‘fallow’). (3) Semi-natural tree and shrub savanna on medium soils without prior cultivation, covered with tall grasses such as *Hyparrhenia involucrata* and the perennial species *Andropogon gayanus*, where use of natural resources is limited due to regulation by law (hereafter referred to as ‘buffer zone’). The third type is located in the buffer zone of the W National Park, while the first two land-cover types can be found in the communal area. Fallows and non-arable land are exposed to similar disturbance intensities (fire, grazing, harvesting) and are freely accessible.

Data collection

Vegetation data were sampled in five censuses from 2008 to 2010. Three censuses were conducted at the end of the dry season (May/Jun 2008, May/Jun 2009 and May/Jun 2010), and two were carried out at the end of the rainy season (Sep/Oct 2008 and Sep/Oct 2009). For each land-cover type, we randomly selected study plots with a size of 1800 m^2 each (non-arable: 12 plots; fallows: 17 plots; buffer zone: 10 plots) wherein we placed four 6.25-m^2 subplots. On each of these subplots, we examined the survival and diameter growth of the juveniles. To allow for an individual-based observation during the study period, all individuals smaller than 1 m were permanently marked. At each census, we measured the basal diameter (cm) and height (cm) of each individual already present or newly appeared on the plot.

Multistate Capture-Recapture Models and Model Fitting Procedure

To determine the survival of the plants, capture-recapture methods were used to estimate demographic parameters (Lahoreau et al. 2004; Gurevitch 2006). As each individual may belong to different diameter classes, we applied multistate capture-recapture models; such models provide estimates for the probabilities at which a plant individual will persist in its current demographic state (survival probability) or will develop to the next state (transition probability) (Shefferson et al. 2001; Kéry & Gregg 2004; Lesica & Crone 2007). The diameter classes were used as a proxy for demographic states; therefore, we defined 11 regular 0.1-cm-wide diameter classes ranging from 0 to 5.0 cm in width. For analysis, only species with more than 50 individuals in total were considered (Appendix S1).

To determine the environmental factors (e.g., land use) affecting survival and transition probabilities, the above-mentioned multistate capture-recapture models were fitted according to the following two-step procedure:

1. First, we fitted the models using all possible combinations and interactions of the factors diameter class, land-cover type and season to determine S (survival probability) and Psi (transition probability). Consequently, for each species, 154 single models containing different factors and interaction terms were fitted using maximum likelihood estimates of survival and transition between diameter classes (Lesica & Crone 2007; Conroy 2009). Following Lesica & Crone (2007) and Kéry et al. (2005), we used a fixed detection probability P = 0 for the uncertain, unobserved state and P = 1 for each individual being observed.

All 154 possible models were ranked by the corrected Akaikie Information Criterion (AICc) (Akaike 1973, Akaike 1981; Burnham et al. 1995). We compared several models and consequently considered the model with the lowest AICc values for further analysis as it best described the data. However, if a model contained fewer parameters than the best model and differed in the AICc value by less than two, we chose this model for further analysis (principle of parsimony) (Burnham & Anderson 2002; Johnson & Omland 2004; Schwarz 2005; Mazerolle 2006).

2. As a second step of the model simplification procedure, we tested the significance of land-cover type on species survival and transition by recalculating the most parsimonious models from step (1) above with merged land-cover types. As an example, we merged non-arable and fallows to determine whether these two land-cover types differed significantly in their influence on the parameters S and Psi. Again, we compared the AICc values of the original model with those of the model with the merged land-cover types and found the optimal model (according to the procedure described above).

Following the procedure used to detect differences between land-cover types, we merged diameter classes until the AICc values decreased. For this, we merged diameter classes when no significant difference between them occurred.

Through model simplification, we gained species-specific diameter classes of a varying range, for each land-cover type. Based on survival and transition probabilities, we constructed species-specific transition matrices (Appendix S2). The detected survival and transition probabilities were converted into six categories, ranging from ‘extremely low’ to ‘extremely high’ (Table 1, Appendix S2). If the transition or survival probabilities were extremely low (<E-06), we defined the corresponding diameter as “critical”, as it is very unlikely that such a low probability (less than one individual out of a million will move to the next diameter class or survive) would allow for the development of a stable population. Based on this categorization, we assessed the potential of each species to survive in the three investigated land-cover types (Table 2). As an example, if a species had a high survival probability (0.5 - <0.95) and a low transition probability (0.01 to <0.25) on non-arable sites, we assumed that the species could survive and grow in this land-cover type and described it as “medium”.

All statistical analyses were implemented in the R (version 2.12.2, R Development Core Team 2010, R Foundation for Statistical Computing, Vienna, AT) package RMark (http://www.phidot.org/software/mark/remark/) to construct models for the MARK program (White & Burnham 1999).

Table 1 Categories for the survival and transition probabilities.

Survival and Transition Probability	
Extremely Low	< 1.0E-06
Very Low	1.0E-06- < 0.01
Low	0.01- < 0.25
Medium	0.25- < 0.5
High	0.5- < 0.95
Extremely High	0.95- 1.00

Table 2 Characterization of species performance based on survival and transition probabilities.

Performance	**Critical diameter**	**Survival probability**	**Transition probability**
1 – Good	No	Extremely high/high	Extremely high/high
2 – Medium	No	Extremely high/high	Medium/low/very low
3 – Poor	No	Medium/low/ very low	Extremely high/ high/medium/low/very low
4 – Critical	Yes	All	All

3.3 Results

We found land-cover type and seasonality were very important factors influencing the survival and transition probabilities of woody savanna species (the optimal model for each species is shown in Appendix S3). The survival and transition probabilities did not differ between land-cover types for only two species; for *Pteleopsis suberosa*, no differences in growing conditions were detected between non-arable sites and fallows, while *Annona senegalensis* showed no difference between non-arable sites and the buffer zone. This may indicate that land use has little effect on species growth and survival for these two species. For *Isoberlinia doka* and *Feretia apodanthera*, the survival and transition probabilities did not depend on seasonality, indicating that the development of young stages of these species may be less limited by drought during the dry season than those of other species.

In the following, we focus on description of patterns detected for the rainy season only, as plant growth, as well as re-sprouting, mainly occurs during the rainy season because many species remain underground or dormant during the dry season in semi-arid ecosystems. We did not detect significant differences in survival and growth between the two seasons for any of the species, aside from a general trend of lower values for the survival probabilities.

Based on the evaluated performance of each species per land-cover type during the rainy season (1 - good, 2 - medium, 3 - poor, 4 - critical), we assigned all species to groups with similar demographic performance for the same land-cover type (Table 3, Fig. 1).

Table 3 Species performance based on survival and transition probabilities in different land-cover types during the rainy season. If the demographic performance varied between diameter classes, we indicated this by reporting two numbers in the cell: (++) good performance, (+) medium performance, (-) poor performance, (- -) critical.

G1: best performance on all land-cover types, G2: best performance on non-arable sites and fallows, G3: best performance on non-arable sites, G4: best performance on fallows, G5: best performance on non-arable sites and in the buffer zone, G6: best performance in the buffer zone. Growth forms: S, shrub, T, tree.

Group	Species	Non-arable	Fallows	Buffer zone
G1	*Dichrostachys cinerea* (S)	++	++	++
G2	*Vitellaria paradoxa* (T)	++*/+	++/+	- -
	Combretum molle (S)	++	++	+
	Terminalia avicennioides (T)	++	++	- -
	Diospyros mespiliformis (S)	++	++	
	Pteleopsis suberosa (S)	++	++	
	Lannea acida (T)	+		- -
	Feretia apodanthera (S)	+	+	
G3	*Combretum nigricans* (S)	++	+/++	
	Detarium microcarpum (S)	++	+	
	Combretum collinum (S)	++	+	- -
	Annona senegalensis (S)	+	-	+
G4	*Stereospermum kunthianum* (T)	+/++	++	+*/++*
	Strychnos spinosa (S)	+*	++	+
	Isoberlinia doka (T)	-	+	- -
	Anogeissus leiocarpa (T)	-	+	-
G5	*Pterocarpus erinaceus* (T)	++	+	++
G6	*Philenoptera laxiflora* (T)	-	- -	+

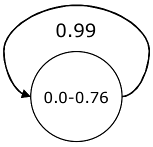
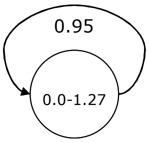
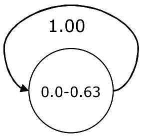
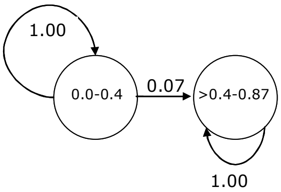
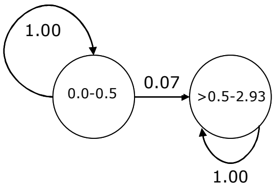
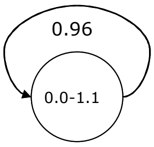
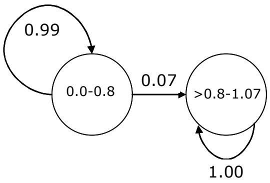
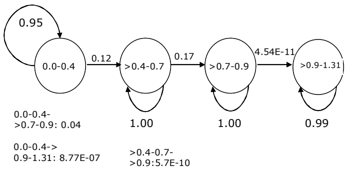
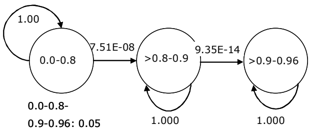
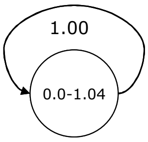
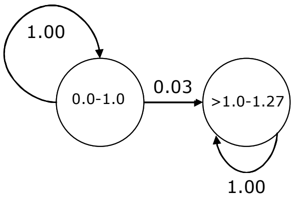
* High recruitment, skipping a diameter class, *Psi* from one diameter class to the diameter class after the next is > 1E-06

No entry: No data or insufficient data set (only a few monitored individuals in total or in a certain diameter class)

We detected six groups (G1-G6) of species. *Dichrostachys cinerea* was the only member of G1, and performed equally well in all land-cover types; thus, we detected no influence of land-cover type on the survival and transition probabilities. The transition probability did not depend on stem diameter for any land-cover type, thus resulting in a single diameter class (Fig. 1). The probability of survival was extremely high for all land-cover types. The second group (G2) contained seven species, *Vitellaria paradoxa*, *Combretum molle*, *Terminalia avicennioides*, *Diospyros mespiliformis*, *Pteleopsis suberosa*, *Lannea acida* and *Feretia apodanthera*, whose seedlings and saplings performed best on non-arable sites and fallows. The species of group G3 (*Combretum nigricans, Detarium microcarpum, C. collinum* and *Annona senegalensis*) performed best on non-arable sites, whereas the species of group G4 (*Sterospermum kunthianum*, *Strychnos spinosa*, *Isoberlinia doka* and *Anogeissus leiocarpa*) exhibited their best demographic performance on fallows. Group G5 only included *Pterocarpus erinaceus*, whose seedlings and saplings performed best on non-arable sites and in the buffer zone. The last group, G6, contained the tree species *Philenoptera laxiflora*, whose juveniles showed the best development in the buffer zone.

By examining the survival and transition rates of juveniles on different land-cover types we investigated their performance in relation to land use. However, it is also important to determine whether the species can develop stable populations. We detected eight woody species, of which two are shrub species and six are tree species, having a critical diameter class (Table 4) in one of the land-cover types. The transition for seedlings and saplings of the shrub species *Annona senegalensis* was critical from the diameter class of 0.4-0.6 cm to the following class of >0.6-1.23 cm on fallows, and for the shrub *Combretum collinum*, the critical transition was from the class of 0.7-

0.9 cm to the class of >0.9-1.31 cm, indicating that both species easily develop in the first diameter classes whereas the later development seems to be more difficult. Of the eight tree species studied, six had a critical diameter class in relation to land use: *Anogeissus leiocarpa*, *Isoberlinia doka*, *Lannea acida*, *Philenoptera laxiflora*, *Terminalia avicennioides* and *Vitellaria paradoxa*.

Group	**Non-arable**	**Fallows**	**Buffer zone**
G1	*Dichrostachys cinerea* (S)		
			
G2	*Feretia apodanthera* (S)		
			
G3	*Combretum collinum* (S)		
			
G4	*Strychnos spinosa* (S)		
			

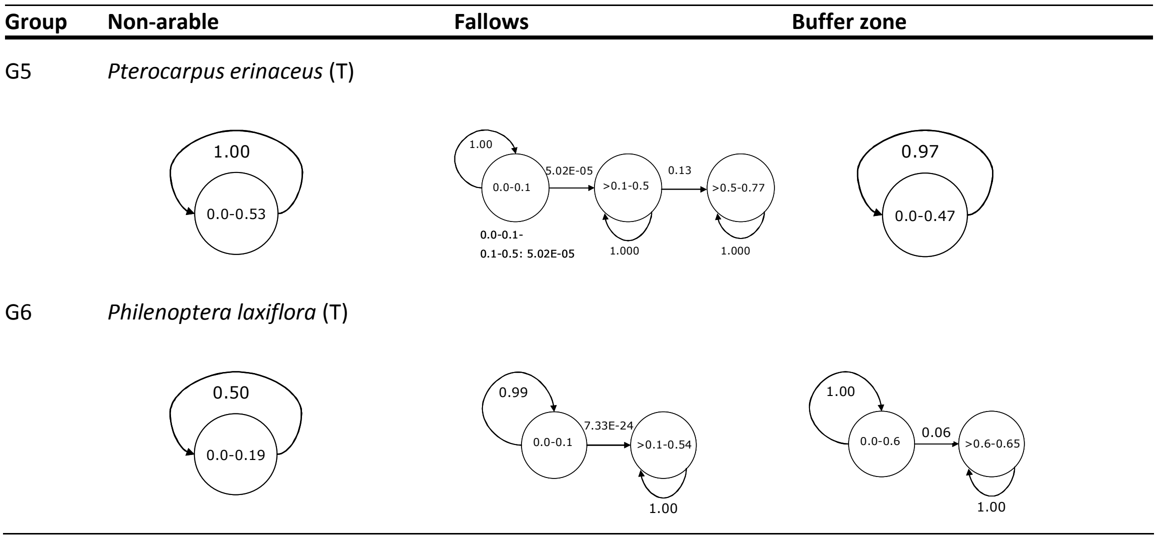


Fig. 2 Life-cycle diagrams separated into six groups formed by species whose seedlings and saplings perform best in relation to the land-cover type (compare with Table 3). The numbers within the circles show the diameter class. For each group, one representative species is shown: (G1) *Dichrostachys cinerea* (S), (G2) *Feretia apodanthera* (S), (G3) *Combretum collinum* (S), (G4) *Strychnos spinosa* (S), (G5) *Pterocarpus erinaceus* (T) and (G6) *Philenoptera laxiflora* (T). G1: best performance on all land-cover types, G2: best performance on non-arable sites and fallows, G3: best performance on non-arable sites, G4: best performance on fallows, G5: best performance on non-arable sites and in the buffer zone, G6: best performance in the buffer zone.

For most of these species, we detected a critical diameter in the buffer zone; for one of them, we detected a critical diameter on non-arable sites, and we observed a critical diameter for fallows in only one case (*Philenoptera laxiflora*). For *A. leiocarpa*, *I. doka*, *L. acida* and *V. paradoxa*, the first diameter class (0.0-0.1 except *I. doka,* 0.0-0.2 cm) already represented the critical stage on non-arable sites (for *A. leiocarpa*) and in the buffer zone, indicating difficulties in developing to the next diameter class after germinating on the site.

Table 4 Critical diameter (Psi =< 1E-06) for transition from one diameter class (cm) to the following for the land-cover types non-arable, fallows and buffer zone.

	Critical diameter[cm] and *Psi* (transition probability) for each land-cover type		
Species	**Non-arable**	**Fallows**	**Buffer zone**
Anogeissus leiocarpa (T)	0.1; *Psi* = 5.063E-14		
Annona senegalensis (S)		0.6; *Psi* = 4.39E-06	
Philenoptera laxiflora (T)		0.1; *Psi* = 7.33E-24	
Combretum collinum (S)			0.9; *Psi* = 4.54E-11
Isoberlinia doka (T)			0.2; *Psi* = 1.94E-10
Lannea acida (T)			0.1; *Psi* = 1.69E-28
Terminalia avicennioides (T)			0.3; *Psi* = 1.25E-07
Vitellaria paradoxa (T)			0.1; *Psi* = 2.28E-14

3.4 Discussion

Our results showed that land-cover type influences the survival and transition probabilities of almost all species, emphasizing the significance of land use. Only the seedlings and saplings of *Dichrostachys cinerea*, assigned to group G1, persisted equally well on all land-cover types, showing an extremely high survival probability irrespective of the stem diameter. This performance corresponds to the description of *D. cinerea* as an invasive species with strong vegetative reproduction through prolific root suckers, good re-sprouting capability and fire protection properties enhancing its competitive strength (Dagar et al. 1978; Orwa et al. 2009; Pare et al. 2009). Moreover, in a previous study (Jurisch et al. 2012), we found high numbers of individuals in the diameter class ranging from 0 to 5 cm for all land-cover types studied, indicating good recruitment. Especially in continuously grazed areas, as is the case in our study area due to the traditional daily rotational grazing system, *D. cinerea* spreads rapidly because livestock removes the herbaceous biomass and causes trampling-induced soil compaction (Nianogo & Thomas 2004; Orwa et al. 2009).

Human land use positively affects growing conditions for the species of group G2 (*Vitellaria paradoxa*, *Combretum molle*, *Terminalia avicennioides*, *Diospyros mespiliformis*, *Pteleopsis suberosa*, *Lannea acida* and *Feretia apodanthera*), with similar effects on non-arable sites and fallows. Based on our results, we predict a very good establishment probability for *V. paradoxa* because its seedlings and saplings had an extremely high survival probability; moreover, the stem diameter rapidly increased between the two censuses, indicating optimal growth conditions for the juveniles. Jurisch et al. (2012) detected large numbers of seedlings and saplings on non-arable sites and fallows, which may result from a high production of fruits, as has been reported for *V. paradoxa* (Makana & Thomas 2006). Due to the extremely high survival probability, we presume that we monitored cohorts of seedlings as well as saplings. For seedlings that germinated during the course of an observed growing season, seedling mortality is supposed to be high in semi-arid areas due to drought stress and fire (Wellington & Noble 1985; Harrington 1991), which was particularly observed in *V. paradoxa* (Teklehaimanot 2004). We instead expect that juveniles of different ages had already established extensive and widespread root systems or storage organs under the soil surface, enabling them to re-sprout after disturbances (Hoffman et al. 2004; Ouedraogo 2006; Grossnickle 2005; Wigley et al. 2009). In frequently disturbed savanna ecosystems, most woody species are capable of regenerating either from seed or vegetative organs, such as root suckers or sprouts (e.g. Midgley 1996; Kruger et al 1997; Bellingham & Sparrow 2000; Ky-Dembele 2008; Appendix 4), resulting in co-occurrence of seedlings and saplings where saplings dominate (Midgley 1996). Due to the strong re-sprouting capability, the detected mortality rates for saplings are low.

Species ecological preferences, which refer to the environmental conditions under which a species is most likely to occur, seem to be more relevant for the seedlings and saplings of species assigned to group G3 (best performance on non-arable sites) and group G4 (best performance on fallows). For the species of group G3 (*Combretum nigricans, Detarium microcarpum, C. collinum* and *Annona senegalensis*), the excellent performance of seedlings and saplings is emphasized by a large number of juveniles on non-arable sites (Jurisch et al. 2012). For the shrub *Detarium microcarpum*, this is probably due to its strong regeneration capacity based on re-sprouting via root suckers (Rietkerk et al. 1998, Bationo et al. 2001), as has also been shown for *A. senegalensis* (Persinos et al. 1964; Menaut & Cesar 1979; Hines & Eckman 1993) and many other savanna shrub species (see Bellefontaine 2005). In addition, the species is well-adapted to shallow skeletal and sandy soils (Arbonnier 2002; Vautier et al. 2007; Appendix S4), where its competitive strength is enhanced by its ability to undergo vegetative reproduction, rapidly and easily producing large quantities of offspring; hypogenous seed germination is an advantageous trait on dry sites (Abrahamson 1980). Our results obtained for juveniles of *A. senegalensis* (best development on non-arable sites) correspond to the species preference for dry rocky soils, whereas the two species of the Combretaceae (*C. nigricans* and *C. collinum*) can be found on all soil types (Arbonnier 2002; Sacandé et al. 2007; Appendix S4).

The survival and growth of seedlings and saplings of group G4 (*Anogeissus leiocarpa*, *Isoberlinia doka*, *Strychnos spinosa* and *Stereospermum kunthianum*) were best on fallows. In contrast to non-arable sites, the soils on fallows are deeper and contain less gravel, as our soil analysis has shown, favoring the development of these species. The species *A. leiocarpa* and *I. doka* in particular prefer medium, well-drained soils, whereas the other two species show wide ecological amplitudes (Kershaw 1968; Arbonnier 2002). The establishment and growth of the juveniles of *S. spinosa* and *S. kunthianum* seem to be more affected by habitat conditions in the juvenile stage. Once established, juveniles of the four species seem to persist well under current land-use processes, based on the high survival probability detected on fallows, irrespective of the stem diameter.

The only species in group G5, *Pterocarpus erinaceus*, performed best in two contrasting habitats: on non-arable sites and in the buffer zone. Both on non-arable sites and in the buffer zone, all diameter classes merged, indicating that survival and transition probabilities were stable between the diameter classes.

The juveniles of the only species in group G6, *Philenoptera laxiflora*, performed best in the buffer zone, whereas they showed poor performance on the other land-cover types. In contrast, the survival and growth of many other species seedlings and saplings tend to be weak or even critical in the buffer zone. Five species showed an extremely low transition probability for this land-cover type. Particularly for trees, the transition from the first diameter class to the following class was extremely low, indicating a critical life stage, as it is very unlikely that such low transition probabilities would allow the development of stable populations. Based on these observations, we consider that those populations were likely to decline in this land-cover type. In grass-dominated savanna ecosystems juveniles compete during the establishment and initial growth phase mainly with stand-forming tall grasses. Such grasses can be frequently found in the buffer zone, namely *Andropogon gayanus* and *Hyparrhenia involucrata*. These grasses may shade out juvenile woody plants and compete for water and nutrients, as above- and below-ground competition by plants growing in the surroundings of a young plant individual greatly affects its survival and growing performance (Harper 1977; Jurena & Archer 2003; Vandenberghe et al. 2006; Riginos 2009). Additionally, the presence of tall grasses provides a high amount of inflammable biomass, increasing the potential for high-intensity fires. Fire significantly decreases the annual recruitment rate of seedlings and saplings and is partly responsible for the shoot die back exhibited by many savanna tree species (Bationo et al. 2001; Luoga et al. 2004; Zida 2007). In communal areas, palatable tall perennial grasses are widely absent due to intensive livestock grazing, which reduces ground-level biomass and thus also reduces fire intensity (Midgley et al. 2010; Nacoulma et al. 2011). Moreover, traditional fire management in communal areas creates a mosaic of burned and unburned sites (Sheuyange et al. 2005; Butz 2009), providing safe sites where fire- and drought-sensitive seedlings may persist (see Setterfield 2002; Zida et al. 2008; Gignoux et al. 2009).

3.5 Conclusion

Our findings show that the survival and growth of woody species seedlings and saplings are strongly related to land use, where most species developed better in the communal area compared to the buffer zone. Human activities (timber harvesting, fire and extensive livestock grazing) have an indirect positive effect on their seedlings and saplings by providing diverse, small-scale habitats that vary in time, such as bare soils, or by reducing vegetation cover. Such opening of the canopy is beneficial for germination of seeds and establishment of new suckers (Goldberg & Werner 1983; Silvertown & Smith 1989; Bakker & de Vries 1992); it also enhances the survival of juveniles by reducing competition for light, water and nutrients.

Many studies deduce from a high recruitment rate that a species is able to withstand human pressure (e.g., Lykke 1998; Mwavu & Witkowski 2009; Schuman et al. 2011); however, this should be considered with caution. As an example, for *A. leiocarpa*, we detected a high number of seedlings on non-arable sites in a previous study, although the transition probability was extremely low between the diameter classes, indicating that growth and recruitment of juveniles rarely occurred on these sites (Jurisch et al. 2012). Accordingly, our findings show that static observations are not necessarily good predictors of future population trends because survival and growth affect the current state of a population (Condit et al. 1998, Feeley et al. 2007).

Land use was shown to significantly affect the survival and growth of all species studied, as demonstrated through the grouping of species according to performance. Werner (1975) showed that the size of plants, and not their age, is more reliable for making predictive statements concerning death and survival. Because the survival probability of all species studied was affected by the diameter class, we suggest a stage-based analysis of population dynamics that accounts for the stem diameter as an appropriate approach for classifying juvenile savanna woody plants rather than defining life stages (see also Gignoux et al. 2009).

Due to the on-going land-use changes leading to habitat loss, the shortening of fallow periods, and over-grazing, diverse sites for juveniles are becoming fewer. This development is more pronounced when the current adult populations are already under high human pressure (e.g. harvesting and pollarding), causing removal and vitality impairment of reproductive individuals. This can reduce the availability of seeds and may thereby lead to a lack of regeneration (Plumptre 1995; Makana & Thomas 2004; McLaren et al. 2005). More demographic studies on survival and mortality rates of populations in their natural habitat — especially in relation to land use— are required to develop species-specific management strategies for allowing a high amount of natural regeneration to occur. This is especially relevant here because our observations have shown that populations of some land-cover types were likely to decline.

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Chapter 4

Land use impact on juvenile densities of woody plants in a semi-arid savanna, West Africa

with Markus Bernhardt-Römermann, Rüdiger Wittig and Karen Hahn

Manuscript submitted

Human land use affects the density of woody species seedlings and saplings by altering the physical, chemical, and biological characteristics of the land, resulting in different land-cover types. To study this effect, we determined seedling and sapling densities on non-arable sites, fallows and in a protected area. We analyzed the influence of land use on juvenile densities for 25 species (16 shrubs, 7 trees) and determined which environmental conditions were related to juvenile densities next to the influence of land use.

We found that the soil acidity, the particle size distribution of the soil, and the vegetation structure differed between land-cover types. In terms of human impact, we detected five groups of species responding similarly to land use. Although we detected significant differences in soil properties, its direct effects on juvenile densities are less pronounced than its indirect effects. By altering the availability of resources, soil properties affect height and cover of all plants growing in the surrounding of a young woody plant, increasing the competition for light, water and nutrients during the establishment and initial growth. These effects are intensified by human land use and vary between land-cover types.

4.1 Introduction

The savanna regions of West Africa are frequently affected by human-induced disturbances. Aside from agricultural activities (crop production and animal husbandry), the harvesting of timber and non-timber forest products affects savanna vegetation. During recent decades, social and economic conditions have changed dramatically (for detailed studies see Descroix et al. 2009; Norris et al. 2010; Ouedraogo et al. 2010), causing habitat loss, the shortening of fallow periods, over-grazing and the removal and vitality impairment of reproductive individuals (e.g., by harvesting and pollarding). This development becomes more pronounced as due to increased human pressure, habitats suitable for juvenile establishment are becoming diminished.

In particular, the seedling and sapling stages are usually a critical phase in the regeneration of woody species, as for plants at these stages the risk of abiotic stress caused by human-induced disturbances (e.g., fire and livestock grazing) as well as soil conditions and biological interactions (intra- and inter-specific plant competition) is very high (Abrahamson 1980; Bond 2008; Jurisch et al. 2012a; 2012b; Prior et al. 2010; Zida 2007). Consequently, seedlings must quickly develop an effective root system to allocate and store nutrients and to gain access to water, which enhances the individual’s ability to tolerate and be resilient to disturbances (Grossnickle 2005; Hoffman et al. 2004; Wigley et al. 2009). The topsoil properties are important for the establishment of young plants, as most of their root biomass is located close to the surface (Jeffrey 1987; Kaonga & Bayliss-Smith 2012; Knoop & Walker 1985; Weltzin & McPherson 1997).

The impact of human land use on the density of seedlings and saplings of woody plants in West African savannas has been determined so far only for single species in comparative studies between protected and non-protected areas (e.g., Djossa et al. 2008; Pare et al. 2009; Schumann et al. 2011) and in relation to management practices (Dhillion & Gustad 2004; Kouami et al. 2009; Ky-Dembele et al. 2007). These studies generally report higher seedling and sapling densities in non-protected areas, on croplands and in villages compared to protected sites and fallows. Prescribed fire, moderate livestock grazing and selective removal of trees were found to have an indirect positive effect on seedling and sapling densities and growth by reducing vegetation cover and thus, reducing intra- and inter-specific plant competition for light, water and nutrients. In contrast, *in situ* experimental studies from semi-arid South Africa have revealed that herbaceous competition was intensified under fertile conditions by enhancing growth rates of grasses. This may lead to a decrease in seedling individual densities, as well as changes in growth rates, morphology, and resource allocation (Bush & van Auken 1995; Kraaij et al. 2006; Staver et al. 2009; van Auken & Bush 1997; van der Waal et al. 2009). Several studies detected that fire and browsing may suppress the recruitment of young plants by removing above-ground plant parts or the entire plant. This is more pronounced in dry climate with low rainfall causing higher water stress and thus, limiting the regeneration potential of plants (Fatubarin 1987; Gijsbers et al. 1994; Kessler & Breman 1991; Menaut 1983; Zida et al. 2007; 2008).

As a result of these studies, one can assume that human land use may have either positive or negative effects on the density of woody species seedlings and saplings due to the change of the physical, chemical, and biological characteristics of the land-cover types caused by human impact. Therefore, we expect to observe a significant effect of habitat conditions altered by human land use on the density of seedlings and saplings (Swaine 1996). We further assume that this effect is related to species' ecological preferences, which refer to the environmental conditions under which the species is most likely to occur. To study this, we investigated patterns of population densities in relation to soil conditions, vegetation structure and land-cover type of a broad set of characteristic savanna species to obtain a better understanding of the influence of land use and related environmental factors on the juvenile stage of woody species.

4.2 Methods

Study site

The study was carried out around Sampeto village (11°40′-12°23′ N and 2°04′-3°05′ E) located in the northern part of Benin at the periphery of the trans-boundary W National Park, one of the largest protected areas in West Africa. Sampeto had 1500 inhabitants in 2002 (INSAE 2002), although this number has most likely increased since the last census. The area belongs to the North-Sudanian vegetation zone, characterized by a semi-arid climate with an average precipitation of 700-1000 mm and a six-month rainy season from May to October (Bonou 2008).

All field data were collected in the surroundings of Sampeto (in maximal distance of 10 km). The communal area of the village represents a typical example of a savanna landscape in West Africa with an alternating mosaic of croplands, fallows and non-arable land. Because the location is at the periphery of a national park (W National Park), we were also able to consider sites that are less altered by human impact – the buffer zone of the national park - and represent semi-natural conditions.

An integral part of land use is extensive livestock breeding of both cattle and small ruminants such as goats and sheep. Mixed livestock in herds of different size are rotationally grazed during the day, affecting all land-cover types through grazing and trampling. The buffer zone is grazed mainly by cattle, but generally less altered by livestock grazing activities compared with the communal area. Fires are irregularly set by the farmers once or twice during the dry season in order to support the re-growth of palatable forbs and grasses and for protection against intensive fires at the end of the dry season. In the buffer zone, early fires are set for management purposes at the beginning of the dry season. The mean fire density was three fires per 1000 ha between 2004 and 2009, and is approximately the same in the buffer zone and the adjacent communal area (SUN 2010, unpubl. data).

Three land-cover types were studied. (1) Tree and shrub savanna on shallow skeletal soils without prior cultivation, but with frequent use of non-timber forest products (NTFPs) and as pasture. This habitat is dominated by the shrub species *Detarium microcarpum* whereas the herbaceous layer is sparsely developed (hereafter referred to as 'non-arable'). (2) Tree and shrub savanna on poor to medium, previously cultivated soils (at least 10 years ago, with different crops), frequent use of NTFPs and as pasture. The canopy layer is composed of different woody plants; such as *Piliostigma thonningii*, *Dichrostachys cinerea*, *Terminalia laxiflora* and *Flueggea virosa*. The herb layer is characterized by *Tephrosia pedicellata*, *Spermacoce ruelliae*; *Pennisetum polystachion*, *Desmodium velutinum* and *Chasmopodium caudatum* (hereafter referred to as 'fallow'). (3) Semi-natural tree and shrub savanna on medium soils covered with tall grasses, such as *Hyparrhenia involucrata* and the perennial species *Andropogon gayanus*, where use of natural resources is limited due to regulation by law (hereafter referred to as 'buffer zone'). The latter is located in the buffer zone of the W National Park, while the first two land-cover types can be found in the communal area. Fallows and non-arable land are exposed to similar disturbance intensities (fire, grazing, harvesting) and are freely accessible.

Data collection

Vegetation data

Seedling and sapling densities were determined on randomly selected plots with a size of 1800m^2; each of these plots was characterized by four 6.25 m^2 subplots. In total, 39 of these 1800m^2 plots were investigated, 12 on non-arable sites, 17 on fallows, and 10 in the buffer zone. On each of the 6.25m^2 subplots, numbers of juveniles were counted, comprising all young, immature individuals of the seedling and sapling stage smaller than 1 m.

To account for weather related annual and seasonal variation, vegetation sampling was repeated five times. Three censuses were conducted at the end of the dry season (May/June 2008, May/June 2009 and May/June 2010), and two were carried out at the end of the rainy season (September/October 2008 and September/October 2009).

Nomenclature follows the African Plant Database (APD, accessed April 2012).

Environmental data

Environmental conditions were characterized by the vegetation structure and soil analysis. Structural characteristics of the land-cover types were described as cover and height of the tree and shrub layer (on plots of 1800 m^2) and the herbaceous layer (on one sub-plot of 100 m^2) in September/October 2007.

On each of the 1800 m^2 plots, we took three randomly placed soil samples of the upper 0-20 cm layer in May 2009. These three sampled were pooled and subsequently analyzed for concentrations of plant-available phosphorous and potassium, organic and inorganic carbon, and nitrogen, cation exchange capacity (CEC, with ion concentrations of sodium, potassium, calcium, and magnesium), particle size distribution (PSD), and pH. Plant-available phosphorous (phosphorus pentoxide, P_2O_5) and potassium (potassium oxide, K_2O) determination was carried out by calcium-acetate-lactate (CAL)-method (Schüller 1969; 1973); pH was measured in aqueous solution against 0.1 M KCl (Meiwes et al. 1984) and 0.01 M $CaCl_2$ solution (DIN 19 684, sheet 1 1977). We determined organic carbonate by the wet combustion method (Lichtenfelder (DIN 19 684, sheet 2 1977) and colorimetric detection using spectral photometer Cadas 100 (Lange). Nitrogen was determined quantitatively by the Kjeldahl-titrimetric method modified by Bremmer (1960, 1965). Cation exchange capacity and ion concentrations were determined in $BaCl_2$ solution buffered with triethanolamine by the Mehlich-extraction method according to DIN 19 684, sheet 8 (1977). PSD for fine soil particles was determined with Köhn-pipette method (DIN 19 683, sheet 1 and 2 1973).

Data analysis

Differences in environmental factors between land-cover types

We calculated the mean of all environmental parameters per land-cover type and used Tukey's multiple comparison tests to search per environmental parameter for differences between land-cover types. Prior to statistical analysis, numerical variables were normalized by scaling them between zero and one. Such standardization is required to make the explanatory variables that were measured on different scales comparable. Furthermore, all environmental variables were checked for possible inter-correlations. Using a correlation threshold of $r^2 > 0.7$, we found that the amount of potassium and potassium oxide were highly correlated ($r^2 = 0.785$) and consequently removed potassium oxide from the further analyses (for Pearson correlation coefficients see Appendix 1).

Influence of land use and environment on juvenile densities

In total, we used 16 shrub and 7 tree species in our analysis. Only species occurring with more than ten individuals in at least two land-cover types were included (for density values see Appendix 2).

The statistical analyses addressed two different issues for each species: (i) to determine the influence of land use on juvenile densities, and (ii) to determine which environmental conditions affect juvenile densities additional to the influence of land use.

To answer the first issue, a linear mixed effect model (LME) with seedling density as response variable (number of individuals per ha) and land-cover type as explanatory variable was calculated. To correct for potential auto-correlation in time, we induced census as random factor. These LMEs were tested for differences between the land-cover types using Tukey's multiple comparison tests. Based on these tests, we merged land-cover types without significant differences, resulting in LMEs showing which land-cover types differ in seedling densities. Using these models, we assigned each tree and shrub species to a certain group. For example, two species that showed no statistical differences in juvenile densities between fallows and non-arable sites, but differed from those in the buffer zone would be grouped together, even though the juvenile density of two species might differ.

To address the environmental conditions which alter juvenile densities, in addition to the influence of land use, we searched for environmental parameters significantly related to each species affiliation group. Only environmental parameters differing between land-cover types were used. These pre-selected factors were taken as explanatory variables in generalized linear models (GLM using juvenile densities as dependent variable) of the 'quasipoisson' family, as this error described the distribution of the residuals best (juvenile densities are count data). We performed a model simplification by omitting non-significant parameters until only significant parameters remained (Crawley 2007).

All statistical analyses were done in R 2.13.2 (R Development Core Team 2011) with the additional package "vegan" (Oksanen 2011), "lme4" (Bates et al. 2011) and "multcomp" (Hothorn et al. 2008).

4.3 Results

Differences in environmental factors between land-cover types

We found 11 environmental parameters differing significantly between the land-cover types: height of herb layer, cover of tree/shrub and herb layer characterizing the vegetation structure and eight soil parameters (Table 1).

On non-arable sites, we detected the highest amount of acid exchangeable cations (H-value), the lowest amount of exchangeable acid cations (BS-value), the lowest pH as well as the lowest percentage cover of the herb layer, which differed significantly to fallows and the buffer zone (Table 1). Site conditions on fallows were intermediate to those conditions on non-arable sites and the buffer zones, as we did not detect any environmental parameter that was significantly higher or lower on fallows compared to the other land-cover-types. The low percentage of clay in the sub-surface and the height of the herb layer, were characteristic for the buffer zone and differed significantly from the communal area (non-arable sites and fallows).

Influence of land use and environment on juvenile densities

The 16 shrub and 7 tree species in scope of our study were assigned to five groups of species (A-E) each responding similar to land use (Table 2, for LME results see Appendix 3). For groups A-D we detected several, but different, soil parameters as significantly related to juvenile densities, whereas no parameter was found for group E (Table 3).

The tree species *Pterocarpus erinaceus* was the only member of group A where juvenile densities differed between all land-cover types. For species of group B (*Annona senegalensis*, *Crossopteryx febrifuga*, *Lannea acida* and *Terminalia avicennioides*) no differences were found between non-arable land and fallows, but they differed from the buffer zone. For group A and B, the height of the herb layer was the only significant environmental parameter explaining differences in juvenile densities between all land-cover types and, and in the case of group B, between the communal area (non-arable and fallows) and the buffer zone. Group C was the largest group, comprising seven shrubs and two tree species with similar densities on non-arable land and in the buffer zone, which differed from those on fallows. The vegetation structure (height of the herb layer and percentage cover of the tree/shrub layer), the amount of exchangeable acid cations (H-value) and the percentage of the coarse-grained silt fraction were the parameters determining differences in the density of juveniles between fallows and those on non-arable sites and the buffer zone. Eight shrub and tree species, whose juvenile densities did not differ between fallows and the buffer zone but on non-arable sites, were assigned to group D. Differences in the percentage cover of the herb layer, pH, H-value and the percentage of clay in the top-soil were the most important soil parameters significantly impacting on juvenile densities of species affiliated to group D. Species of group E (one tree, two shrubs) showed no influence of land use on juvenile abundances (Tables 2, 3).

Table 1 Mean (± S.E.) of environmental parameters (soil parameters and vegetation structural data) per land-cover type, different letters (a, b and c) indicate significant differences ($p < 0.05$, highlighted as bold).

Soil parameter	**Non-arable (n=12)**	**Fallows (n=17)**	**Buffer zone (n=10)**
Cover tree/shrub layer [%]	**29.8 ± 4.71 a**	19.7 ± 1.29 ab	13.3 ± 2.1 b
H-value	**73.2 ± 9.12 a**	49.5 ± 4.29 b	38.1 ± 5.14 b
Medium silt [%]	**9.3 ± 0.52 a**	8.1 ± 0.3 b	8.6 ± 0.47 ab
Clay < 2µm [%]	**21.1 ± 1.34 a**	18.6 ± 1.04 a	13.4 ± 0.6 b
K_2O [mg/100g]	6.0 ± 0.36 a	**8.4 ± 0.73 b**	7.8 ± 0.77 ab
Height herb layer [cm]	50.2 ± 12.46 a	42.8 ± 6.32 a	**184 ± 5.42 b**
Cover herb layer [%]	48.6 ± 3.68 a	62.4 ± 4.25 b	**71.9 ± 2.61 b**
Coarse silt [%]	32.4 ± 1.35 ab	31.2 ± 1.69 a	**38.6 ± 1.78 b**
pH	4.8 ± 3.07 a	5.4 ± 2.83 b	**5.6 ± 3.85 b**
K^+ [mmol$_c$/kg]	0.8 ± 0.05 a	1.1 ± 0.11 ab	**1.4 ± 0.16 b**
BS-value	34 ± 3.27 a	48.3 ± 2.07 b	**54.9 ± 2.78 b**
C/N-ratio	20.1 ± 2.08 a	22 ± 2.18 a	20.4 ± 2.51 a
Ca^{2+}[mmol$_c$/kg]	25.9 ± 1.17 a	35.4 ± 3.89 a	34.6 ± 5.21 a
CECpot [cmol$_c$/kg]	108 ± 9.09 a	96.9 ± 7.88 a	85.1 ± 10.67 a
Coarse sand [%]	7.9 ± 1.54 a	8.6 ± 1.89 a	6.4 ± 2.22 a
C-organic [%]	1.8 ± 0.16 a	1.7 ± 0.18 a	1.5 ± 0.16 a
Fine sand [%]	18.2 ± 1.2 a	21.4 ± 1.45 a	22.7 ± 1.15 a
Fine silt [%]	4.1 ± 0.22 a	3.8 ± 0.23 a	3.9 ± 0.15 a
Medium sand [%]	7.1 ± 0.61 a	7.9 ± 0.65 a	6.5 ± 0.36 a
Mg^{2+} [mmol$_c$/kg]	7.7 ± 0.78 a	10.5 ± 0.85 a	10.7 ± 1.2 a
Na^+ [mmol$_c$/kg]	0.4 ± 0.07 a	0.3 ± 0.03 a	0.3 ± 0.04 a
N-total [%]	0.1 ± 0.01 a	0.1 ± 0 a	0.1 ± 0.01 a
P_2O_5 [mg/100g]	0.3 ± 0.05 a	0.3 ± 0.02 a	0.3 ± 0.03 a
S-value	34.8 ± 1.36a	47.4 ± 4.6 a	47 ± 6.31 a

Table 2 Juvenile densities [100 m^2] of the 25 analyzed woody species. Densities are presented per land-cover type (non-arable land: n=12, fallows: n=17 and buffer zone: n=10). Similarity between land-cover types is marked by (&), dissimilarity by (≠).Growth form: S: shrub, T: tree.

		Land-cover type		
Species	**Family**	**Non-arable**	**Fallows**	**Buffer zone**
group A: non-arable ≠ fallows ≠ buffer zone				
Pterocarpus erinaceus (T)	Fabaceae	23 ± 3.1	10 ± 1.7	38 ± 5.4
group B: non-arable & fallows ≠ buffer zone				
Annona senegalensis (S)	Annonaceae	43 ± 6.4	62 ± 5.8	0 ± 0.5
Crossopteryx febrifuga (S)	Rubiaceae	15 ± 3.4	10 ± 1.7	23 ± 5.0
Lannea acida (T)	Anacardiaceae	26 ± 4.4	36 ± 4.1	2 ± 1.1
Terminalia avicennioides (T)	Combretaceae	36 ± 6.1	49 ± 5.4	10 ± 3.2
group C: non-arable & buffer zone ≠ fallows				
Acacia hockii (S)	Mimosaceae	0 ± 0.0	13 ± 3.2	2 ± 1.0
Anogeissus leiocarpa (T)	Combretaceae	27 ± 7.0	79 ± 14.7	12 ± 34
Combretum collinum (S)	Combretaceae	45 ± 5.0	133 ± 15.7	31 ± 7.8
Dichrostachys cinerea (S)	Mimosaceae	126 ± 25.8	223 ± 29.6	14 ± 4.6
Diospyros mespiliformis (S)	Ebenaceae	1 ± 0.7	54 ± 11.2	2 ± 1.0
Feretia apodanthera (S)	Rubiaceae	7 ± 1.7	68 ± 11.8	2 ± 1.0
Gardenia ternifolia (S)	Rubiaceae	22 ± 5.4	13 ± 2.0	14 ± 3.7
Piliostigma thonningii (S)	Caesalpiniaceae	13 ± 2.2	43 ± 4.3	4 ± 1.3
Strychnos spinosa (S)	Strychnaceae	35 ± 5.8	26 ± 3.4	57 ± 7.6
Vitellaria paradoxa (T)	Sapotaceae	40 ± 13.5	85 ± 15.8	14 ± 2.9
group D: fallows & buffer zone ≠ non-arable				
Combretum glutinosum (S)	Combretaceae	23 ± 4.0	4 ± 1.1	4 ± 1.3
Combretum nigricans (S)	Combretaceae	93 ± 16.1	34 ± 5.5	10 ± 2.3
Detarium microcarpum (S)	Caesalpiniaceae	461 ± 53.7	45 ± 6.7	0 ± 0.0
Isoberlinia doka (T)	Caesalpiniaceae	12 ± 2.7	43 ± 4.9	35 ± 6.3
Philenoptera laxiflora (T)	Fabaceae	1 ± 0.6	19 ± 4.8	30 ± 5.2
Pteleopsis suberosa (T)	Combretaceae	222 ± 41.8	71 ± 9.8	2 ± 1.0
Stereospermum kunthianum (T)	Bignoniaceae	95 ± 9.4	44 ± 5.3	30 ± 4.9
group E: non-arable & fallows & buffer zone				
Bombax costatum (T)	Bombacaceae	7 ± 1.6	9 ± 1.8	8 ± 1.8
Combretum molle (S)	Combretaceae	68 ± 9.6	65 ± 6.7	69 ± 13.4
Gardenia aqualla (S)	Rubiaceae	4 ± 1.8	9 ± 3.0	8 ± 2.3

Table 3 Influence of environmental factors on juvenile densities by species affiliation groups A-E. The GLMs were fitted using juvenile densities as dependent variable, and environmental variables (numerical) as explanatory variables. Family = quasipoisson.

group A: non-arable ≠ fallows ≠ buffer zone

	Estimate	S.E.	*t* value	Pr (>|t|)
Intercept	5.63	0.21	26.6	<0.001***
Height herb layer [cm]	0.55	0.17	3.2	0.003**

group B: non-arable & fallows ≠ buffer zone

	Estimate	S.E.	*t* value	Pr (>|t|)
Intercept	6.02	0.14	42.9	<0.001***
Height herb layer cm]	-0.48	0.17	-2.9	0.005**

group C: non-arable & buffer zone ≠ fallows

	Estimate	S.E.	*t* value	Pr (>|t|)
Intercept	63.75	0.15	45.9	<0.001***
Height herb layer [cm]	-0.64	0.17	-3.7	<0.001***
Cover tree/shrub layer [%]	0.29	0.13	2.2	0.026*
H-value	-0.45	0.17	-2.7	0.007**
Medium silt [%]	-0.29	0.13	-2.3	0.023*

group D: non-arable ≠ fallows & buffer zone

	Estimate	S.E.	*t* value	Pr (>|t|)
(Intercept)	6.34	0.16	39.4	<0.001***
Cover herb layer [%]	-0.34	0.17	-2.0	0.043*
pH	-0.62	0.23	-2.7	0.007**
H-value	0.61	0.14	4.3	<0.001***
Clay < 2µm [%]	-0.49	0.14	-3.4	<0.001***

group E: non-arable & fallows & buffer zone

	Estimate	S.E.	*t* value	Pr (>|t|)
(Intercept)	6.10	0.20	30.4	<0.001***

4.4 Discussion

Differences in environmental factors between land-cover types

We detected chemical and physical soil properties, as well as characteristics of the vegetation structure, as factors differing between the land-cover types non-arable, fallows and the buffer zone. In contrast to the buffer zone, pH and percentage base saturation (BS-value) were increased in the communal area (non-arable sites and fallows). Comparable results were also observed by Hahn (1996) who stressed the physical soil properties as determining the occurrence of vegetation types in West African savannas. However, as also found by Orthmann (2005), we additionally detected soil acidity and alkalinity as important factors differing between land-cover types.

Influence of land use and environment on juvenile densities

Land use was shown to significantly affect juvenile densities of almost all studied species. For the tree species *Pterocarpus erinaceus* juvenile density differed between all land-cover types (group A) and was highest in the buffer zone followed by fallows and non-arable sites. This pattern was related to differences in the vegetation structure (height of the herb layer) in the studied land-cover types. In general, in grass-dominated savanna ecosystems, juveniles compete during the establishment and initial growth mainly with stand-forming tall grasses. Such grasses as *Andropogon gayanus* and *Hyparrhenia involucrata* can be frequently found in high abundances in the buffer zone. However, we detected a high number of juveniles of *P. erinaceus* in the buffer zone; thus, we suppose that other factors besides the competition between young woody plants and grasses are responsible for the contrasting performance pattern. This species is one of the five most important fodder tree species in the study area (L. Houessou, pers. comm.) and is pruned to provide additional forage for the livestock during the dry season. Higher densities of large reproductive trees were found on fallows compared to the buffer zone (Appendix S3) as many mature trees are maintained when land is cleared for agriculture due to the immediate value of the foliage for the cattle. This may influence the relative abundance of regeneration detectable on a site (Milton 1995). Aside from the fact that cutting of large stems and pollarding in the buffer zone is prohibited and can have a significant impact on reproduction and on population viability over the long-term (Dhillion & Gustad 2004; Gaoue & Ticktin 2008; Hall & Bawa 1993; Peters 1990), high juvenile densities may be due to a reduced grazing intensity in the buffer zone as young leaves of this species are preferably consumed by livestock (Bayer 1990; Duvall 2008; Glèlè Kakaï et al. 2009).

For several study species, juvenile densities in the buffer zone differed significantly from those densities on non-arable sites and on fallows (group B). Except for *Crossopteryx febrifuga*, juvenile densities were significantly lower in the buffer zone compared to juvenile densities in the communal area. In the case of *C. febrifuga*, we suppose that the high grazing pressure in the communal area may reduce the number of young plants; the species re-sprouts early after the dry season and is preferably browsed by cattle as our grazing observations have shown. For the buffer zone our results imply that the high amount of silt relates to an increased water-holding capacity compared to non-arable sites and fallows. Thus, coupled with a high percentage base saturation, the soils in the buffer zone provide ideal growing conditions for plants. On sites where nutrient availability and water supply are high, grasses, in particular, can quickly form an almost continuous vegetation cover and may repress juvenile woody plants by competing for light, water and nutrients during their establishment and initial growth phase (Harper 1977; Jurena & Archer 2003; Riginos 2009; Vandenberghe et al. 2006). This corresponds to the findings from Mwavu et al. (2009) who detected competition by the ground vegetation as the most important factor reducing the survivorship of slower-growing, young woody plants. As detected in this study, the result is a reduced seedling density. Additionally, the tall grasses increase the fuel load and therefore, the potential for high-intensity fires causing a decrease in juvenile densities due to fire-induced mortality (Bationo et al. 2001; Luoga et al. 2004; Zida 2007). However, burning may stimulate the growth of surviving species and the colonization of species because of the release of plant nutrients and through a range of indirect effects, e.g. decreased shade, higher soil temperatures and reduced competition affecting the growing performance of young plants (‘ash-bed’ effect, Harper 1977; Jeffrey 1987; Riginos 2009; Vandenberghe et al. 2006).

For species affiliated to group C, beneficial effects through human-induced disturbances positively affect juvenile densities, as their juvenile densities are highest on fallows (but compare *Gardenia ternifolia* and *Strychnos spinosa*). These species are well adapted to the alternating cycles of cultivation and fallows like the shrub *Combretum collinum* (Nacoulma et al. 2011), and *Piliostigma thonningii* which is known as invasive species on fallows regenerating from the remaining rootstock left after the field clearing (Arbonnier 2002; Bellefontaine 2005; Nikiema 2005). Human activities can have an indirect positive effect on seedlings and saplings by providing diverse, small-scale habitats that vary in time, such as bare soils on fallows, or by reducing vegetation cover. We found that percentage cover of the tree and shrub layer and the height of the herb layer positively affect juvenile densities on fallows. Such opening of the canopy is beneficial for the germination of seeds; in particular pioneer species like *Anogeissus leiocarpa*, whose seeds primarily germinate on bare soils, are favored on fallows compared to sites with a dense vegetation cover (Bognounou et al. 2010; Sacande & Sanogo 2007).

For species assigned to group D (non-arable sites differed from fallows and the buffer zone), high juvenile densities of some species (*Detarium microcarpum*, *Combretum glutinosum*, *C. nigricans*, *Pteleopsis suberosa* and *Stereospermum kunthianum*) might be related to species ecological preferences or tolerance to specific soil conditions, such as increased soil acidity. The soils of non-arable sites were more acidic than those on fallows and in the buffer zone (high H-value and low pH); nevertheless, the soils were only slightly acidic which promotes nutrient availability and plant growth. However, for two species, *Isoberlinia doka* and *Philenoptera laxiflora*, we detected the lowest juvenile density on non-arable sites compared to fallows and the buffer zone. Although Arbonnier (2002) indicated habitat preferences for *I. doka* to loamy, well-drained soils, we suppose that rather human-induced changes in the population structure affect juvenile densities of this species (Jurisch et al. 2012a). Low numbers of juveniles may be due to a low density of mature individuals on non-arable sites, producing less offspring, or in the case of *P. laxiflora*, leaves are preferably browsed or used as fodder for goats (Arbonnier 2002, L. Houessou, pers. comm.), which may limit the number of juveniles and reduce the population viability as well (Hall & Bawa 1993; Dhillion & Gustad 2004; Gaoue & Ticktin 2008). For *I. doka*, some studies showed that the density of seedlings and saplings was more abundant below mature trees as the main dispersal mode of the species is dropping the seeds from pods under the mother tree and suckering that encourage aggregated distribution (Bationo et al. 2005, Dourma et al. 2006). The species *P. laxiflora* mainly reproduces by seed, thus, low numbers of juveniles may be due to the lack of reproductive individuals. In comparison, for *D. microcarpum*, *C. nigricans*, *P. suberosa* and *S. kunthianum*, the number of mature individuals were highest on non-arable sites compared to fallows and the buffer zone. Together with its ability to undergo vegetative reproduction, these species dominate on these sites.

Group E contained species showing no differences in juvenile densities between all land-cover types. For *Bombax costatum* and *Gardenia aqualla*, we detected an overall low density of juveniles, whereas juvenile densities of *Combretum molle* were high in all land-cover types. In a former study, we detected a similar pattern for sub-adult and adult individuals of *C. molle*, in relation to land use (Jurisch et al. 2012a). This species is not site-specific and show wide ecological amplitudes (Arbonnier 2002; Orwa et al. 2009). The species-specific characteristics, to reproduce vegetatively and to re-sprout after damaging, enhance its competitive strength and allow its persistence in many habitats (see Bond & Midgley 2001; Devineau & Fournier 2005; Drobnik et al. 2011; Lavorel et al. 1997). However, *G. aqualla* preferably grows in shady depressions or on alluvial terraces and has a scattered distribution by nature (Arbonnier 2002) which might result in this low number of juveniles in all land-cover types. The affiliation of *B. costatum* to this group might indicate an overall harvesting pressure across the species in all land-cover types; the wood of this tree species is eligible as construction material and its fibers are mainly used as filling, especially for mattresses and pillows (Arbonnier 2002; Oyen 2011). The flowers are the main ingredient for a sauce and were often collected through cutting of the entire branch. As it was mentioned before, the removal of large reproductive trees and plant parts can reduce the availability of seeds and might reduce the overall density of juveniles in an area if the impact is not compensated by their life histories as is the case for *B. costatum* (Gaoue & Ticktin

2008; Ticktin 2004; Schumann et al. 2011). Furthermore, its leaves are highly digestible and eaten by livestock, further reducing the number of young individuals.

Conclusion

Land use was shown to significantly affect juvenile densities of almost all studied woody species, as demonstrated by grouping of species according to their observed densities. Almost all species showed higher juvenile densities in the communal area compared to the buffer zone. We determined that the soil acidity and physical properties of the soil sub-surface horizon and vegetation structure are important factors differing between the land-cover types non-arable, fallows and the buffer zone. Although we detected significant differences in soil properties, their direct effects on juvenile densities are less pronounced than their indirect effects by altering the availability of resources (water and nutrients) for plants. Particularly in the buffer zone, the effect of below- and above-ground competition for space, light, water and nutrients may rather limit establishment and growth of seedlings and saplings, indicating a strong impact of human activities on plant populations by altering the relative ratio between grasses and woody plants (see Bond 2008; Sankaran et al. 2008; Scholes & Archer 1997). We showed that physical soil properties affect growing conditions for juveniles on non-arable sites and on fallows; especially through its effect on the amount of water that can be held and on the distribution of water within the soil. A good water-holding capacity of the soil might extend the growing season for a longer time by preserving soil water into the dry season or between rainfalls (McNaughton et al. 1983) and thus, enhances the establishment of juveniles. For plants growing on non-arable sites, drought resistance as well as early development of an effective root system to gain access to water may be an important feature enhancing the individual’s ability to low rainfall.

Due to the ongoing land use changes causing habitat loss, the shortening of fallow periods, and over-grazing, diverse sites for juveniles are becoming diminished. This development becomes more pronounced as the current adult populations are already under high human pressure (e.g., harvesting and pollarding), causing removal and impairment of the vitality of reproductive individuals. This can reduce the availability of seeds and may lead to a lack of regeneration (Plumptre 1995; Makana & Thomas 2006; McLaren et al. 2005). More studies on populations in their natural habitat, specifically in relation to land use and environmental conditions, are required to develop species-specific management strategies for allowing a high amount of natural regeneration to occur.

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Chapter 5

Conclusion

In Africa, the conversion of savanna, woodlands and forests into croplands has risen dramatically during the last few decades, driven mainly by the expansion of subsistence requirements of the growing human population (Graetz 1994, Houghton 1994, Reid et al. 2000, Niang et al. 2008, Reij et al. 2005). As a result of the stepwise land-use change, the landscape becomes fragmented and consists of patches of more or less native vegetation interspersed with a matrix of different land use systems, including agriculture (Stoate et al. 2001, Green et al. 2005, Abdullah & Nakagoshi 2006). The critical issue of the expansion of agriculture is not just the area of conversion, but also the structural and functional changes of the remaining sites (Graetz 1994, Higgins et al. 1999). At these sites, the ongoing exploitation of timber and non-timber forest products, temporary grazing and fire, contributes to degradation through overuse and modifies demographic parameters such as germination, seedling and sapling growth and mortality rates (Graetz 1994, Guariguata & Pinard 1998, Vermeulen et al. 2011) and therefore, affects the population structure of woody plants. In addition, natural events such as fluctuations in recruitment rates and establishment failures, affect the population structure, and lead to over-aged populations with gaps in diameter classes. The fact that most of the occurring species provide valuable NTFPs to fulfill subsistence needs for the rural population or contribute notably to the total household income (Kristensen & Balslev 2003; Lykke et al. 2004, Heubach 2011), underlines the importance of gaining more knowledge of all woody plants to conserve these important natural resources. In the context of growing land-use pressure, a thorough knowledge of plant population biology and ecological preferences of all woody plants is important to evaluate the consequences of this development on savanna woody plants (see Skarpe 1991, Obiri et al. 2001, Wezel & Lykke 2008).

By analyzing the population structure of a large number of woody savanna species under semi-natural conditions in comparison to the population structure in communal areas more altered by human impact (**chapter 2**), it was shown that land-cover type influenced size-class distribution. Our findings show that some woody plant populations are affected by human-induced disturbances (e.g., *Burkea africana*, *Isoberlinia doka*, *Lannea acida* and *Pterocarpus erinaceus*) while others perform very well under the current land use system (e.g., *Detarium microcarpum*, *Combretum molle* and *Vitellaria paradoxa*). They show well-shaped size-class distributions with high numbers of juveniles and a gradual decline with increasing stem diameter. For many species, only certain stages of the life-cycle or size-classes are affected by land use practices, respectively. However, within **chapter 3**, we showed that the survival and growth of woody species seedlings and saplings are strongly related to land use. Almost all species developed better in the communal area compared to the buffer zone, showing high survival and growth rates. Human activities have an indirect positive effect on seedlings and saplings by providing diverse, small-scale habitats that vary in time, such as bare soils, or by reducing vegetation cover. The population of some tree species, *Anogeissus leiocarpa, Isoberlinia doka*, *Lannea acida* and *Terminalia avicennioides* performed best in the communal area and are likely to decline in the buffer zone as the detected transition probabilities were extremely low. This pattern is explained by the beneficial effect of on open canopy for the germination of seeds and the establishment of new suckers (Goldberg & Werner 1983, Silvertown & Smith 1989, Bakker & Devries 1992). Such opening of the vegetation cover also enhances the survival of juveniles by altering the relative ratio between grasses and woody plants and therefore, reducing competition for light, water and nutrients (see Bond 2008, Sankaran et al. 2008, Scholes & Archer 1997). This assumption was proved by the results presented in **chapter 4**, which shows that vegetation structure (height and percentage cover of the herb layer) is an important factor affecting juvenile densities.

This study also detected soil reaction and physical soil properties as being important factors differing between land-cover types. I was able to show that physical soil properties affect growing conditions for juveniles on non-arable sites and on fallows, noticeably through its effect on water-holding capacity and distribution of water within the soil. A sufficient water-holding capacity of the soil might extend the growing season for a longer time by preserving soil water into the dry season or between rainfalls (McNaughton et al. 1983) enhancing juvenile establishment.

A major conclusion to be drawn from this thesis is that land use influences savanna vegetation in a complex way and does not necessarily lead to a decline or loss of tree populations and species. It is rather that in a constantly changing landscape, as a result of human-induced disturbances, populations of ubiquitous and some common species can be stable over time. The abundance of some species tends to decline consistently, whereas others benefit from human disturbance (Abbadie et al. 2011). However, by means of different statistical methods applied to the data, I was able to identify groups of species responding in extraordinarily similar ways to land use. In each single study, different species were affiliated to a certain group showing no statistical differences regarding either their size-class distribution as it is shown in **chapter 2**, their survival and transition probabilities (**chapter 3**) or their juvenile densities (**chapter 4**). Although all studies focused on different demographical aspects to describe and evaluate the current state of populations of savanna woody plants, some general patterns and common trends can be discerned.

Approximately one third of the species studied showed a well-shaped size-class distribution with high recruitment rates regardless of land-cover type. Their competitive strength is higher when compared to other species, as they are able to tolerate human-induced disturbances, such as coppicing, fire and grazing, by vegetative reproduction, fire resistance traits and re-sprouting. Some of them are ubiquitous species, partly invasive and show wide ecological amplitudes (e.g., *Combretum molle*, *Dichrostachys cinerea* and *Piliostigma thonningii*), whereas others achieve their competitive strength under native environmental conditions (e.g., *Annona senegalensis*, *Combretum collinum*, *C. glutinosum*, *Crossopteryx febrifuga*, *Detarium microcarpum* and *Pteleopsis suberosa*). The latter species are most likely to occur on non-arable sites, which are not well suited for agricultural use due to its soil and relief conditions. The population of *Vitellaria paradoxa* is facilitated by traditionally managed agro-forestry systems. This tree has a high socioeconomic importance and is spared when woodland is cleared for agriculture (Boffa 1999, Petit 2003, Augusseau *et al.* 2006, Heubach et al. 2011). Individuals of all diameter classes are often maintained on fallows and non-arable sites (Lovett & Haq 2000) resulting in a well-shape size-class distribution as shown in chapter 2. *V. paradoxa* may benefit directly from humans as it is of high local and regional value for the human population.

Approximately one-third of the studied species were trees where I found a strong influence of local land use on size-class distribution and therefore on population structure (e.g., *Anogeissus leiocarpa*, *Burkea africana*, *Isoberlinia doka, Lannea acida* and *Pterocarpus erinaceus*). Many of these species developed best in young stages in the communal area (non-arable sites and fallows) compared to protected areas as I detected high densities of seedlings and saplings on these sites. However, for most of theses species, individuals in the medium and large diameter classes were lacking. This may be due to the exploitation of appropriate individuals for firewood and construction material. As my studies revealed that environmental conditions and human land use significantly decrease the annual recruitment rate of seedlings and saplings and for some populations, the annual recruitment was extremely low and thus it is expected that those populations are likely to decline. My findings correspond to other studies on population structure of savanna woody plants, where a change of land-cover types from one with predominance of large-single trunked trees to one dominated by shrubs and small trees due to a lack of individuals in certain size classes is expected (Lykke 1998; Ouedraogo 2006; Vincke et al. 2010; see also Bond & Midgley 2001). Hence, I presume that this progression leads towards a homogenization of the vegetation where only those species that are well adapted to frequent disturbances through their ability to persist in one stage of the life cycle and re-develop after adverse environmental conditions will dominate. This development is more pronounced in communal areas experiencing continual degradation due to intense expansion of agriculture, habitat fragmentation and increased disturbance frequency. Hence, there is a need for more studies in communal areas as these areas are larger than protected areas and the few remaining semi-natural sites are likely to decrease in the future. Repeated density studies analyzing survivorship and transition probabilities over a number of seasons as well as long-term in-situ experiments in settlement areas, should be undertaken in order to understand the population of woody plants in settlement areas. A challenge will be the development of strategies to protect species within a landscape under cultivation.

The last third of the studied species present an inhomogeneous group including species showing different and partly opposite trends in their population structure and dynamics. For most of them, I recorded high juvenile densities, particularly on fallows, but a lack of individuals in medium and large size classes. Some species show explicit habitat preferences, for example, *Feretia apodanthera* and *Diospyros mespiliformis*, which are often found on termite mounds or in (gallery) forests (Lawesson 1990, Ellery et al. 1993, Hovestadt et al. 1999). Other species such as *Gardenia aqualla*, *G. erubescens*, *G ternifolia* and *Stereospermum kunthianum* have a scattered or clumped distribution by nature (Arbonnier 2002), which might result in an under-representation of these species within my study. Due to ongoing land-use changes leading to habitat loss and the shortening of fallow periods, those sites for juveniles are becoming fewer and human pressure (e.g., harvesting and pollarding) on the current adult populations is likely to increase, causing removal and vitality impairment of reproductive individuals. As mentioned above, my findings provide an insight into the structure and dynamics of those common, but less dominant species; thus, there is an urgent need for further basic studies to assess the impact of land use and ecological preferences of these species.

Summary

Savanna regions in West Africa are valuable cultural landscapes and provide a wide range of ecosystem services for human well-being and are frequently affected by human-induced disturbances. Aside from agricultural activities (crop production and animal husbandry), the harvesting of timber and non-timber forest products is crucial for household income, alimentation and medicinal purposes. Most indigenous woody species have undergone increasing anthropogenic pressure as social and economic conditions have changed dramatically during recent decades (for detailed studies see Descroix et al. 2009, Norris et al. 2010, Ouedraogo et al. 2010), resulting in further habitat fragmentation and increased disturbance severity. In the context of land-use change, there is an urgent need to better understand and evaluate the impact of land-use on savanna vegetation, particularly on the population biology of common savanna woody species.

In the first study (chapter 2), I investigated the population structure described by size-class distribution (SCD) of 30 indigenous woody species (1) to explore the effect of land use on the population structure of woody savanna species; and (2) to search for species with similar population structures related to comparable ecological preferences. General linear models were applied to reveal the influence of the three land-cover types studied and to identify comparable population structures of species with similar ecological preferences. I identified five groups for shrub species and four groups for tree species with different population structures and comparable ecological preferences. In terms of human impact, I detected four groups of species responding similarly to land use. Notably for trees, I found a strong influence of local land use on SCD and hence, population structures. The SCD of shrub species tends to be more related to species’ ecological preferences. Some of the shrub species may be

characterized as ubiquitous species as their SCD is neither related to land use nor to ecological preferences, indicating a high tolerance to disturbance. The observed results show that land use has significant implications on local woody species composition.

As the seedling and sapling stages are usually a critical phase in regeneration, in **chapter 3** I asked additionally to the previous description of the population structure of woody plant populations, if survival and growth of seedlings and saplings of woody savanna species are related to habitat conditions and land use. To determine the environmental factors (e.g., land use) affecting survival and transition probabilities, individuals of 18 common woody species were monitored for 2.5 years; data were analyzed using multistate capture-recapture models. I detected six groups of species with similar survival and transition probabilities. For one of these groups I found no correlation to land use whereas the other groups comprise species with distinct preferences for different land-cover types. Most species developed better in the communal area compared to the protected areas. Five species (one shrub and four trees), showed an extremely low transition probability for the latter land-cover type. For some species groups, differences in plant performance were explained by a human induced opening of the canopy: a process beneficial for the germination of seeds and enhances the survival of juveniles by reducing the competition for light, water and nutrients. Other species showed their best demographic performance in the communal area on non-arable sites with unfavorable environmental conditions and resulting in small-scale heterogeneity (mosaic of bare ground and areas with low herbaceous cover), whereas five species were shown to decline in the protected area.

In the last study (**chapter 4**), I investigated patterns of population densities in relation to soil conditions, vegetation structure and land-cover type of a broad set of characteristic savanna species to obtain a better understanding of the influence of land use and related environmental factors on the juvenile stage of woody species. I applied Tukey's multiple comparison tests and statistical modeling (linear mixed effect models, LME and generalized linear models, GLM) in order to (1) analyze the influence of land use on juvenile densities for 25 species (16 shrubs, 7 trees) and (2) determine which

environmental conditions were related to juvenile densities next to the influence of land use. In terms of human impact, I detected five groups of species responding similarly to land use according to their observed densities. Almost all species showed higher juvenile densities in the communal area compared to the buffer zone. Soil reaction, as well as physical properties of the soil sub-surface horizon and vegetation structure was identified, as important factors differing between the land-cover types non-arable, fallows and the buffer zone. Although significant differences were detected in soil properties, their direct effects on juvenile densities are less pronounced than their indirect effects by altering the availability of resources (water and nutrients) for plants. Particularly in the buffer zone, the effect of below- and aboveground competition for space, light, water and nutrients may rather limit establishment and growth of seedlings and saplings, indicating a strong impact of human activities on plant populations by altering the ratio between grasses and woody plants. My findings provide an insight into the structure and dynamics of common, dominant and less dominant savanna woody plants in a communal and a protected area. There is a need for further basic studies to assess the impact of land use and ecological preferences of all species, including repeated density studies that look at survivorship and transition probabilities over a number of seasons as well as long-term in-situ experiments in settlement areas in order to better understand woody plant populations in settlement areas as the few remaining semi-natural sites are likely to decrease in the future. A challenge will be the development of strategies to protect species within a landscape under cultivation.

Zusammenfassung

Die Savannenökosysteme Westafrikas sind wie überall in den Tropen geprägt von einer kontinuierlichen, gräserdominierten Krautschicht und einer mehr oder weniger dicht ausgebildeten Baum- und Strauchschicht. Seit mehreren Jahrtausenden siedeln Menschen in den Savannengebieten Westafrikas und leben von der Vielfalt natürlicher Ressourcen und Produkte, die dieser Lebensraum bereithält. Infolge menschlicher Tätigkeit haben sich Struktur und Dynamik von Savannen stark verändert, so dass uns heute eine Landschaft begegnet, die stark von menschlicher Nutzung geprägt ist. Eine typische Form der Landnutzung in Westafrika ist die Landwechselwirtschaft, bei welcher der Ackernutzung eine langjährige Brachephase folgt. Es wird eine Vielzahl von Feldfrüchten angebaut, vor allem Mais, Hirse, Sorghum und Jams für den Eigenbedarf, sowie für den Verkauf bestimmte Kulturpflanzen (*cash crops*) wie Baumwolle, Erdnüsse und Cashew. Neben dem Ackerbau spielt die Haltung und Zucht von Rindern und kleinen Wiederkäuern wie Ziegen und Schafen eine bedeutende Rolle. Als Weideland dienen Brachen, nicht kultivierbare Standorte und abgeerntete Felder. Neben Ackerbau und Viehzucht ist die Verwendung von Wildpflanzen (sogenannte Nichtholzprodukte wie Blätter, Borke, Früchte und Wurzeln) in der Medizin, der täglichen Ernährung und im Haushalt fest in den traditionellen Lebensgewohnheiten verankert. Darüber hinaus bedeuten sie für viele Familien eine zusätzliche Einkommensquelle und dienen in Krisenzeiten, z.B. durch Ernteausfälle ausgelösten Hungerszeiten, als maßgebliche (finanzielle) Rücklage. Von der Vielzahl an nutzbaren Wildpflanzen liefern insbesondere Gehölze, sowohl Baum- als auch Straucharten, wertvolle Produkte. Aufgrund ihrer sozioökonomischen und kulturellen Bedeutung werden einige Baumarten bei der Rodung von Savannenflächen zu Ackerflächen ausgenommen. Dazu gehören der Shea-Butterbaum (*Vitellaria paradoxa* C.F.Gaertn), der Baobab (*Adansonia digitata* L.), die Tamarinde (*Tamarindus indica* L.) und der Néré (*Parkia biglobosa* (Jacq.) R.Br. ex G.Don).

Da sich die Umwelt- und Lebensverhältnisse für die Bevölkerung in Westafrika stark verändert haben, ist innerhalb der letzten Jahrzehnte der Nutzungsdruck auf die meisten autochthonen Savannengehölze stark angestiegen. Neben den Auswirkungen des globalen Klimawandels (zunehmende Variabilität der Niederschläge, höheres Erosionsrisiko) vollziehen sich gesellschaftliche (Bevölkerungswachstum, Migration, Konkurrenz um Flächen) und ökonomische (Globalisierung, Ausrichtung der Landwirtschaft auf die Anforderungen des Weltmarkts) Veränderungen. Dies führte zur Veränderung der traditionellen Landwechselwirtschaft und der Ausweitung landwirtschaftlicher Kulturflächen. Neben der Verkürzung oder dem Aussetzen der traditionellen 15-20-jährigen Brachezeiten werden verstärkt mineralische Dünger und Pflanzenschutzmittel eingesetzt. Mit der Ausweitung des Anbaus marktfähiger Agrarprodukte findet häufig eine Mechanisierung der Feldarbeit statt. Diese Veränderungen führen zu einer Fragmentierung und Isolation der verbleibenden naturnahen Habitate, in welchen die Häufigkeit und Intensität der Beeinträchtigungen und Störungen, die auf die Vegetation wirken, zunehmen. Da autochthone Bäume und Sträucher von der Bevölkerung meist nicht gepflanzt werden, ihre Produkte jedoch auch zukünftigen Generationen zur Verfügung stehen sollen, ist es daher dringend erforderlich, vor allem vor dem Hintergrund des kontinuierlich stattfindenden Landnutzungswandel, den Einfluss der Landnutzung auf Gehölzpflanzen besser verstehen und bewerten zu können.

Die vorliegende Arbeit untersucht den Einfluss der Landnutzung auf die Struktur und Dynamik von Gehölzpopulationen in einer ausgewählten Savannenlandschaft im Norden Benins. Das Untersuchungsgebiet befindet sich in der Peripherie des „W Nationalparks“ und umfasst sowohl das Siedlungsgebiet als auch die Pufferzone des Nationalparks. Die enge räumliche Nähe von unterschiedlich stark genutzten Flächen gestattet es, den Einfluss geringer Landnutzung (unregelmäßige Beweidung, kontrolliertes Feuerregime, keine frühere Ackernutzung) und intensiver

Landnutzung (regelmäßige Beweidung, Nutzung von Holz- und Nichtholzprodukten, variierendes Feuerregime, teilweise ehemalige Ackernutzung) auf die Struktur und Dynamik von Gehölzpopulationen zu untersuchen. Eine Population umfasst eine Gruppe von Individuen einer Art, die im gleichen Gebiet zur gleichen Zeit vorkommen und über eine spezifische Struktur, sei es eine räumliche oder Größenklassenstruktur verfügen. Der Begriff der Populationsstruktur umschreibt nachfolgend die Größenklassenstruktur einer Population, also das Verhältnis zwischen juvenilen, sub-adulten und adulten Individuen. Dieses Verhältnis verändert sich kontinuierlich. Die Frage über die zugrundeliegenden Mechanismen und die Ursache dieser Veränderungen, denen Prozesse wie Entstehen, Wachsen und Sterben von Individuen zugrunde liegen, beantwortet die Populationsdynamik.

Die erste Studie (**Kapitel 2**) beschreibt den Einfluss der Landnutzung auf die Populationsstruktur von 30 typischen Savannengehölzen. Hierbei sollen Arten ermittelt werden, die eine ähnliche Populationsstruktur und vergleichbare ökologische Standortansprüche aufweisen. Diese, wie auch die nachfolgenden Studien wurden auf nicht-kultivierbaren Savannenstandorten und Ackerbrachen im Siedlungsgebiet und in der Pufferzone des Nationalparks durchgeführt. In jeder dieser Landnutzungskategorie wurden auf repräsentativen Flächen Höhe und Durchmesser aller Gehölze, sowohl des Jungwuchses als auch der sub-adulten und adulten Individuen erfasst. Für die Auswertung wurden generalisierte lineare Modelle angewandt, um zum einen Arten mit ähnlicher Populationsstruktur zu identifizieren und zum anderen, den Einfluss der Landnutzung auf die Populationsstruktur jeder Gehölzart zu ermitteln. Beim Vergleich der Größenklassenverteilung der untersuchten Arten konnten fünf Gruppen für die Straucharten und vier Gruppen für die Baumarten ermittelt werden, wobei die zu einer Gruppe gehörenden Arten eine vergleichbare Populationsstruktur aufwiesen. Hinsichtlich des Einflusses der Landnutzung auf Gehölze konnten vier Artengruppen gebildet werden, deren Populationsstruktur in ähnlicher Weise den Einfluss dieses Faktors abbildet. Anhand der Zugehörigkeit der Einzelarten zu den gebildeten Gruppen wurde abschließend bewertet, in welchem Maße die Landnutzung einen Einfluss auf die Populationsstruktur hat. Einige Baumarten waren stark von der Landnutzung beeinflusst, meist jedoch nur in bestimmten Entwicklungsstadien. So beeinträchtigt die Präsenz der bis zu drei Meter hohen Gräser in der Pufferzone vor allem den Jungwuchs in der Entwicklung (durch inter-spezifischer Konkurrenz und Steigerung der Feuerintensität). Das Fehlen mittlerer und großer Durchmesserklassen kann auf einen direkten Nutzungseinfluss, z.B. durch die Entnahme von Stämmen zur Verwendung als Brenn- und Bauholz, aber auch auf natürliche Gegebenheiten, z.B. die Häufigkeit und Verbreitung von Arten im Untersuchungsgebiet, zurückgeführt werden. Für viele Straucharten hingegen hatten anthropogen bedingte Störungen keinen Einfluss auf die Populationsstruktur. Dies zeigte sich in einer hohen Anzahl an Jungwuchs und einer ausreichenden Anzahl an Individuen in den sub-adulten und adulten Größenklassen, was für stabile Population kennzeichnend ist. Diese Arten können als Ubiquisten bezeichnet werden. Neben Arten ohne besondere Standortansprüche zeigten einige Gehölzarten nur unter bestimmten Standortbedingungen eine stabile Populationsstruktur, wenn sie dort aufgrund der für sie optimalen Bedingungen eine höhere Konkurrenzfähigkeit gegenüber anderen Arten aufwiesen.

In den beiden folgenden Studien (**Kapitel 3 und 4**) stand der Jungwuchs der Gehölze im Mittelpunkt der Betrachtungen. In diesem sensiblen Lebensabschnitt können eine Reihe von abiotischen (z.B. Feuer, Wasser- und Nährstoffverfügbarkeit) und biotischen Faktoren (z.B. Herbivorie, inter- und intraspezifische Konkurrenz) die Etablierung und Entwicklung der jungen Pflanzen beeinträchtigen. In Kapitel 3 widmete ich mich dem Einfluss der Landnutzung auf das Überleben und das Wachstum junger Gehölzpflanzen kleiner als einem Meter. Hierfür wurden 18 Gehölzarten regelmäßig über einen Zeitraum von zweieinhalb Jahren auf Dauerflächen erfasst. Die Überlebens-wahrscheinlichkeit und die Wahrscheinlichkeit mit der ein Individuum von einer Durchmesserklasse in die folgende wächst (Übergangswahrscheinlichkeit) wurden mithilfe der *multistate capture-recapture* Methode modelliert. Es konnten Artengruppen gebildet werden, die ähnliche Überlebens- und Wachstumsraten in den drei untersuchten Landnutzungskategorien aufwiesen. Die Ergebnisse zeigen, dass Landnutzung einen starken Einfluss auf das Überleben und Wachstum der meisten untersuchten Gehölzarten hat. Lediglich eine Art zeigte keine Reaktion auf Landnutzung. Für die Mehrheit der Arten war die Überlebens- und Übergangswahrscheinlichkeit im Siedlungsgebiet größer als in der Pufferzone. Langfristig ist die Stabilität einiger Gehölzpopulationen in der Pufferzone gefährdet, da zu wenig Jungwuchs zu sub-adulten oder adulten Individuen heranwächst. Die hohen Überlebens- und Wachstumsraten einiger Arten im Siedlungsgebiet sind auf positiv rückwirkende Effekte der menschlichen Nutzung zurückzuführen. So reduziert die kleinräumige Öffnung der Kraut- und Gehölzschicht die Konkurrenz der jungen Gehölze mit benachbarten Pflanzen um Raum, Licht, Wasser und Nährstoffe. Gleichfalls entsteht durch Verbiss und Tritt der Weidetiere und die in Zeitpunkt, Intensität und Frequenz variierenden Feuer ein kleinräumiges Mosaik aus vegetationsfreien und dichter mit Vegetation bestandenen Standorten, was sich infolge der veränderten Konkurrenzverhältnisse zwischen Gräsern und Gehölzen positiv auf die Entwicklung einiger Arten auswirkt. Korrespondierend zu den Ergebnissen der vorausgehenden Studie spiegeln sich artspezifische Habitatpräferenzen in Struktur und Dynamik der Population wieder, wie hier in den hohen Überlebens- und Wachstumsraten. Arten, die unter für sie optimalen ökologischen Bedingungen wachsen sind dort sind im Vergleich zu anderen Arten konkurrenzfähiger, z.B. durch die Fähigkeit zur vegetativen Vermehrung oder Neuaustrieb nach Schädigung. Wie ich in meiner Studie zeigen konnte, stellt die Fähigkeit zum Neuaustrieb und zur vegetativen Reproduktion in häufigen von Störungen beeinflussten Savannenökosystemen eine wichtige Eigenschaft dar und wird z.B. in den hohen Überlebensraten deutlich.

Die letzte Studie (**Kapitel 4**) beschäftigt sich vertiefend mit dem Einfluss von Landnutzung und weiteren Umweltfaktoren auf die Abundanz von Jungwuchs. In die Analyse wurden sowohl physikalische und chemische Bodenparameter als auch strukturelle Parameter, wie Höhe und Deckung der Krautschicht, einbezogen. Mit Hilfe eines mehrstufigen Tukey Vergleichstest wurde zunächst überprüft, welche der

Umweltfaktoren signifikant verschieden zwischen den Landnutzungskategorien sind. In einem weiteren Schritt wurden statistische Modelle (lineare gemischte Modelle und generalisierte lineare Modelle) angewandt, um pro Art einerseits den Einfluss der Landnutzung auf die Abundanz des Jungwuchses zu bestimmen und andererseits die Umweltfaktoren kenntlich zu machen, die die Abundanz des Jungwuchses beeinflussen. Erwartungsgemäß zu den Ergebnissen der vorausgegangenen Studien hatte die Landnutzung auf die Abundanz des Jungwuchses einen sehr starken Einfluss. Es wurden fünf Artengruppen gebildet, in denen die Abundanz des Jungwuchses in verschiedenen Landnutzungskategorien ähnlich war. Die höchste Anzahl an Jungpflanzen wurde für das Siedlungsgebiet nachgewiesen. Neben bodenphysikalischen Eigenschaften und der Bodenazidität, war die Höhe der Krautschicht signifikant verschieden innerhalb der Landnutzungskategorien. Der direkte Einfluss dieser Faktoren auf den Jungwuchs ist jedoch weniger bedeutsam, vielmehr wirken sie indirekt auf den Jungwuchs in dem sie die Verfügbarkeit von Ressourcen (Wasser und Nährstoffe) für die Pflanzen beeinflussen. Dieser Effekt tritt deutlich in der Pufferzone hervor, in welcher die unter- und oberirdische Konkurrenz der Gehölzpflanzen mit den Gräsern um Raum, Licht, Wasser und Nährstoffe die Etablierung und das Wachstum des Jungwuchses beeinträchtigen kann. Insbesondere im Siedungsgebiet beeinflussen bodenphysikalische Eigenschaften die Wachstumsbedingungen der Pflanzen, indem sie die Wasserspeicherkapazität des Bodens und die Verteilung des Bodenwassers im Bodenkörper beeinflussen. So kann bspw. infolge einer guten Wasserkapazität des Bodens die Wachstumsperiode junge Gehölze verlängert werden, wodurch diese über einen längeren Zeitraum Nährstoffe aufnehmen können, um so z.B. nach Störungen schnell und kräftig austreiben zu können.

Die Ergebnisse der vorliegenden Arbeit verdeutlichen, dass der Einfluss der Landnutzung auf die Struktur und Dynamik von Gehölzpopulationen sehr komplex und vielschichtig ist. Bemerkenswert ist, dass anthropogener Einfluss nicht zwangsläufig einen Rückgang der Population oder einen Verlust von Arten bewirkt. Basierend auf meinen Ergebnissen und der Vergleich mit anderen Studien schließe ich, dass in einer sich durch anthropogenen Einfluss kontinuierlich verändernden Landschaft, vor allem ubiquitäre Arten und einige wenige häufige und weit verbreitete Arten, auf lange Sicht stabile Populationen aufweisen werden. Einige Arten scheinen von den durch den Menschen ausgelösten Störungen zu profitieren, während dieser Einfluss andere Populationen negativ beeinflusst. Hierfür wurden zahlreiche Beispiele gegeben. Allerdings sind infolge der anhaltenden Landnutzungsintensivierung Savannenhabitate einem immer größeren Risiko der Zerstörung ausgesetzt, so dass sich der Nutzungsdruck auf die verbleibenden Flächen und Arten noch mehr erhöhen wird. Indem ich in meine Untersuchungen eine große Anzahl von Gehölzarten integriert habe, erweitern meine Studien das Wissen zur Ökologie und Populationsbiologie vieler typischer Savannengehölze. Darüber hinaus zeigen alle Studien eine herausragende Gemeinsamkeit: In jeder Einzelstudie war es mir möglich, Arten, die statistische Gemeinsamkeiten hinsichtlich ihrer Populationsstruktur (Kapitel 2), ihrer Überlebens- und Übergangswahrscheinlichkeit (Kapitel 3) oder ihrer Abundanz (Kapitel 4) in Bezug zur Landnutzung aufwiesen, zusammenzuführen und übergeordnete Artengruppen zu bilden, was bisher nur sehr selten in Untersuchungen vorgenommen wurde. Obwohl in allen Einzelstudien verschiedene demografische Kenngrößen betrachtet werden, lassen sich allgemeingültige und generelle Trends ableiten.

Etwa ein Drittel der untersuchten Arten zeigte eine stabile Größenklassenverteilung mit einer hohen Anzahl von Jungwuchs und einer stetig abnehmenden Anzahl von Individuen in größeren Größenklassen unabhängig von der Landnutzung. Einige dieser Arten sind Ubiquisten, wie z.B. *Combretum molle*, *Dichrostachys cinerea* und *Piliostigma thonningii*, während andere auf Standorten dominieren, auf welchen sie für sie optimale Wachstumsbedingungen vorfinden (z.B. *Annona senegalensis*, *Combretum collinum*, *C. glutinosum*, *Crossopteryx febrifuga*, *Detarium microcarpum* und *Pteleopsis suberosa*). Die stabile Populationsstruktur des Sheabutter-Baum, *Vitellaria paradoxa*, ist direkt durch menschlichen Einfluss begünstigt. Diese Art hat eine weite ökonomische Bedeutung für die Bevölkerung und wird bspw. beim Roden der Savanne für neue Ackerflächen stehen gelassen.

Ein Drittel der untersuchten Arten waren Bäume, für welche ich einen starken Einfluss der Landnutzung auf die Populationsstruktur feststellen konnte (z.B. *Anogeissus leiocarpa*, *Burkea africana*, *Isoberlinia doka, Lannea acida* und *Pterocarpus erinaceus*). Viele der genannten Arten entwickelten sich in den frühen Phasen des Lebenszyklus im Siedlungsbereich besser als im Vergleich zur Schutzzone, was durch eine höhere Anzahl an Jungwuchs deutlich wurde. Für die meisten Arten wurden allerdings nur wenige oder gar keine sub-adulten und adulten Individuen gefunden, was sehr wahrscheinlich in der intensiven Nutzung dieser Gehölze als Bau- und Brennholz begründet liegt. Meine Studien belegen, dass Umweltbedingungen und Landnutzung die jährlichen Wachstumsraten von jungen Gehölzindividuen signifikant reduzieren. Bei einigen Arten war der Zuwachs so gering, dass die Stabilität der Populationen langfristig gefährdet ist, da zu wenige Juvenile zu sub-adulten oder adulten Individuen heranwachsen. Einhergehend mit einer Überalterung der Bestände führt diese zu einer Veränderung der Landschaft, von einer, von großen Solitärbäumen gekennzeichnete Landschaft, hin zu einer von niedrigwüchsigen Bäumen und Sträuchern dominierten. Diese Tendenz wurde bereits einigen Studien beschrieben und wird im Siedlungsgebiet stärker sichtbar werden als in Schutzgebieten, da Habitate im Siedlungsgebiet infolge der Ausweitung der landwirtschaftlichen Nutzfläche stärker beeinträchtigt und gestört sind.

Das letzte Drittel der untersuchten Arten bildet eine inhomogene Gruppe, in welcher Arten enthalten sind, deren Populationsstruktur und -dynamik verschiedene und mitunter gegenläufige Muster aufweist. Die meisten von ihnen hatten eine hohe Anzahl von jungen Individuen, jedoch wenige oder fehlende Individuen in den größeren Größenklassen. Einige Arten verfügen über ausgeprägte Habitatpräferenzen (z.B. *Feretia apodanthera* und *Diospyros mespiliformis*), während andere eher geklumpt oder zerstreut vorkommen (z.B. *Gardenia aqualla*, *G. erubescens*, *G ternifolia* und *Stereospermum kunthianum*). Dies kann zu einer Unterrepräsentation dieser Arten in den Studien geführt haben.

Neben der Tatsache, dass über die meisten meiner untersuchten Gehölzarten keine Informationen zum Zustand der Populationen vorliegen, werden fast alle von der Bevölkerung in vielfältiger Weise genutzt. Dies unterstreicht die Bedeutung, die Kenntnisse über die Arten zu vertiefen, damit sie auch langfristig von der Bevölkerung genutzt werden können. Eine Herausforderung stellt die Entwicklung geeigneter Maßnahmen zum nachhaltigen Schutz von Arten im Siedlungsgebiet dar, da diese Standorte flächenmäßig bedeutsamer sind als Schutzgebiete und die wenigen verbliebenen naturnahen Habitate in Zukunft weniger werden. Langfristig angelegte Wiederholungsaufnahmen, *in situ* Experimente und Grundlagenstudien zur besseren Kenntnis der Populationsbiologie und der Ökologie der Arten unter verschiedenen Landnutzungssystemen sind hierfür unerlässlich.

References

Abbadie, L. & Lensi, R. 1990. Carbon and nitrogen mineralization and denitrification in a humid savanna of West Africa (Lamto, Ivory-Coast). *Acta Oecologica* 11: 717-728.

Abdullah, S.A. & Nakagoshi, N. 2006. Changes in landscape spatial pattern in the highly developing state of Selangor, peninsular Malaysia. *Landscape and Urban Planning* 77: 263-275.

Abrahamson, W.G. 1980. Demography and vegetative reproduction. In: Solbrig, O.T. (ed.) *Demography and evolution in plant populations*, pp. 89-106. University of California Press, Berkeley, US.

Acacio, V., Holmgren, M., Jansen, P.A. & Schrotter, O. 2007. Multiple recruitment limitation causes arrested succession in Mediterranean cork oak systems. *Ecosystems* 10: 1220-1230.

African Plant Database (version 3.4.0). Conservatoire et Jardin botaniques de la Ville de Genève and South African National Biodiversity Institute, Pretoria, URL: http://www.ville-ge.ch/musinfo/bd/cjb/africa/ (Accessed April 2012).

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, B.N. & Csaki, F. (eds.) *Second International Symposium on Information theory*, pp. 267-281. Akademiai Kiado, Budapest, HU.

Akaike, H. 1981. Likelihood of a model and information criteria. *Journal of Econometrics* 16: 3-14.

Alexandre, D.-Y. & Kaïré, M. 2001. Les productions des jachères africaines à climat soudanien (Bois et produits divers). In: Floret, C. & Pontannier, R. (eds.) *La Jachère en Afrique Tropicale- Rôle et aménagement, alternatives*, pp. 169-199. John Libbey Eurotext, Paris, FR.

Arbonnier, M. 2002. *Arbres, arbustes et lianes des zones sèches d'Afrique de l'Ouest.* 2nd ed. CIRAD, MNHN, Paris, FR.

Augusseau, X., Nikiema, P. & Torquebiau, E. 2006. Tree biodiversity, land dynamics and farmers' strategies on the agricultural frontier of southwestern Burkina Faso. *Biodiversity* and *Conservation* 15: 613-630.

Avocevou-Ayisso, C., Sinsin, B., Adegbidi, A., Dossou, G. & van Damme, P. 2009. Sustainable use of non-timber forest products: Impact of fruit harvesting on *Pentadesma butyracea* regeneration and financial analysis of its products trade in Benin. *Forest Ecology and Management* 257: 1930-1938.

Bakker, J.P & de Vries, Y. 1992. Germination and early establishment of lower salt-marsh species in grazed and mown salt marsh. *Journal of Vegetation Science* 3: 247-252.

Bates, D., Maechler, M. & Bolker, B. 2011. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42. http://CRAN.R-project.org/package= lme4 mixed-effects models using S4 classes. R package version 0.999375-42. URL: http://CRAN.R-project.org/package=lme4.

Bationo, B.A., Ouedraogo, S.J. & Guinko, S. 2001. Stratégies de régénération naturelle de *Detarium microcarpum* Guill. et Perr. dans la forêt classée de Nazinon (Burkina Faso). *Fruits* 56: 271-285.

Bationo, B.A., Ouedraogo, S.J. & Guinko, S. 2001. The longevity of seed and the constraints of survival of seedlings of *Afzelia africana* Sm. in a woody savannah in Burkina Faso. *Annals of Forest Science* 58: 69-75.

Baudron, F., Corbeels, M., Monicat, F. & Giller, K.E. 2009. Cotton expansion and biodiversity loss in African savannahs, opportunities and challenges for conservation agriculture: a review paper based on two case studies. *Biodiversity and Conservation* 18: 2625-2644.

Bayer, W. 1990. Use of native browse by Fulani cattle in central Nigeria. *Agroforestry Systems* 12:217-228.

Bellefontaine, R. 2005. Pour de nombreux ligneux, la reproduction sexuée n'est pas la seule voie : analyse de 875 cas - Texte introductif, tableau et bibliographie. *Sécheresse* 1 E: 1-39.

Bellingham, P.J. & Sparrow, A.D. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409-416.

Biaou, S.S.H., Holmgren, M., Sterck, F.J. & Mohren, G.M.J. 2011. Stress-driven changes in the strength of facilitation on tree seedling establishment in West African woodlands. *Biotropica* 43: 23-30.

Bissels, S., Holzel, N. & Otte, N. 2004. Population structure of the threatened perennial *Serratula tinctoria* in relation to vegetation and management. *Applied Vegetation* Science 7: 267-274.

Boffa, J.-M. 1999. *Agroforestry parklands in sub-Saharan Africa*. [FAO conservation guide 34], Food and Agricultural Organization, Rome, IT.

Bognounou, F., Thiombiano, A., Oden, P.C. & Guinko, S. 2010. Seed provenance and latitudinal gradient effects on seed germination capacity and seedling establishment of five indigenous species in Burkina Faso. *Tropical Ecology* 51: 207-220.

Bognounou, F., Tigabu, M., Savadogo, P., Thiombiano, A., Boussim, I.J., Oden, P.C. & Guinko, S. 2010. Regeneration of five Combretaceae species along a latitudinal gradient in Sahelo-Sudanian zone of Burkina Faso. *Annals of Forest Science* 67: 306-315.

Bond, W.J. 2008. What limits trees in C-4 grasslands and savannas? *Annual Review of Ecology Evolution and Systematics* 39: 641-659.

Bond, W.J. & Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology & Evolution* 16: 45-51.

Bond, W.J. & Midgley, J.J. 2003. The evolutionary ecology of sprouting in woody plants. *International Journal of Plant Sciences* 164: S103-S114.

Bond, W.J. & VanWilgen, B.W. 1996. *Fire and plants*. 1st ed. Chapman & Hall, London, UK.

Bond, W.J. 2008. What limits trees in C-4 grasslands and savannas? *Annual Review of Ecology Evolution and Systematics* 39: 641-659.

Bonou, A. 2008. *Estimation de la valeur économique des Produits Forestier Non Ligneux (PFNL) d'origine végétale dans le village Sampéto (commune de Banikoara).* Ph.D. thesis, University of Abomey-Calavi, Abomey-Calavi, BJ.

Boulière, F. & Hadley, M. 1983. Present-day savannas: an overview. In: Boulière, F. (ed.) *Tropical Savannas*, pp. 1-17, [Ecosystems of the world 13]. Elsevier, Amsterdam, NL.

Brady, N.C. & Weil, R.R. 1999. *The nature and properties of soils*. 12th ed. Prentice-Hall, Upper Saddle River, US.

Breman, H. & Kessler, J.J. 1995. *Woody plants in agro-ecosystems of semi-arid regions: with an emphasis on the Sahelian countries*. 1st ed. Springer, Berlin, DE.

Bremner, J.M. 1960. Determination of nitrogen in soil by the Kjeldahl method. *Journal* of *Agricultural Science* 55: 11-33.

Bremner, J.M. 1965. Total nitrogen. In Black, C.A. (ed.) *Methods of soil analysis. Part 2. Chemical and microbiological properties*, pp. 1149-1178. American Society of Agronomy, Madison, US.

Brink, A.B. & Eva, H.D. 2009. Monitoring 25 years of land cover change dynamics in Africa: A sample based remote sensing approach. *Applied Geography* 29: 501-512.

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

Brown, J.R. & Archer, S. 1999. Shrub invasion of grassland: Recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80: 2385-2396.

Burgman, M.A. & Lamont, B.B. 1992. A stochastic-model for the viability of *Banksia cuneata* populations - environmental, demographic and genetic effects. *Journal of Applied Ecology*. 29: 719-727.

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. Springer, New York, US.

Burnham, K.P., White, G.C. & Anderson, D.R. 1995. Model selection strategy in the analysis of capture-recapture data. *Biometrics* 51: 888-898.

Bush, J.K. & Vanauken, O.W. 1995. Woody plant growth related to planting time and clipping of a C-4 grass. *Ecology* 76: 1603-1609.

Butz, R.J. 2009. Traditional fire management: historical fire regimes and land use change in pastoral East Africa. *International Journal of Wildland Fire* 18: 442-450.

Byakagaba, P., Eilu, G., Okullo, J.B.L., Tumwebaze, S.B. & Mwavu, E.N. 2011. Population structure and regeneration status of *Vitellaria paradoxa* (C.F. Gaertn.) under different land management regimes in Uganda. *Agricultural Journal* 6: 14-22.

Cardon, D. & Jansen, P.C.M. 2005. *Philenoptera laxiflora* (Guill. & Perr.) Roberty. [Internet] Record from Protabase. Jansen, P.C.M. & Cardon, D. (eds). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l’Afrique tropicale), Wageningen, NL. URL: http://database.prota.org/search.htm. (Accessed May 2012).

Chandrasekharan, C. 1995. Terminology, definition and classification of forest products other than wood. In: Food and Agricultural Organization (ed.) *Report of the International Expert Consultation on Non-Wood Forest Products 3 - Yogyakarta, Indonesia 17-27 January*, pp. 345-380. Food and Agricultural Organization of the United Nations, Rome, IT.

Condit, R., Sukumar, R., Hubbell, S.P. & Foster, R.B. 1998. Predicting population trends from size distributions: A direct test in a tropical tree community. *American Naturalist* 152: 495-509.

Conroy, M.J. 2009. Application of capture-recapture to addressing questions in evolutionary ecology. In: Thompson, D.L., Cooch, E.G. Cooch & Conroy, M.J. (eds.) *Modeling demographic processes in marked populations*, pp. 131-156. Springer, New York, US.

Crawley, M.J. 2007. *The R book*. John Wiley & Sons, Ltd., London, UK.

Dagar, J.C., Singh, V.P. & Mall, L.P. 1978. Regeneration in plants growing on eroded soil. *Annals of Arid Zone* 17: 68-74.

Descroix, L., Mahe, G., Lebel, T., Favreau, G., Galle, S., Gautier, E., Olivry, J.C., Albergel, J., Amogu, O., Cappelaere, B., Dessouassi, R., Diedhiou, A., Le Breton, E., Mamadou, I. & Sighomnou, D. 2009. Spatio-temporal variability of hydrological regimes around the boundaries between Sahelian and Sudanian areas of West Africa: A synthesis. *Journal of Hydrology* 375: 90-102.

Devineau, J.L. & Fournier, A. 2005. To what extent can simple plant biological traits account for the response of the herbaceous layer to environmental changes in fallow-savanna vegetation (West Burkina Faso, West Africa)? *Flora* 200: 361-375.

Dhillion, S.S. & Gustad, G. 2004. Local management practices influence the viability of the baobab (*Adansonia digitata* Linn.) in different land use types, Cinzana, Mali. *Agriculture*, *Ecosystems* & *Environment* 101: 85-103.

DIN – Deutsches Institut für Normung 19683-2. 1973. *Bodenuntersuchungsverfahren im landwirtschaftlichen Wasserbau – Physikalische Laboruntersuchungen – Bestimmung der Korngrößenzusammensetzung nach Vorbehandlung mit Natriumpyrophospha*t. Deutsches Institut für Normung e.V., Beuth Verlag, Berlin, DE.

DIN – Deutsches Institut für Normung 19684-1. 1977. *Bodenuntersuchungsverfahren im landwirtschaftlichen Wasserbau – Chemische Laboruntersuchungen – Bestimmung des pH-Wertes des Bodens und Ermittlung des Kalkbedarfs*. Deutsches Institut für Normung e.V., Beuth, Berlin, DE.

DIN – Deutsches Institut für Normung 19684-2. 1977. *Bodenuntersuchungsverfahren im landwirtschaftlichen Wasserbau – Chemische Laboruntersuchungen – Bestimmung des Humusgehaltes im Boden*. Deutsches Institut für Normung e.V., Beuth, Berlin, DE.

DIN – Deutsches Institut für Normung 19684-8. 1977. *Bodenuntersuchungsverfahren im landwirtschaftlichen Wasserbau – Chemische Laboruntersuchungen – Bestimmung der Austauschkapazität des Bodens und der austauschbaren Kationen*. Deutsches Institut für Normung e.V., Beuth, Berlin, DE.

DIN – Deutsches Institut für Normung 19683-1 1973. *Bodenuntersuchungsverfahren im landwirtschaftlichen Wasserbau – Physikalische Laboruntersuchungen Bestimmung der Korngrößenzusammensetzung durch Siebung*. Deutsches Institut für Normung e.V., Beuth, Berlin, DE.

Djossa, B.A., Fahr, J., Wiegand, T., Ayihouenou, B.E., Kalko, E.K. & Sinsin, B.A. 2008. Land use impact on *Vitellaria paradoxa* C.F. Gaerten. stand structure and distribution patterns: a comparison of Biosphere Reserve of Pendjari in Atacora district in Benin. *Agroforestry Systems* 72: 205-220.

Dourma, M., Guelly, K.A., Kokou, K., Batawila, K., Wala, K., Bellefontaine, R. & Akpagana, K. 2006. Multiplication par drageonnage d'*Isoberlinia doka* et *I. tomentosa* au sein des formations arborées du Nord-Togo. *Bois et Forêts des Tropiques* 288: 49-57.

Drobnik, J., Römermann, C., Bernhardt-Römermann, M. & Poschlod, P. 2011. Adaptation of plant functional group composition to management changes in calcareous grassland. A*griculture*, *Ecosystems* & *Environment* 145: 29-37.

Duvall, C.S. 2008. *Pterocarpus erinaceus* Poir. In: Louppe, D., Oteng-Amoako, A.A. & Brink, M. (eds.) *Plant Resources of Tropical Africa* 7*(1). Timbers 1*, pp. 478-482. PROTA Foundation, Wageningen, NL/Bachhuys Publishers, Leiden, NL.

Ellery, W.N., Ellery, K. & Mccarthy, T.S. 1993. Plant distribution in islands of the Okavango Delta, Botswana: determinants and feedback interactions. *African Journal* of *Ecology* 31: 118-134.

Etejere, E.O., Fawole, M.O. & Sani, A. 1982. Studies on the seed germination of *Parkia clapertoniana*. *Turrialba* 32: 181-185.

Fandohan, A.B., Assogbadjo, A.E., Kakai, R.L.G., Sinsin, B. & van Damme. P. 2010. Impact of habitat type on the conservation status of tamarind (*Tamarindus indic*a L.) populations in the W National Park of Benin. *Fruits* 65: 11-19.

Fatubarin, A. 1987. Observations on the natural regeneration of the woody plants in a savanna ecosystem in Nigeria. *Tropical Ecology* 28:1-8.

Feeley, K.J., Davies, S.J., Noor, M.N.S., Kassim, A.R. & Tan, S. 2007. Do current stem size distributions predict future population changes? An empirical test of intraspecific patterns in tropical trees at two spatial scales. *Journal of Tropical Ecology* 23: 191-198.

Fensham, R.J. & Bowman, D.M.J.S. 1992. Stand structure and the influence of overwood on regeneration in tropical Eucalypt forest on Melville-Island. *Australian Journal of Botany* 40: 335-352.

FAO – Food and Agricultural Organization. 1983. The progression from arable cropping to integrated crop and livestock production. In: Food and Agricultural Organization (ed.) *Integrating crops and livestock in West Africa*, pp. 1-112. Food and Agriculture Organization of the United Nations, Rome, IT.

FAO – Food and Agricultural Organization. 2011. The state of forest resources - a regional analysis. In: Food and Agricultural Organization (ed.) *State of world's forests 2011*. Food and Agriculture Organization of the United Nations, Rome, IT.

FAO – Food and Agricultural Organization. 1999. FAO Forestry – Towards a harmonised definition of non- wood forest products. *Unasylva* 198, Vol. 50.

Gaoue, O.G. & Ticktin, T. 2008. Impacts of bark and foliage harvest on *Khaya senegalensis* (Meliaceae) reproductive performance in Benin. *Journal of Applied Ecology* 45: 34-40.

Garcia, E. (2011): A tutorial on correlation coefficients. URL: http://irthoughts.wordpress.com/2010/07/08/a-tutorial-on-correlation-coefficients/ (Accessed March 2012).

Gignoux, J., Clobert, J. & Menaut, J.C. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* 110: 576-583.

Gignoux, J., Lahoreau, G., Julliard, R. & Barot, S. 2009. Establishment and early persistence of tree seedlings in an annually burned savanna. *Journal of Ecology* 97: 484-495.

Gijsberg, H.J.M., Kessler, J.J. & Knevel, M.K. 1994. Dynamics and natural regeneration of woody species in farmed parklands in the Sahel region (Province of Passore, Burkina Faso). *Forest Ecology and Management* 64: 1-12.

Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.M.N. & Swift, M.J. 1997. Agricultural intensification, soil biodiversity and agroecosystem function. *Applied Soil Ecology* 6: 3-16.

Gillon, D. 1983. The fire problem in tropical savannas. In: Bourlière, F. (ed.) *Tropical savannas*, pp. 617-642, [Ecosystems of the world 13]. Elsevier, Amsterdam, NL.

Glèlè KakaÏ, R., Assogbadjo, A.E., Sinsin, B. & Pelz, D. 2009. Structure spatiale et régénération naturelle de *Pterocarpus erinaceus* Poir en zone soudanienne au Bénin. *Revue Ivoirienne des Sciences et Technologie* 19: 199-212.

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

Goldammer, J. & Ronde, C. 2004. *Wildland fire management handbook for Sub-Sahara Africa*. Global Fire Monitoring Center (GFMC), Freiburg, DE.

Goldberg, D.E. & Werner, P.A. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of Goldenrods (*Solidago* spp.). *Oecologia* 60: 149-155.

Gong, X., Marklund, L.G. & Tsuij, S. 2009. Land use classification proposed to be used in the system of integrated environmental and economic accounting (SEEA). In: Food and Agricultural Organization (ed.) *14th Meeting of the London Group on Environmental Accounting Canberra 2009*, pp. 1-18. Food and Agriculture Organization of the United Nations, Rome, IT.

Graetz, D. 1994. Grasslands. In: Meyer, W.B. & Turner II, B.L. (eds.) *Changes in land use and land cover: a global perspective*, pp. 125-147. Cambridge University Press, Cambridge, UK.

Green, R.E., Cornell, S.J., Scharlemann, J.P.W. & Balmford, A. 2005. Farming and the fate of wild nature. *Science* 307: 550-555.

Grime, J.P. 2002. *Plant strategies, vegetation processes, and ecosystem properties*. 2nd ed. Wiley, Chichester, UK.

Grossnickle, S.C. 2005. Importance of root growth in overcoming planting stress. *New Forests* 30: 273-294.

Guariguata, M.R. & Pinard, M.A. 1998. Ecological knowledge of regeneration from seed in neotropical forest trees: Implications for natural forest management. *Forest Ecology and Management* 112: 87-99.

Gurevitch, J., Scheiner, S.M. & Fox, G.A. 2006. Population structure, growth, and decline. In: Gurevitch, J., Scheiner, S.M. & Fox, G.A. (eds.) *The ecology of plants*, pp. 101-127. Sinauer Associates, Sunderland, US.

Gwali, S., Okullo, P., Hafashimana, D. & Byabashaija, D.M. 2010. Diversity and composition of trees and shrubs in Kasagala forest: a semiarid savannah woodland in central Uganda. *African Journal* of *Ecology* 48: 111-118.

Hahn, K. 1996. *Die Pflanzengesellschaften der Savannen im Südosten Burkina Fasos (Westafrika). Ihre Beeinflussung durch den Menschen und die naturräumlichen Gegebenheiten*. Ph.D. thesis, University of Frankfurt, Frankfurt, DE.

Hall, P. & Bawa, K. 1993. Methods to assess the impact of extraction of non-timber tropical forest products on plant-populations. *Economic Botany* 47: 234-247.

Harper, J.L. 1977. *Population biology of plants*. 1st ed. Academic Press, London, UK.

Harrington, G.N. 1991. Effects of soil-moisture on shrub seedling survival in a semiarid grassland. *Ecology* 72: 1138-1149.

Heubach, K. 2011. *The socio-economic importance of non-timber forest products for rural livelihoods in West African savanna ecosystems: current status and future trends*. Ph.D. thesis, University of Frankfurt, Frankfurt, DE.

Heubach, K., Wittig, R., Nuppenau, E.A. & Hahn, K. 2011. The economic importance of non-timber forest products (NTFPs) for livelihood maintenance of rural west African communities: A case study from northern Benin. *Ecological Economics* 70: 1991-2001.

Higgins, S.I., Shackleton, C.M. & Robinson, E.R. 1999. Changes in woody community structure and composition under constrasting landuse systems in a semi-arid savanna, South Africa. *Journal* of *Biogeography* 26: 619-627.

Higgins, S.I., Bond, W.J. & Trollope, W.S.W. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213-229.

Hines, D.A. & Eckman, K. 1993. *Indigenous multipurpose trees of Tanzania: Uses and economic benefits for people*. 1st ed. Ottawa, CA.

Hoffmann, W.A. 1998. Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal* of *Applied Ecology*. 35: 422-433.

Hoffmann, W.A. & Solbrig, O.T. 2003. The role of topkill in the differential response of savanna woody species to fire. *Forest Ecology and Management* 180: 273-286.

Hoffmann, W.A., Orthen, B. & Franco, A. C. 2004. Constraints to seedling success of savanna and forest trees across the savanna-forest boundary. *Oecologia* 140: 252-260.

Hood, L.A., Swaine, M.D. & Mason, P.A. 2004. The influence of spatial patterns of damping-off disease and arbuscular mycorrhizal colonization on tree seedling establishment in Ghanaian tropical forest soil. *Journal of Ecology* 92: 816-823.

Hothorn, T., Bretz, F. & Westfall, P. 2008. Simultaneous inference in general parametric models. *Biometrical Journal* 50: 346-363.

Hough, J.L. 1993. Why burn the bush - social approaches to bush fire management in West-African national parks. *Biological Conservation* 65: 23-28.

Houghton, R.A. 1994. The worldwide extent of land-use change. *Bioscience* 44: 305-313.

Hovestadt, T., Yao, P. & Linsenmair, K.E. 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoe National Park, Ivory Coast). *Plant Ecology* 144: 1-25.

Huntley, B.J. & Walker, B.H. 1982. *Ecology of Tropical Savannas*. 1st ed. Springer-Verlag, Berlin, DE.

INSAE – Institut National de la Statistique et de l'Analyse Economique. 2002. *Troisième recensement général de la population et de l'habitat. La population de l'Alibori, villages et quartiers de ville*. unpublished data.

Jeffrey, D.W. 1987. *Soil-plant relationships: an ecological approach*. 1st ed. Croom Helm, London, UK.

Johnson, J.B. & Omland, K.S. 2004. Model selection in ecology and evolution. *Trends in Ecology & Evolution* 19: 101-108.

Jurena, P.N. & Archer, S. 2003. Woody plant establishment and spatial heterogeneity in grasslands. *Ecology* 84: 907-919.

Jurisch, K., Wittig, R., Hahn, K. & Bernhardt-Römermann, M. 2012a. Population structure of woody plants in relation to land use in a semi-arid savanna, West Africa. *Biotropica*. DOI: 10.1111/j.1744-7429.2012.00864.x

Jurisch, K., Wittig, R., Hahn, K. & Bernhardt-Römermann, M. 2012b. Land-use impact on the growth and survival of seedlings and saplings in West African savannas. *Journal of Vegetation Science*. DOI: 10.1111/j.1654-1103.2012.01444.x.

Kaonga, M.L. & Bayliss-Smith, T.P. 2012. A conceptual model for carbon dynamics for improved fallows in the tropics. In: Kaonga, M.L. (ed.) *Agroforestry for Biodiversity and Ecosystem Services - Science and Practice*, pp. 23-44. InTech.

Kelly, B.A., Hardy, O.J. & Bouvet, J.M. 2004. Size class distribution and spatial pattern of *Vitellaria paradoxa* in relation to farmers' practices in Mali. *Agroforestry Systems* 60: 3-11.

Kéré, U. 1998. Végétation et utilisation des plantes spontanées dans la région de Tenkodogo (Burkina Faso). *Etudes sur la flore et la végetation du Burkina Faso et des pays avoisinants* 4: 3-55.

Kershaw, K.A. 1968. A survey of the vegetation in Zaria Province, N. Nigeria. *Plant Ecology* 15: 244-268

Kéry, M. & Gregg, K.B. 2004. Demographic analysis of dormancy and survival in the terrestrial orchid *Cypripedium reginae*. *Journal of Ecology* 92: 686-695.

Kéry, M., Gregg, K.B. & Schaub, M. 2005. Demographic estimation methods for plants with unobservable life-states. *Oikos* 108: 307-320.

Kessler, J.J. & Breman, H. 1991. The potential of agroforestry to increase primary production in the Sahelian and Sudanian zones of West Africa. *Agroforestry Systems* 13: 41-62.

Kindt, R., Kalinganire, A., Larwanou, M., Belem, M., Dakouo, J.M., Bayala, J. & Kaire, M. 2008. Species accumulation within land use and tree diameter categories in Burkina Faso, Mali, Niger and Senegal. *Biodiversity* and *Conservation* 17: 1883-1905.

Kjeldahl, J.Z. 1883. A new method for the determination of nitrogen in organic bodies. *Analytical Chemistry* 22: 366.

Knoop, W.T. & Walker, B.H. 1985. Interactions of woody and herbaceous vegetation in a Southern African Savanna. *Journal of Ecology* 73:235-253.

Köhn, M. (1929): Korngrößenanalyse vermittels Pipettanalyse. *Tonindustrie-Zeitung* 53: 729–731.

Kouami, K., Yaovi, N. & Honan, A. 2009. Impact of charcoal production on woody plant species in West Africa: A case study in Togo. *Scientific Research and Essays* 4: 881-893.

Kraaij, T. & Milton, S.J. 2006. Vegetation changes (1995-2004) in semi-arid Karoo shrubland, South Africa: Effects of rainfall, wild herbivores and change in land use. *Journal* of *Arid Environments* 64: 174-192.

Kristensen, M. & Balslev, H. 2003. Perceptions, use and availability of woody plants among the Gourounsi in Burkina Faso. *Biodiversity and Conservation* 12: 1715-1739.

Krohmer, J., Hahn-Hadjali, K. & Wittig, R. 2006. Utilisation de la flore sauvage par des populations peules au Burkina Faso et Bénin. *Etudes sur la flore et la végetation du Burkina Faso et des pays avoisinants* 10: 33-48.

Kruger, L.M., Midgley, J.J. & Cowling, R.M. 1997. Resprouters vs reseeders in South African forest trees; A model based on forest canopy height. *Functional Ecology* 11: 101-105.

Kwit, C., Horvitz, C.C. & Platt, W.J. 2004. Conserving slow-growing, long-lived tree species: Input from the demography of a rare understory conifer, *Taxus floridana*. *Conservation Biology* 18: 432-443.

Ky-Dembele, C., Tigabu, M., Bayala, J., Ouedraogo, S.J. & Oden, P.C. 2007. The relative importance of different regeneration mechanisms in a selectively cut savanna-woodland in Burkina Faso, West Africa. *Forest Ecology and Management* 243: 28-38.

Ky-Dembele, C., Tigabu,M., Bayala,J., Ouedraogo,S.J. & Oden,P.C. 2008. Comparison between clonal and sexual plantlets of *Detarium microcarpum* Guill. & Perr., a savanna tree species in Burkina Faso. *African Journal of Ecology* 46: 602-611.

Laake, J. & Rexstad, E. 2008. RMark - an alternative approach to building linear models in MARK. URL: http://www.phidot.org/software/mark/rmark/.

Lahoreau, G., Gignoux, J. & Julliard, R. 2004. Exploring mark-resighting-recovery models to study savannah tree demographics. *Animal Biodiversity and Conservation* 27: 549-560.

Lambin, E.F., Geist, H.J. & Lepers, E. 2003. Dynamics of land-use and land-cover change in tropical regions. *Annual* Review of *Environment* and *Resources* 28: 205-241.

Laris, P. 2002. Burning the seasonal mosaic: Preventative burning strategies in the wooded savanna of southern Mali. *Human Ecology* 30: 155-186.

Lavorel, S., McIntyre, S., Landsberg, J. & Forbes, T.D.A. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends *in Ecology &* Evolution 12: 474-478.

Lawes, M.J., Joubert, R., Griffiths, M.E., Boudreau, S. & Chapman, C.A. 2007. The effect of the spatial scale of recruitment on tree diversity in Afromontane forest fragments. *Biological Conservation* 139: 447-456.

Lawesson, J. E. 1990. Sahelian woody vegetation in Senegal. *Vegetatio* 86: 161-174.

Lesica, P. & Crone, E.E. 2007. Causes and consequences of prolonged dormancy for an iteroparous geophyte, *Silene spaldingii*. *Journal of Ecology* 95: 1360-1369.

Lovett, P.N. & Haq, N. 2000. Evidence for anthropic selection of the sheanut tree (*Vitellaria paradoxa*). *Agroforestry Systems* 48: 273-288.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2002. Harvested and standing wood stocks in protected and communal miombo woodlands of eastern Tanzania. *Forest Ecology and Management* 164: 15-30.

Luoga, E.J., Witkowski, E.T.F. & Balkwill, K. 2004. Regeneration by coppicing (resprouting) of miombo (African savanna) trees in relation to land use. *Forest Ecology and Management* 189: 23-35.

Lykke, A.M. 1998. Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodiversity and Conservation* 7: 1261-1275.

Lykke, A.M., Kristensen, M.K. & Ganaba, S. 2004. Valuation of local use and dynamics of 56 woody species in the Sahel. *Biodiversity and Conservation* 13: 1961-1990.

Makana, J.R. & Thomas, S.C. 2006. Impacts of selective logging and agricultural clearing on forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo. *Biodiversity and Conservation* 15: 1375-1397.

Matson, P.A., Parton, W.J., Power, A.G. & Swift, M.J. 1997. Agricultural intensification and ecosystem properties. *Science* 277: 504-509.

Mazerolle, M.J. 2006. Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia* 27: 169-180.

Mbow, C., Nielsen, T.T. & Rasmussen, K. 2000. Savanna fires in east-central Senegal: Distribution patterns, resource management and perceptions. *Human Ecology* 28: 561-583.

McLaren, K.P., McDonald, M.A., Hall, J.B. & Healey, J.R. 2005. Predicting species response to disturbance from size class distributions of adults and saplings in a Jamaican tropical dry forest. *Plant Ecology* 181: 69-84.

Mcnaughton, S.J., Wallace, L.L. & Coughenour, M.B. 1983. Plant Adaptation in an ecosystem context - effects of defoliation, nitrogen, and water on growth of an African C-4 sedge. *Ecology* 64: 307-318.

Mehlich, A. 1953. Determination of P, Ca, Mg, K, Na, and NH4. North Carolina Soil Test Division (Mimeo 1953).

Meiwes, K.J. 1984. Chemische Untersuchungsverfahren zur Charakterisierung und Bewertung der Versauerung in Waldböden. *Berichte des Forschungszentrums für Waldökologie* 7, Göttingen, DE.

Menaut, J.C. & Cesar, J. 1979. Structure and primary productivity of Lamto Savannas, Ivory Coast. *Ecology* 60: 1197-1210.

Menaut, J.C. 1983. The vegetation of African savannas. In: Bourlière, F. (ed.) *Tropical savannas*, pp. 109-134, [Ecosystems of the world 13]. Elsevier, Amsterdam, NL.

Mendoza, I., Gomez-Aparicio, L., Zamora, R. & Matias, L. 2009. Recruitment limitation of forest communities in a degraded Mediterranean landscape. *Journal of Vegetation Science* 20: 367-376.

Midgley, J.J. 1996. Why the world's vegetation is not totally dominated by resprouting plants; because resprouters are shorter than reseeders. *Ecography* 19: 92-95.

Midgley, J.J., Lawes, M.J. & Chamaille-Jammes, S. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany* 58: 1-11.

Midoko-Iponga, D., Krug, C.B. & Milton, S.J. 2005. Competition and herbivory influence growth and survival of shrubs on old fields: Implications for restoration of renosterveld shrubland. *Journal of Vegetation Science* 16: 685-692.

Milton, S.J. 1995. Spatial and Temporal Patterns in the Emergence and Survival of Seedlings in Arid Karoo Shrubland. *Journal of Applied Ecology* 32: 145-156.

Mücher, C.A., Stomph, T.J. & Fresco, L.O. 1993. *Proposal for a global land use classification*. FAO/ITC/WAU, Rome/Wageningen, IT/NL.

Mwavu, E.N. & Witkowski, E.T.F. 2008. Land-use and cover changes (1988-2002) around Budongo Forest Reserve, Nw Uganda: Implications for forest and woodland sustainability. *Land Degradation & Development* 19: 606-622.

Mwavu, E.N. & Witkowski, E.T.F. 2009. Population structure and regeneration of multiple-use tree species in a semi-deciduous African tropical rainforest: Implications for primate conservation. *Forest Ecology and Management* 258: 840-849.

Mwavu, E.N. & Witkowski, E.T.F. 2009. Seedling regeneration, environment and management in a semi-deciduous African tropical rain forest. *Journal of Vegetation science* 20: 791-804.

Nacoulma, B.M.I., Schumann, K., Traoré, S., Bernhardt-Römermann, M., Hahn, K., Wittig, R. & Thiombiano, A. 2011. Impacts of land-use on West African savanna vegetation: a comparison between protected and communal area in Burkina Faso. *Biodiversity and Conservation* 20: 3341-3362.

Niang, A., Ozer, A. & Ozer, P. 2008. Fifty years of landscape evolution in Southwestern Mauritania by means of aerial photos. *Journal* of *Arid Environments* 72: 97-107.

Nianogo, A. & Thomas, I. 2004. Forest-livestock interactions in West Africa. The African Forest Forum [Lessons learnt on sustainable forest management in Africa]. URL: http://www.afforum.org/publications.html?start=3.

Nikiema, A. 2005. *Agroforestry parkland species diversity: uses and management in semi-arid West Africa (Burkina Faso).* PhD thesis, Wageningen University, Wageningen, NL.

Norris, K., Asase, A., Collen, B., Gockowksi, J., Mason, J., Phalan, B. & Wade, A. 2010. Biodiversity in a forest-agriculture mosaic - The changing face of West African rainforests. *Biological Conservation* 143: 2341-2350.

Nye, P.H. & Greenland, D.J. 1960. *The soil under shifting cultivation*. [Technical Communication no. 156], Commenwealth Agricultural Bureaux, Oxfordshire, UK.

Nzunda, E.F., Griffiths, M.E. & Lawes, M.J 2007. Multi-stemmed trees in subtropical coastal dune forest: Survival strategy in response to chronic disturbance. *Journal* of Vegetation *Science* 18: 693-700.

Nzunda, E.F., Griffiths, M.E. & Lawes, M.J. 2008. Resprouting enhances seedling persistence in a subtropical coastal dune forest. *African Journal of Ecology* 46: 32-38.

Obiri, J., Lawes, M. & Mukolwe, M. 2002. The dynamics and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecology and Management* 166: 131-148.

Okigbo, B.N. 1985. Land use and production potentials of African savanna. In: Tothill, J. C. & Mott, J.J. (eds.) *International Savanna Symposium – Ecology and management of the world's savannas*, pp. 95-106, Australian Academy of Science, Bucks, AU.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Sstevens, M.H.H. & Wagner, H. 2011. Vegan: Community Ecology Package. R package version 2.0-2. URL: http://CRAN.R-project.org/package=vegan.

Orthmann, B. 2005. *Vegetation ecology of a woodland-savanna mosaic in central Benin (West Africa): ecosystem analysis with a focus on the impact of selective logging*. Ph.D. thesis, University of Rostock, Rostock, DE.

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

Ouedraogo, A. 2006. *Diversité et dynamique de la végétation ligneuse de la partie orientale du Burkina Faso*. Ph.D. thesis, University of Ouagadougou, Ouagadougou, BF.

Ouedraogo, I., Tigabu, M., Savadogo, P., Compaore, H., Oden, P.C. & Ouadba, J.M. 2010. Land cover change and its relation with population dynamics in Burkina Faso, West Africa. *Land Degradation & Development* 21: 453-462.

Oyen, L.P.A. 2011. *Bombax costatum* Pellegr. & Vuillet. [Internet] Record from PROTA4U. Brink, M. & Achigan-Dako, E.G. (eds.) PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen. URL: http://www.prota4u.org/search.asp. (Accessed May 2012).

Pare, S., Savadogo, P., Tigabu, M., Oden, P.C. & Ouadba, J.M. 2009. Regeneration and spatial distribution of seedling populations in Sudanian dry forests in relation to conservation status and human pressure. *Tropical Ecology* 50: 339-353.

Persinos, G.J., Quimby, M.W. & Schermerhorn, J.W. 1964. A preliminary pharmacognostical study of ten Nigerian plants. *Economic Botany* 18: 329-341.

Peters, C.M. 1990. Population ecology and management of forest fruit trees in Peruvian Amazonia. In: Anderson, A.B. (ed.) A*lternatives to deforestation: Steps toward sustainable use of the amazon rain forest*, pp. 86-90. Columbia University Press, New York, US.

Petit, S. 2003. Parklands with fodder trees: a Fulbe response to environmental and social changes. *Applied Geography* 23: 205-225.

Plumptre, A.J. 1995. The importance of 'seed trees' for the natural regeneration of selectively logged tropical forest. *Commonwealth Forestry Review* 74: 253-258.

Poschlod, P., Hoffmann, J. & Bernhardt-Römermann, M. 2011. Effect of grassland management on the age and reproduction structure of *Helianthemum nummularium* and *Lotus corniculatus* populations. *Preslia* 83: 421-435.

Powell, D.C. 2005. How to measure a big tree. UmatillaNational Forest's big-tree website. http://www.fs.fed.us/r6/uma/nr/silv/Tree%20Measurements. Accessed 04 August 2010.

Pretzsch, H. 2002. *Grundlagen der Waldwachstumsforschung*. Parey, Berlin, DE.

Prior, L.D., Williams, R.J. & Bowman, D.M.J.S. 2010. Experimental evidence that fire causes a tree recruitment bottleneck in an Australian tropical savanna. *Journal of Tropical Ecology* 26: 595-603.

Pulido, F.J. & Diaz, M. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. *Ecoscience* 12: 92-102.

Pulido, F.J., Diaz, M. & de Trucios, S.J.H. 2001. Size structure and regeneration of Spanish holm oak *Quercus ilex* forests and dehesas: effects of agroforestry use on their long-term sustainability. *Forest Ecology and Management* 146: 1-13.

R Development Core Team. 2010. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, AT.

Razanamandranto, S., Tigabu, M., Neya, S. & Oden, P.C. 2004. Effects of gut treatment on recovery and germinability of bovine and ovine ingested seeds of four woody species from the Sudanian savanna in West Africa. *Flora* 199: 389-397.

Reid, R.S. & Ellis, J.E. 1995. Impacts of pastoralists on woodlands in South Turkana, Kenya - Livestock-Mediated Tree Recruitment. *Ecological Applications* 5: 978-992.

Reid, R.S., Kruska, R.L., Muthui, N., Taye, A., Wotton, S., Wilson, C.J. & Mulatu, W. 2000. Land-use and land-cover dynamics in response to changes in climatic, biological and socio-political forces: the case of southwestern Ethiopia. *Landscape Ecology* 15: 339-355.

Reij, C., Tappan, G. & Belemvire, A. 2005. Changing land management practices and vegetation on the Central Plateau of Burkina Faso (1968-2002). *Journal* of *Arid Environments* 63: 642-659.

Rietkerk, M., Blijdorp, R. & Slingerland, M. 1998. Cutting and resprouting of *Detarium microcarpum* and herbaceous forage availability in a semiarid environment in Burkina Faso. *Agroforestry Systems* 41: 201-211.

Riginos, C. 2009. Grass competition suppresses savanna tree growth across multiple demographic stages. *Ecology* 90: 335-340.

Ruthenberg, H. 1980. *Farming systems in the Tropics*. 3rd ed. Clarendon Press, Oxford, UK.

Sacande M. & Sanogo, S. 2007. *Anogeissus leiocarpus (DC.)* Guill. & Perr. *Seed Leaflet* 109.

Sacandé, M., Sanon, M. & Schmidt, L. 2007. *Combretum nigricans* Lepr. ex Guill. & Perr. *Seed Leaflet* 130.

Sankaran, M., Ratnam, J. & Hanan, N.P. 2004. Tree-grass coexistence in savannas revisited - insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* 7: 480-490.

Sankaran, M., Ratnam, J. & Hanan, N. 2008. Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography* 17: 236-245.

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

Schüller, H. 1969. Die CAL–Methode, eine neue Methode zur Bestimmung des pflanzen-verfügbaren Phosphates in Böden. *Zeitschrift für Pflanzenernährung und Bodenkunde* 123: 63-48.

Schüller, H.1973. Über die Untersuchung von Böden mit hohen Carbonatgehalten. *Landwirtschaftliche Forschung* 26, Sonderheft 28/1: 140–155.

Schumann, K., Wittig, R., Thiombiano, A., Becker, U. & Hahn, K. 2010. Impact of land-use type and bark- and leaf-harvesting on population structure and fruit production of the baobab tree (*Adansonia digitata* L.) in a semi-arid savanna, West Africa. *Forest Ecology and Management* 260: 2035-2044.

Schumann, K., Wittig, R., Thiombiano, A., Becker, U. & Hahn, K. 2011. Impact of land-use type and harvesting on population structure of a non-timber forest product-providing tree in a semi-arid savanna, West Africa. *Biological Conservation* 144: 2369-2376.

Schwarz, C.J. 2005. Multistate Models. In: Amstrup, S.C., McDonald, T.L. & Manly, B.F.J. (eds.) *Handbook of Capture-Recapture Analysis*, pp. 165-195. Princeton University Press, Princeton, New Jersey, US.

Setterfield, S.A. 2002. Seedling establishment in an Australian tropical savanna: effects of seed supply, soil disturbance and fire. *Journal of Applied Ecology* 39: 949-959.

Shefferson, R.P., Sandercock, B.K., Proper, J. & Beissinger, S.R. 2001. Estimating dormancy and survival of a rare herbaceous perennial using mark-recapture models. *Ecology* 82: 145-156.

Sheuyange, A., Oba, G. & Weladji, R.B. 2005. Effects of anthropogenic fire history on savanna vegetation in northeastern Namibia. *Journal of Environmental Management* 75: 189-198.

Sieglstetter, R., Hahn, K. & Wittig, R. 2011. The use of woody species in northern Benin. *Flora et Vegetatio Sudano-Sambesica* 14: 19-23.

Shorrocks, B. 2007. *The biology of African savannas*. Oxford University Press, Oxford, UK.

Silvertown, J. & Charlesworth, D. 2007. *Introduction to plant population biology.* Blackwell Publishing, Oxford, UK.

Silvertown, J. & Smith, B. 1989. Germination and population structure of spear thistle *Cirsium vulgare* in relation to experimentally controlled sheep grazing. *Oecologia* 81: 369-373.

Skarpe, C. 1991. Impact of grazing in savanna ecosystems. *Ambio* 20: 351-356.

Sokpon, N. & Biaou, S.H.. 2002. The use of diameter distributions in sustained-use management of remnant forests in Benin: case of Bassila forest reserve in North Benin. *Forest Ecology* and *Management* 161: 13-25.

Staver, A.C., Bond, W.J., Stock, W.D., van Rensburg, S.J. & Waldram, M.S. 2009. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications* 19: 1909-1919.

Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., de Snoo, G.R. & Eden, P. 2001. Ecological impacts of arable intensification in Europe. *Journal* of *Environmental Management* 63: 337-365.

SUN (Tools for management and Sustainable Use of Natural vegetation in West Africa). 2010. Periodic Activity Report. unpublished data.

Swaine, M.D. 1996. Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology* 84: 419-428.

Teklehaimanot, Z. 2004. Exploiting the potential of indigenous agroforestry trees: *Parkia biglobosa* and *Vitellaria paradoxa* in sub-Saharan Africa. *Agroforestry Systems* 61: 207-220.

Ticktin, T. 2004. The ecological implications of harvesting non-timber forest products. *Journal of Applied Ecology* 41: 11-21.

Todd, S.W. & Hoffman, M.T. 1999. A fence-line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. *Plant Ecology* 142: 169-178.

Trollope, W.S.W. 1984. Fire in savanna. In: Booysen, P.D.V. & Tainton, N.M. (eds.) *Ecological effects of fire in South African ecosystems*, pp. 199-218. Springer, Berlin, DE.

Turner, B.L. & Meyer, W.B. 1994: C*hanges in land use and land cover: a global perspective*. Cambridge University Press, Cambridge, UK.

Van der Waal, C., de Kroon, H., de Boer, W.F., Heitkoenig, I.M., Skidmore, A.K., de Knegt, H.J., van Langevelde, F., van Wieren, S.E., Grant, R.C., Page, B.R., Slotow, R., Kohl, E.M., Mwakiwa, E. & Prins, H.H. 2009. Water and nutrients alter herbaceous competitive effects on tree seedlings in a semi-arid savanna. *Journal of Ecology* 97: 430-439.

Van der Waal, C., Kool, A., Meijer, S.S., Kohl, E., Heitkoenig, I.M., de Boer, W.F., van Langevelde, F., Grant, R.C., Peel, M.J., Slotow, R., de Knegt, H.J., Prins, H.H. & de Kroon, H. 2011. Large herbivores may alter vegetation structure of semi-arid savannas through soil nutrient mediation. *Oecologia* 165: 1095-1107.

Van Langevelde, F., van de Vijver, C.A.D.M., Kumar, L., van de Koppel, J., de Ridder, N., van Andel, J., Skidmore, A.K., Hearne, J.W., Stroosnijder, L., Bond, W.J., Prins, H.H.T. & Rietkerk, M. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology* 84: 337-350.

Vanauken, O.W. & Bush, J.K. 1997. The importance of neighbors, soil pH, phosphorus, and nitrogen for the growth of two C-4 grasses. *International Journal of Plant Sciences* 158: 325-331.

Vanauken, O.W. & Bush, J.K. 1989. *Prosopis glandulosa*-growth - Influence of nutrients and simulated grazing of *Bouteloua curtipendula*. *Ecology* 70: 512-516.

Vandenberghe, C., Frelechoux, F., Gadallah, F. & Buttler, A. 2006. Competitive effects of herbaceous vegetation on tree seedling emergence, growth and survival: Does gap size matter? *Journal of Vegetation Science* 17: 481-488.

Vautier, H., Sanon, M.D. & Sacande, M. 2007a. *Combretum glutinosum* Perrot ex. DC. *Seed leaflet* 128.

Vautier, H., Sanon, M.D. & Sacande, M. 2007b. *Detarium microcarpum* Guill. & Perr. *Seed leaflet* 122.

Veenendaal, E.M., Swaine, M.D., Agyeman, V.K., Blay, D., Abebrese, I.K. & Mullins, C.E. 1996. Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology* 84: 83-90.

Vermeulen, C., Dubiez, E., Proces, P., Mukumary, S.D., Yamba, T.Y., Mutambwe, S., Peltier, R., Marien, J.N. & Doucet, J.L. 2011. Land issues, exploitation of natural resources, and Forests of Rural Communities in the periphery of Kinshasa, DRC. *Biotechnologie Agronomie Societe et Environnement* 15: 535-544.

Vincke, C., Diedhiou, I. & Grouzis, M. 2010. Long term dynamics and structure of woody vegetation in the Ferlo (Senegal). *Journal* of *Arid Environments* 74: 268-276.

Vodouhe, F.G., Coulibaly, O., Greene, C. & Sinsin, B. 2009. Estimating the local value of non-timber forest products to Pendjari Biosphere Reserve dwellers in Benin. *Economic Botany* 63: 397-412.

Wellington, A.B. & Noble, I.R. 1985. Seed dynamics and factors limiting recruitment of the Mallee *Eucalyptus incrassata* in semi-arid, Southeastern Australia. *Journal of Ecology* 73: 657-666.

Weltzin, J.F. & McPherson, G.R. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* 112: 156-164.

Werner, P.A. 1975. Predictions of fate from rosette size in teasel (*Dipsacus fullonum*-L). *Oecologia* 20: 197-201.

Werner, P.A. 2005. Impact of feral water buffalo and fire on growth and survival of mature savanna trees: An experimental field study in Kakadu National Park, northern Australia. *Austral Ecology* 30: 625-647.

Wezel, A. & Lykke, A.M. 2006. Woody vegetation change in Sahelian West Africa: evidence from local knowledge. *Environment*, *Development and Sustainability* 8: 553-567.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46: 120-139.

Wiegand, T., Milton, S.J. & Wissel, C. 1995. A simulation-model for a shrub ecosystem in the semiarid Karoo, South-Africa. *Ecology* 76: 2205-2221.

Wigley, B.J., Cramer, M.D. & Bond, W.J. 2009. Sapling survival in a frequently burnt savanna: mobilisation of carbon reserves in *Acacia karroo*. *Plant Ecology* 203: 1-11.

Wilson, B.G. & Witkowski, E.T.F. 2003. Seed banks, bark thickness and change in age and size structure (1978-1999) of the African savanna tree, *Burkea africana*. *Plant Ecology* 167: 151-162.

Wittig, R., Koenig, K., Schmidt, M. & Szarzynski, J. 2007. A study of climate change and anthropogenic impacts in West Africa. *Environmental Science and Pollution Research* 14: 182-189.

Zida, D. 2007. *Impacts of forest management regimes of ligneous regeneration in the Sudanian savanna of Burkina Faso*. Ph.D. thesis, Umeå University, Umeå, SE.

Zida, D., Sawadogo, L., Tigabu, M., Tiveau, D. & Oden, P.C. 2007. Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. *Forest Ecology and Management* 243: 102-115.

Zida, D., Tigabu, M., Sawadogo, L. & Oden, P.C. 2008. Initial seedling morphological characteristics and field performance of two Sudanian savanna species in relation to nursery production period and watering regimes. *Forest Ecology and Management* 255: 2151-2162.

Zida, D., Tigabu, M., Sawadogo, L., Tiveau, D. & Oden, P.C. 2008. Long-term effects of prescribed early fire, grazing and selective tree cutting on seedling populations in the Sudanian savanna of Burkina Faso. *African Journal of Ecology* 47: 97-108.

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Appendix

Appendix – Chapter 2

Table S1 List of species that were excluded from the analysis as they had less than 10 individuals in total in all sampled plots. The figures are numbers of individuals (N individuals) sampled in each land-cover type. Total numbers of individual are further divided according to their development stage: juveniles, sub-adult and adult. Plots sampled on non-arable land: n=23, fallows: n=20 and buffer zone: n=21.

			N individuals: juveniles			**N individuals: sub-adults**			**N individuals: adults**		
Life-form	**Family**	**Species**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**
shrub	Fabaceae - Mimosoideae	*Acacia seyal* Delile	NA	NA	NA	0	1	0	0	0	1
shrub	Fabaceae - Mimosoideae	*Acacia sieberiana* DC.	NA	NA	NA	0	0	3	0	0	1
tree	Fabaceae - Caesalpinioideae	*Afzelia africana* Sm. ex Pers.	NA	NA	NA	0	0	0	2	0	0
tree	Fabaceae - Mimosoideae	*Albizia chevalieri* Harms	NA	NA	NA	0	0	0	0	1	1
tree	Meliaceae	*Azadirachta indica* A.Juss.	NA	NA	NA	0	1	0	0	0	0
tree	Balanitaceae	*Balanites aegyptiaca* (L.) Delile	NA	NA	NA	0	1	0	0	0	0
shrub	Fabaceae	*Bobgunnia madagascariensis* (Desv.) J.H.Kirkbr. & Wiersema	NA	NA	NA	0	1	0	0	0	0
tree	Bombacaceae	*Bombax costatum* Pellegr. & Vuill.	NA	NA	NA	2	1	3	0	1	1
tree	Fabaceae - Caesalpinioideae	*Cassia sieberiana* DC.	NA	NA	NA	1	1	0	0	0	0
tree	Fabaceae - Caesalpinioideae	*Daniellia oliveri* (Rolfe) Hutch. & Dalziel	NA	NA	NA	0	0	0	2	0	0
tree	Moraceae	*Ficus ovata* Vahl	NA	NA	NA	2	0	0	2	1	0
tree	Moraceae	*Ficus platyphylla* Delile	NA	NA	NA	0	0	1	0	0	2
tree	Moraceae	*Ficus spec*	NA	NA	NA	1	0	0	1	3	0
tree	Meliaceae	*Khaya senegalensis* (Desr.) A.Juss.	NA	NA	NA	0	0	2	0	0	0
shrub	Rubiaceae	*Mitragyna inermis* (Willd.) Kuntze	NA	NA	NA	0	1	0	0	0	0
shrub	Opiliaceae	*Opilia amentacea* Roxb.	NA	NA	NA	2	4	2	0	0	0
shrub	Chrysobalanaceae	*Parinari curatellifolia* Planch. ex Benth.	NA	NA	NA	6	0	0	0	0	0
tree	Fabaceae - Mimosoideae	*Parkia biglobosa* (Jacq.) R.Br. ex G.Don	NA	NA	NA	1	0	1	0	5	1
shrub	Rubiaceae	*Sarcocephalus latifolius* (Sm.) E.A.Bruce	NA	NA	NA	0	4	0	0	1	0
shrub	Rhamnaceae	*Ziziphus abyssinica* A.Rich.	NA	NA	NA	3	0	1	0	0	0
shrub	Rhamnaceae	*Ziziphus mauritiana* Lam.	NA	NA	NA	0	0	2	0	0	0

Table S2 Results of Generalized linear model (GLM) for shrubs (n=18). The maximum model was fitted with number of individuals as dependent variable, and size class (numerical) and species names (factor) as explanatory variables. Family = Gamma.

	Estimate	**S.E.**	***t* value**	**Pr (>|t|)**
Intercept_S1	-0.0026716	0.0003039	-8.792	<2e-16***
dbh-class-mean : S1	0.0018651	0.0002015	9.257	<2e-16***
S2	-0.0071242	0.0005852	-12.174	<2e-16***
S3	-0.0132067	0.0011442	-11.542	<2e-16***
S4	-0.0133019	0.0024032	-5.535	3.97E-08***
S5	-0.0216701	0.0054446	-3.98	7.39E-05***
dbh-class-mean : S2	0.0052194	0.0003845	13.574	<2e-16***
dbh-class-mean : S3	0.0091065	0.0007609	11.968	<2e-16***
dbh-class-mean : S4	0.0089275	0.0016017	5.574	3.21e-08***
dbh-class-mean : S5	0.0156874	0.0035935	4.366	1.40e-05***
Residual deviance: 672.84 on 1002 df				

Table S3 Results of Generalized linear model (GLM) for trees (n=12). The maximum model was fitted with number of individuals as dependent variable, and size class (numerical) and species names (factor) as explanatory variables. Family = Gamma.

	Estimate	**S.E.**	***t* value**	**Pr (>|t|)**
Intercept_T1	-1.51E-02	1.15E-03	-13.186	<2e-16***
dbh-class-mean : T1	6.22E-03	4.58E-04	13.576	<2e-16***
T2	-1.99E-03	1.51E-03	-1.316	0.18881
T3	3.15E-05	4.80E-03	0.007	0.99476
T4	-1.78E-02	6.61E-03	-2.683	0.0075**
dbh-class-mean : T2	9.65E-04	6.02E-04	1.603	0.10946
dbh-class-mean : T3	3.70E-04	1.91E-03	0.194	0.84661
dbh-class-mean : T4	7.25E-03	2.65E-03	2.74	0.00633**
Residual deviance: 338.47 on 580 df				

Table S4 Group affiliation of the 30 analyzed woody species depending on size-class distribution in relation to land-cover type (plots sampled on non-arable land: n=23, fallow: n=20 and buffer zone: n=21). Similarity between land-cover types is marked by (&), dissimilarity by (≠). Additionally presented is the total number of individuals (N individuals) sampled in each land-cover type, further divided according to their development stage: juveniles, sub-adult and adult.

			N individuals: juveniles			**N individuals: sub-adults**			**N individuals: adults**		
Life-form	**Family**	**Species**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**
group A: non-arable&fallows&buffer zone											
shrub	Combretaceae	*Combretum molle* R.Br. ex G.Don	60	62	54	125	159	181	25	35	29
shrub	Fabaceae - Mimosoideae	*Dichrostachys cinerea* (L.) Wight & Arn.	80	171	31	1	6	8	0	1	0
shrub	Ebenaceae	*Diospyros mespiliformis* Hochst. ex A.DC.	2	47	1	2	6	3	1	4	4
shrub	Rubiaceae	*Feretia apodanthera* Delile	9	57	13	7	29	22	3	22	4
shrub	Rubiaceae	*Gardenia erubescens* Stapf & Hutch.	10	7	1	40	50	5	1	4	0
shrub	Rubiaceae	*Gardenia ternifolia* Schumach. & Thonn.	14	11	20	20	20	27	1	2	2
tree	Fabaceae - Faboideae	*Pericopsis laxiflora* (Benth.) Meeuwen	3	0	3	19	9	6	9	1	10
tree	Fabaceae	*Philenoptera laxiflora* (Guill. & Perr.) Roberty	10	21	37	0	4	6	0	0	10
tree	Fabaceae - Caesalpinioideae	*Piliostigma thonningii* (Schumach.) Milne-Redh.	18	34	7	61	162	66	5	30	11
tree	Fabaceae - Mimosoideae	*Prosopis africana* (Guill. & Perr.) Taub.	3	2	5	8	3	5	4	5	8
tree	Fabaceae - Faboideae	*Pterocarpus erinaceus* Poir.	22	9	60	2	1	5	8	9	8
tree	Bignoniaceae	*Stereospermum kunthianum* Cham.	95	42	55	2	4	4	2	0	0
shrub	Strychnaceae	*Strychnos spinosa* Lam.	37	15	46	183	27	111	15	105	2
tree	Fabaceae - Faboideae	*Xeroderris stuhlmannii* (Taub.) Mendonça & E.C.Sousa	5	3	6	13	8	18	6	0	9
group B: non-arable&fallows≠buffer zone											
shrub	Euphorbiaceae	*Bridelia ferruginea* Benth.	1	0	0	2	7	1	0	2	1
shrub	Combretaceae	*Combretum collinum* Fresen.	76	90	27	123	109	44	13	14	4
shrub	Combretaceae	*Combretum nigricans* Lepr. ex Guill. & Perr.	71	30	7	36	35	7	9	18	0
shrub	Rubiaceae	*Gardenia aqualla* Stapf & Hutch.	12	9	12	9	26	28	1	0	5
shrub	Annonaceae	*Hexalobus monopetalus* (A.Rich.) Engl. & Diels	8	7	0	5	16	20	5	2	9
tree	Fabaceae - Caesalpinioideae	*Isoberlinia doka* Craib & Stapf	14	44	63	15	34	45	37	48	145

Table S4 (continued)

			N individuals: juveniles			**N individuals: sub-adults**			**N individuals: adults**		
Life-form	**Family**	**Species**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**
tree	Anacardiaceae	*Lannea acida* A.Rich.	33	47	53	24	23	17	23	19	50
tree	Combretaceae	*Terminalia avicennioides* Guill. & Perr.	34	52	16	67	79	38	25	12	7
tree	Sapotaceae	*Vitellaria paradoxa* C.F.Gaertn.	34	81	24	71	89	66	60	54	87
group C: non-arable&buffer zone≠fallows											
shrub	Annonaceae	*Annona senegalensis* Pers.	63	49	5	177	49	25	25	5	1
tree	Combretaceae	*Anogeissus leiocarpa* (DC.) Guill. & Perr.	26	82	6	22	52	11	4	19	11
tree	Fabaceae - Caesalpinioideae	*Burkea africana* Hook.	31	7	14	42	25	12	62	33	18
shrub	Rubiaceae	*Crossopteryx febrifuga* (Afzel. ex G.Don) Benth.	24	8	12	166	44	70	80	9	38
group D: non-arable≠fallows≠buffer zone											
shrub	Combretaceae	*Combretum glutinosum* Perr. ex DC.	29	5	2	142	80	35	29	20	4
shrub	Fabaceae - Caesalpinioideae	*Detarium microcarpum* Guill. & Perr.	398	32	1	695	27	1	225	8	7
shrub	Combretaceae	*Pteleopsis suberosa* Engl. & Diels	172	47	1	54	10	4	11	2	0

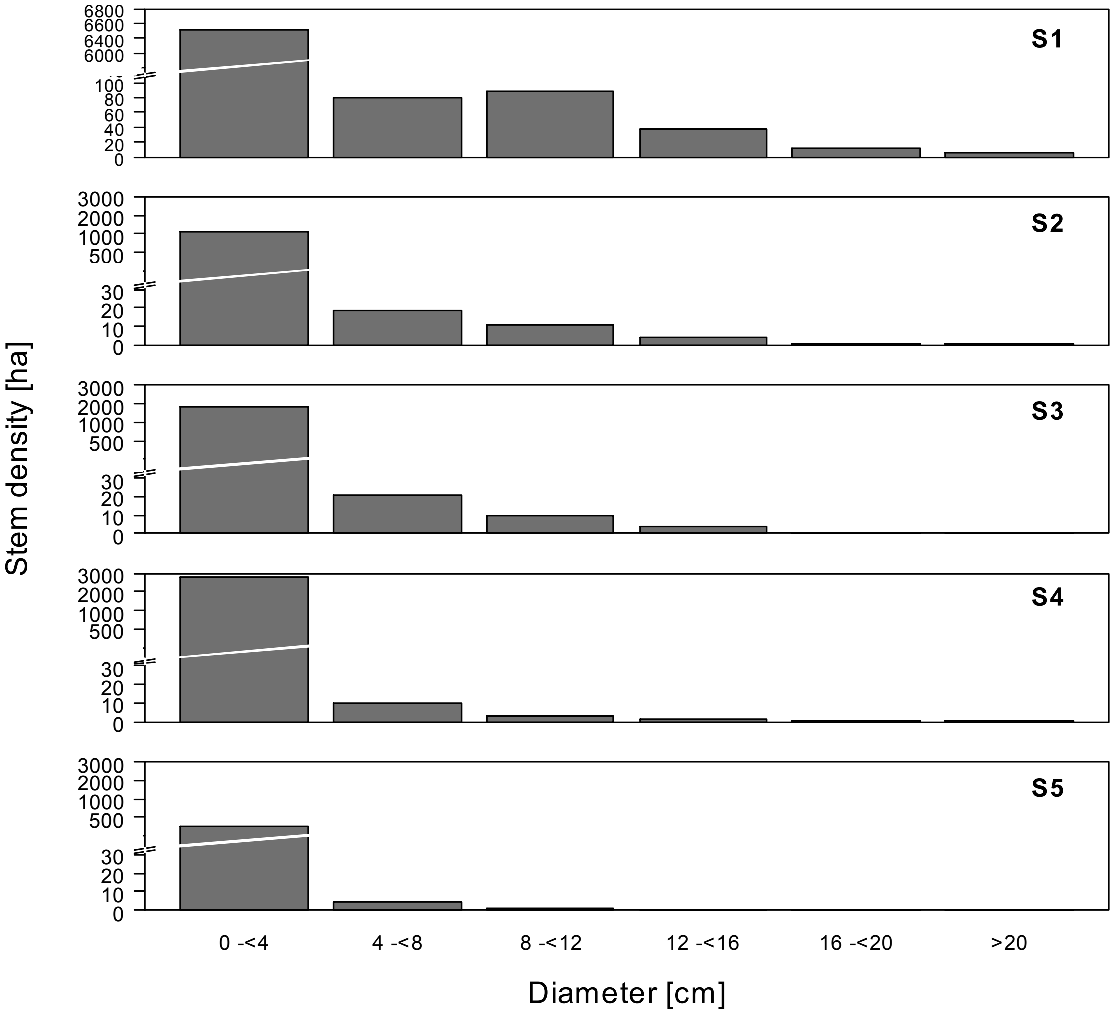


Fig. S1 Size-class distributions (stem density per ha vs. diameter classes) of the analyzed shrubs separated into five groups (S1-S5) formed by species with similar distribution patterns (compare Table 1). For each group one representative species is shown: S1- *Detarium microcarpum*, S2- *Combretum molle*, S3- *Combretum collinum*, S4- *Pteleopsis suberosa*, S5- *Gardenia ternifolia*.

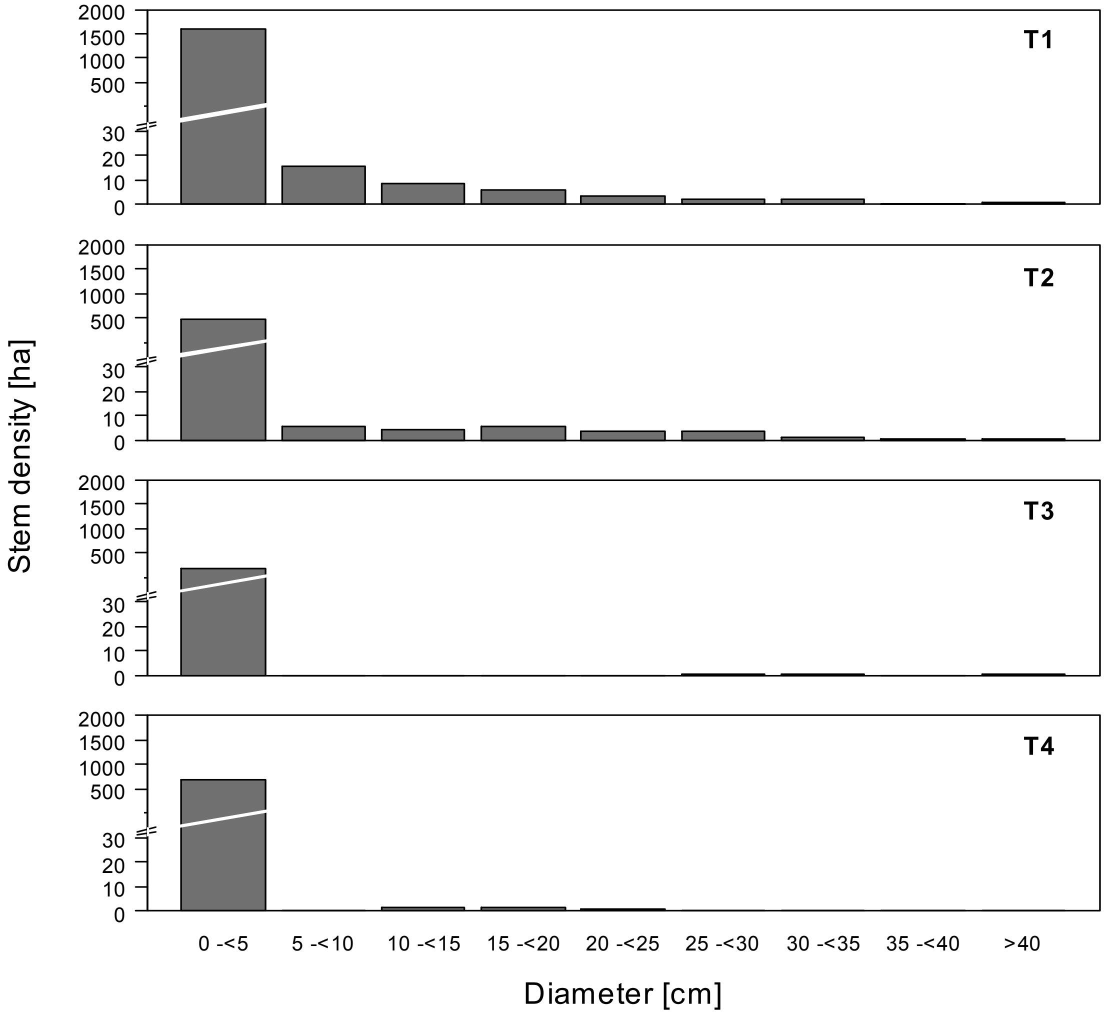
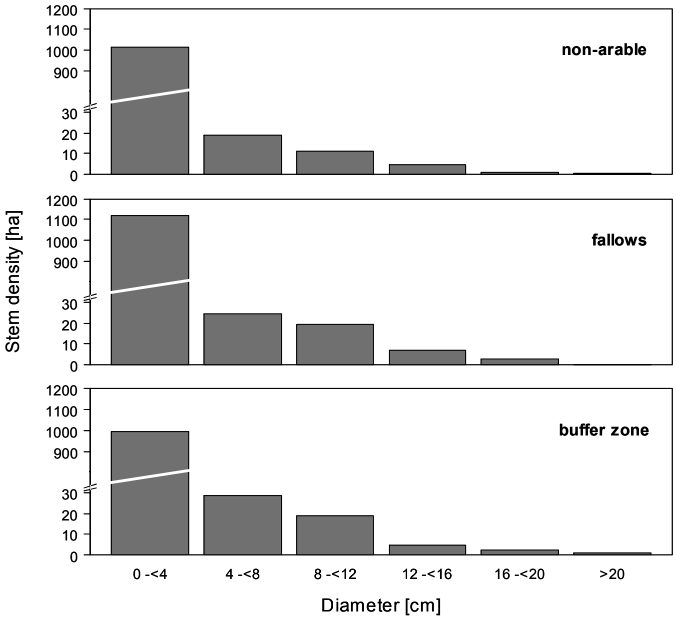
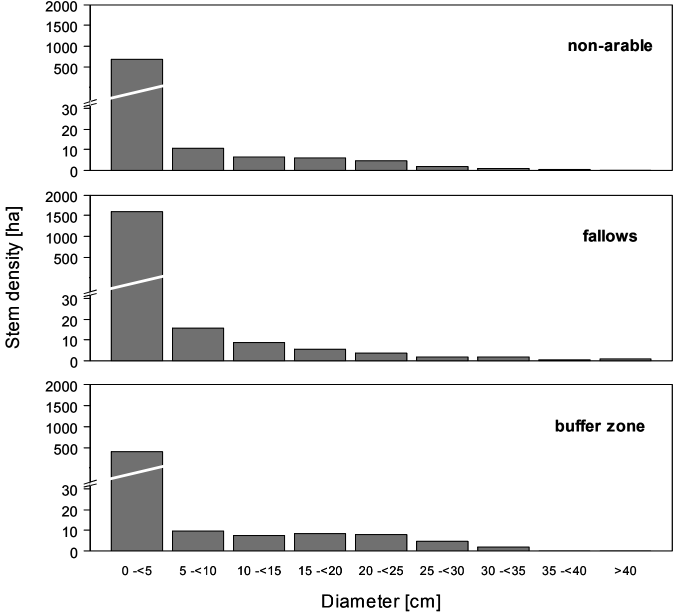


Fig. S2 Size-class distributions (stem density per ha vs. diameter classes) of the analyzed trees separated into four groups (T1-T4) formed by species with similar distribution patterns (compare Table 3). For each group one representative species is shown: T1- *Vitellaria paradoxa*, T2- *Burkea africana*, T3- *Pterocarpus erinaceus*, T4- *Philenoptera laxiflora*.

(A)


A - Combretum molle
non-arable
fallows
buffer zone
Stem density [ha]
0
10
20
30
900
1000
1100
1200
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

(B)


B - Vitellaria paradoxa
non-arable
fallows
buffer zone
Stem density [ha]
0
10
20
30
500
1000
1500
2000
0 -<5
5 -<10
10 -<15
15 -<20
20 -<25
25 -<30
30 -<35
35 -<40
>40
Diameter [cm]

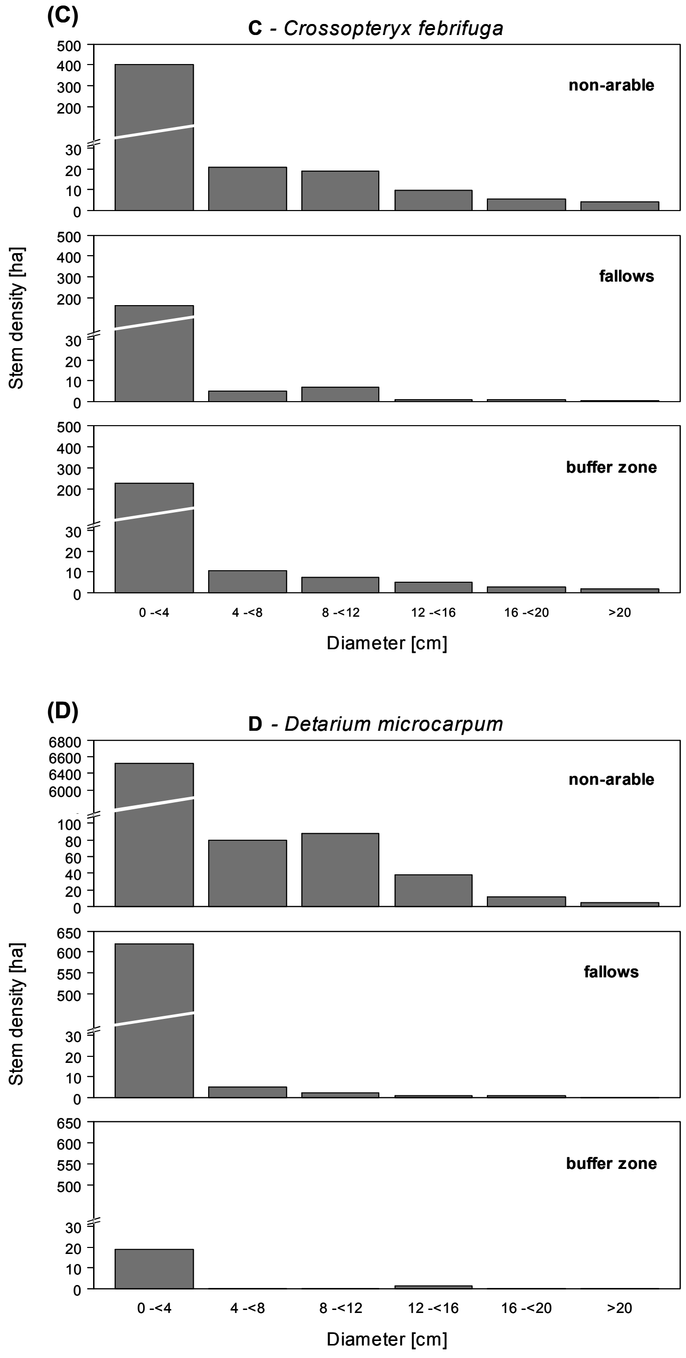
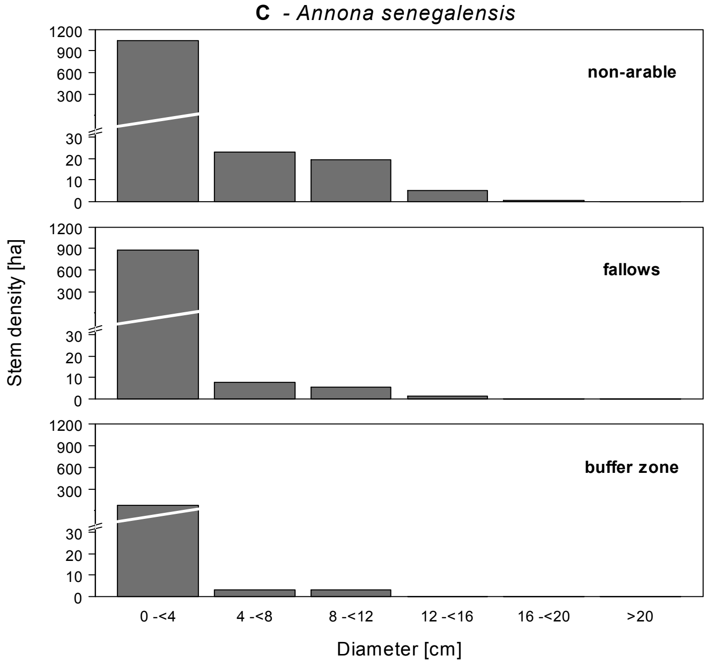
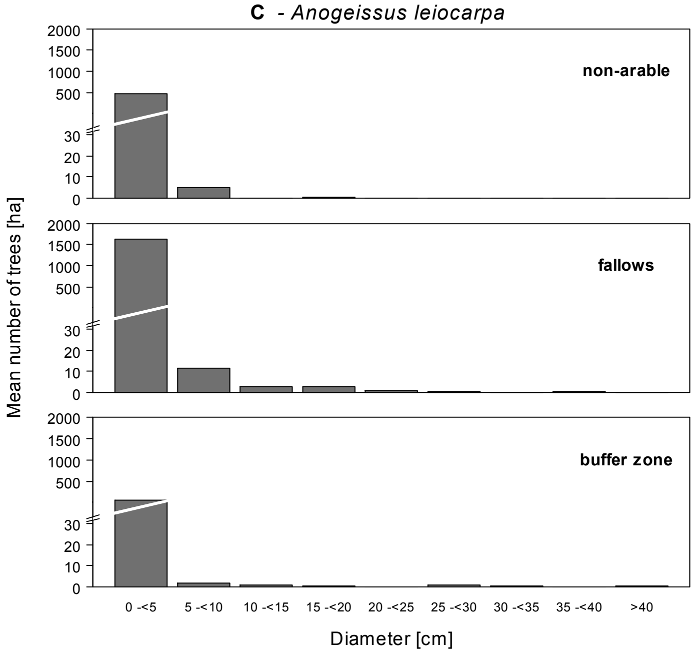
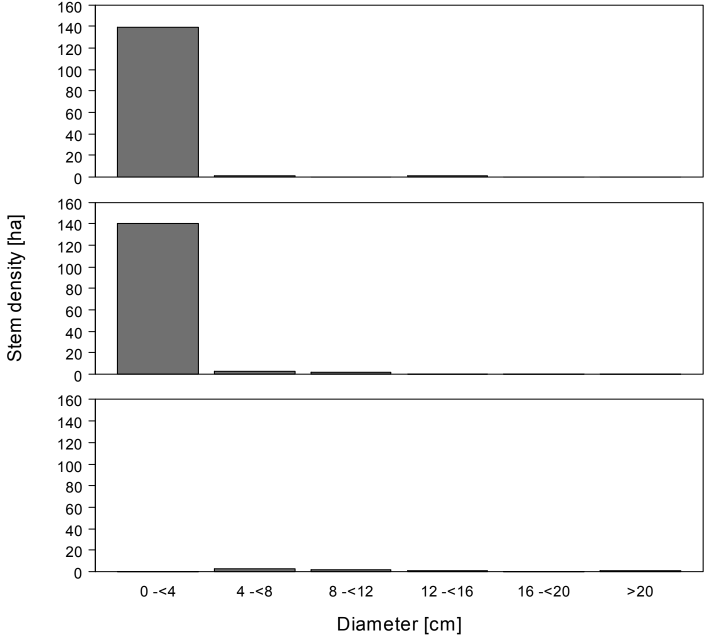


Fig. S3 Size-class distributions (stem density per ha vs. diameter class) of the analyzed woody species separated into four groups formed by species with similar distribution patterns in relation to land-cover type (compare Table 3). For each group one representative species is shown: (A) *Combretum molle*, (B) *Vitellaria paradoxa*, (C) *Crossopteryx febrifuga*, (D) *Detarium microcarpum***.**

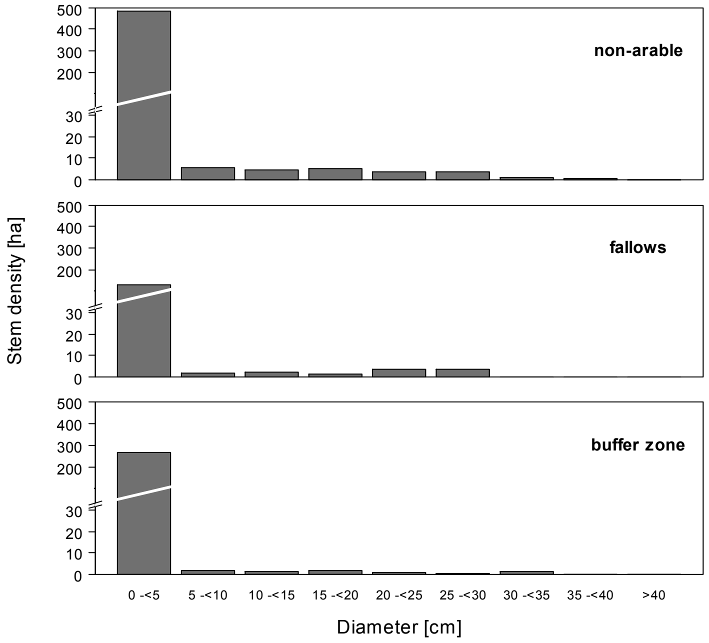
A: non-arable&fallows&buffer zone, **B**: non-arable&fallows≠buffer zone, **C**: non-arable&buffer zone≠fallows, **D**: non-arable≠fallows≠buffer zone. Similarity between land-cover types is marked by (&), dissimilarity by (≠).


C - *Annona senegalensis*
Stem density [ha]
1200
900
600
300
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

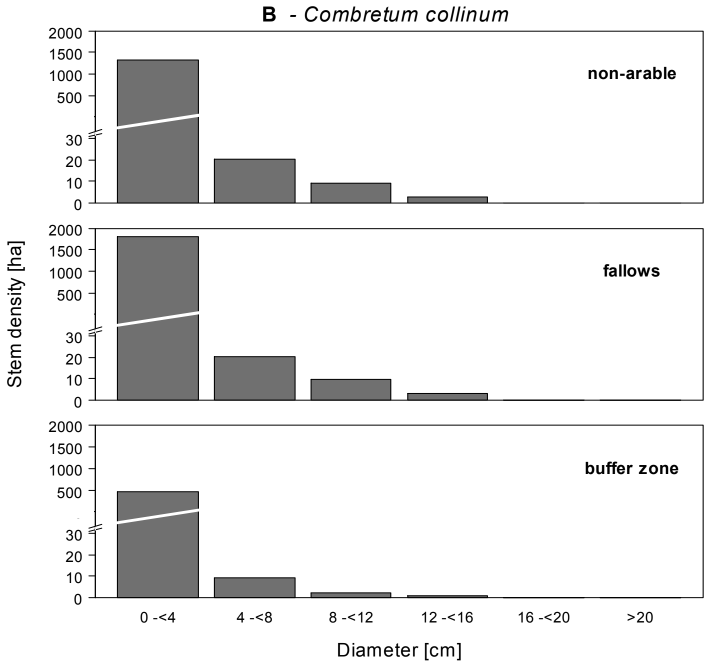

C - *Anogeissus leiocarpa*
Mean number of trees [ha]
2000
1500
1000
500
30
20
10
0
non-arable
fallows
buffer zone
0 -<5
5 -<10
10 -<15
15 -<20
20 -<25
25 -<30
30 -<35
35 -<40
>40
Diameter [cm]

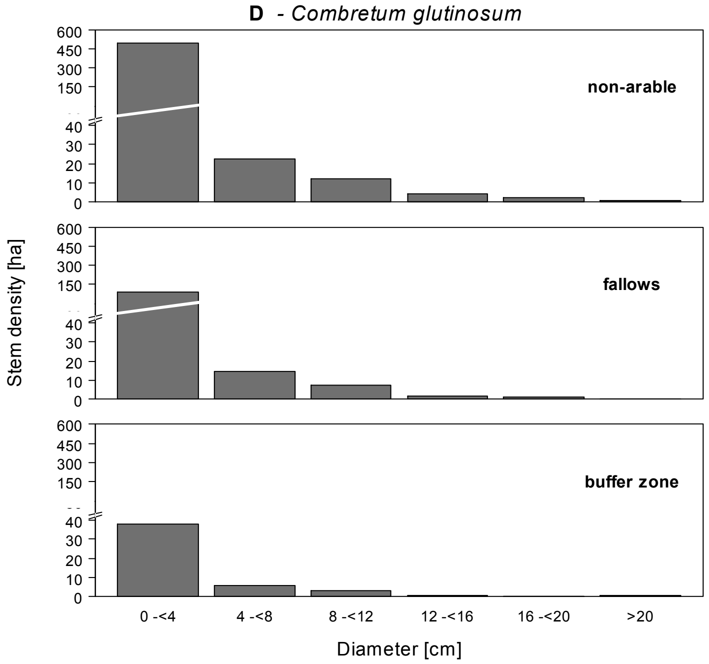


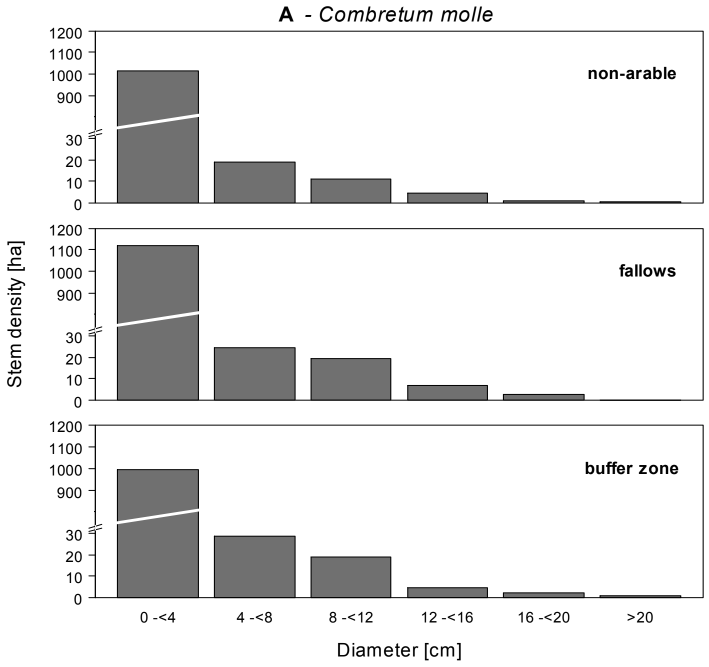
B - *Bridelia ferruginea*

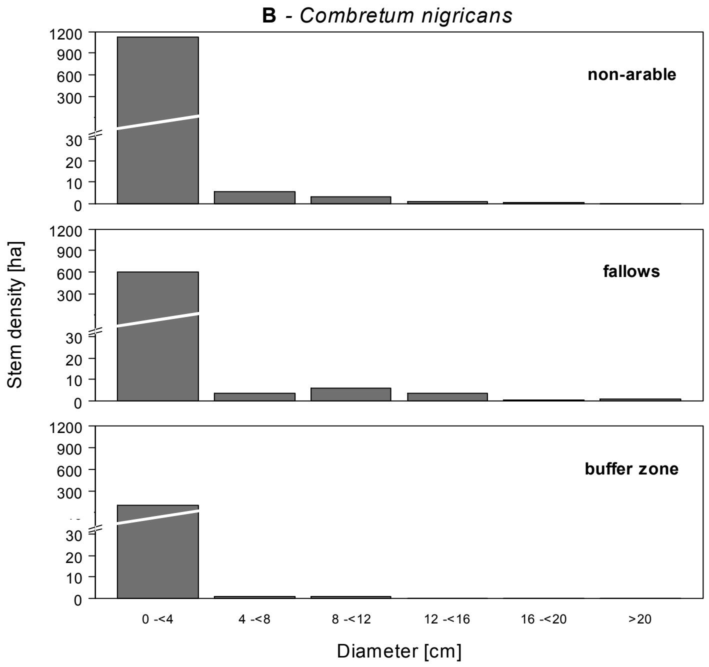


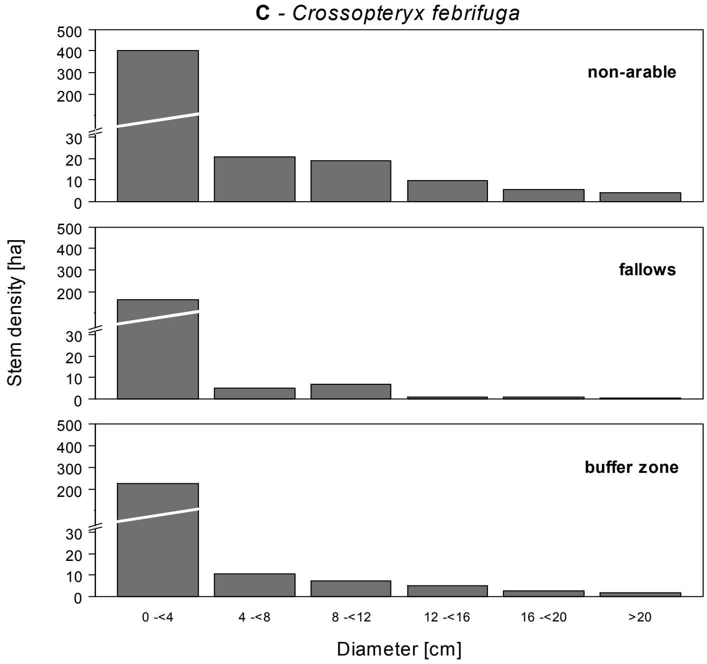
C - *Burkea africana*

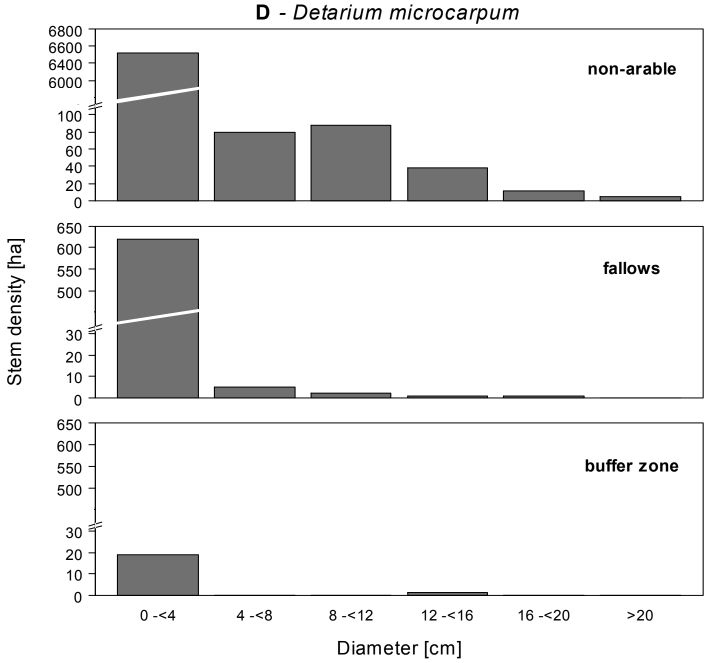

B - Combretum collinum
Stem density [ha]
2000
1500
1000
500
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

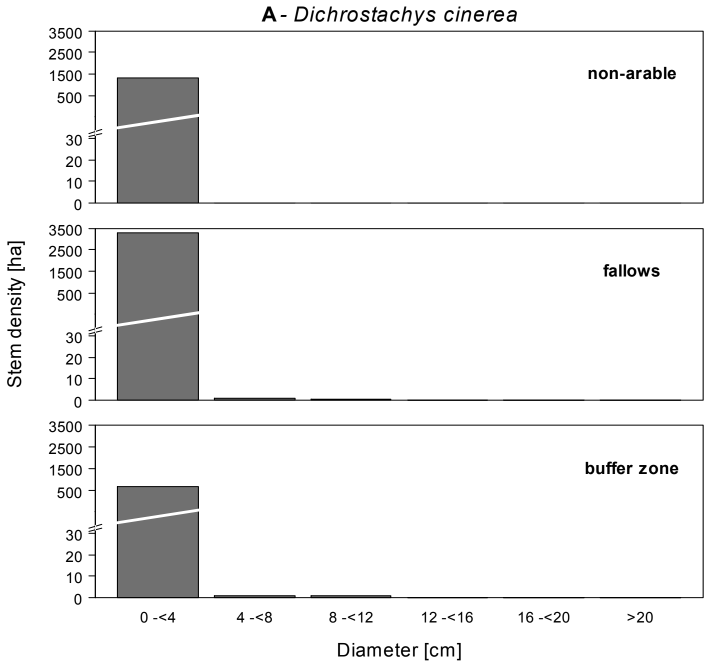

D - Combretum glutinosum
Stem density [ha]
600
450
300
150
40
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]


A - *Combretum molle*
non-arable
fallows
buffer zone
Stem density [ha]
1200
1100
1000
900
30
20
10
0
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

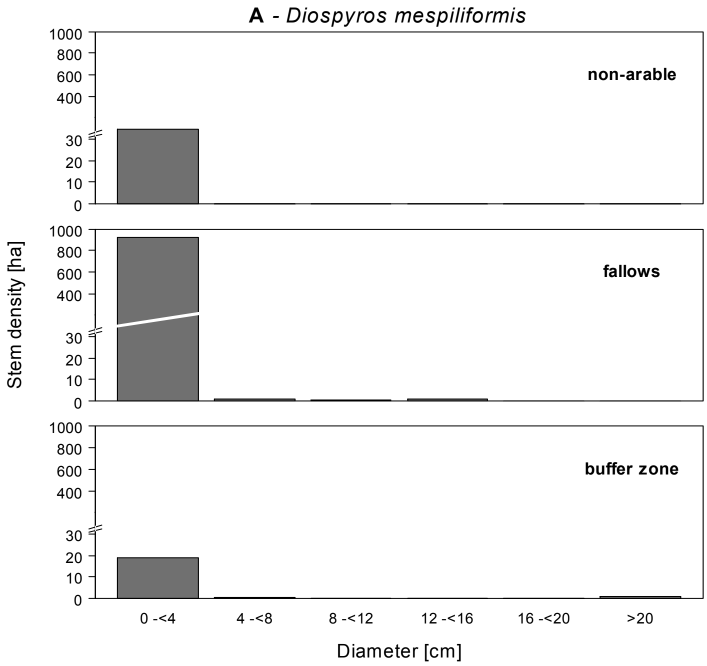

B - *Combretum nigricans*
non-arable
fallows
buffer zone
Stem density [ha]
1200
900
600
300
30
20
10
0
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]


C - Crossopteryx febrifuga
non-arable
fallows
buffer zone
Stem density [ha]
500
400
300
200
30
20
10
0
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

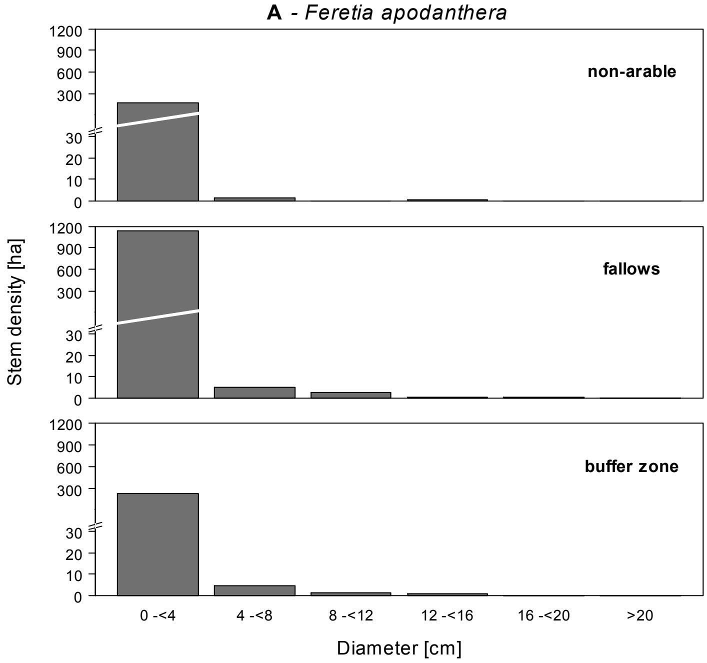

D - Detarium microcarpum
non-arable
fallows
buffer zone
Stem density [ha]
6800
6600
6400
6000
100
80
60
40
20
0
650
600
550
500
30
20
10
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

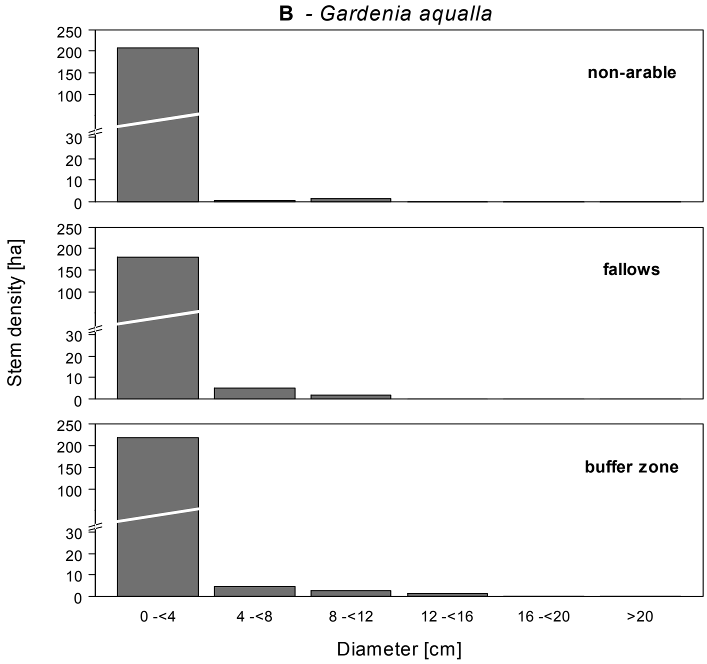


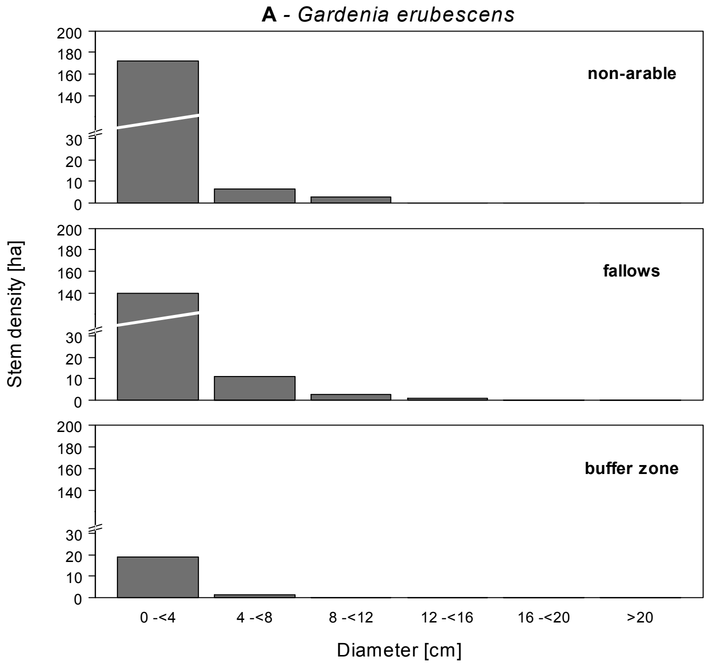
A- *Dichrostachys cinerea*

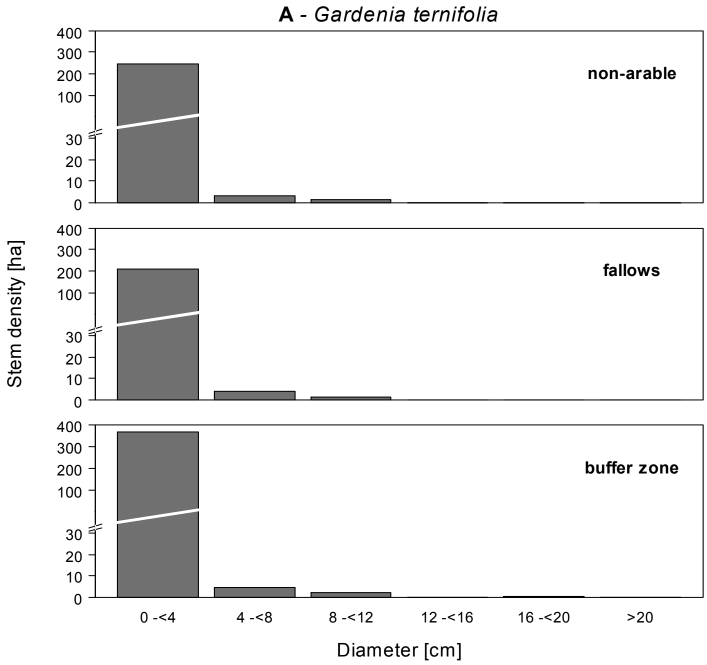


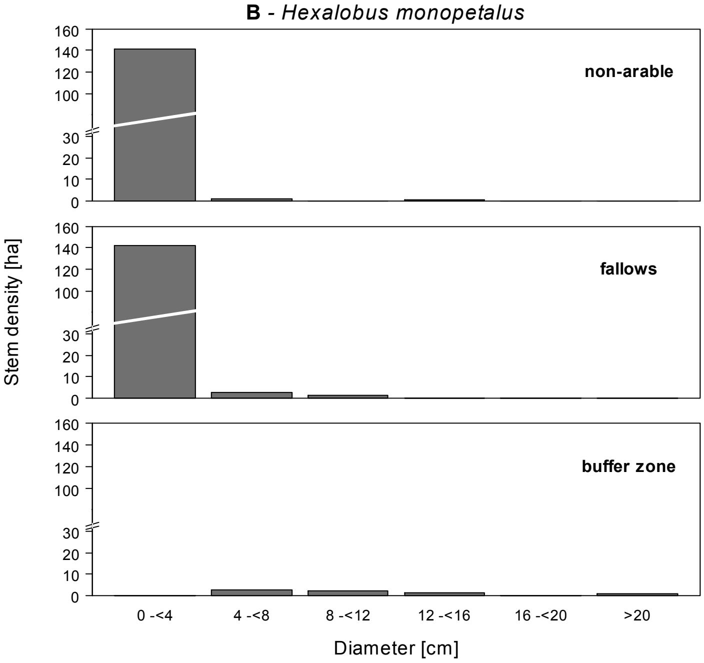
A - *Diospyros mespiliformis*

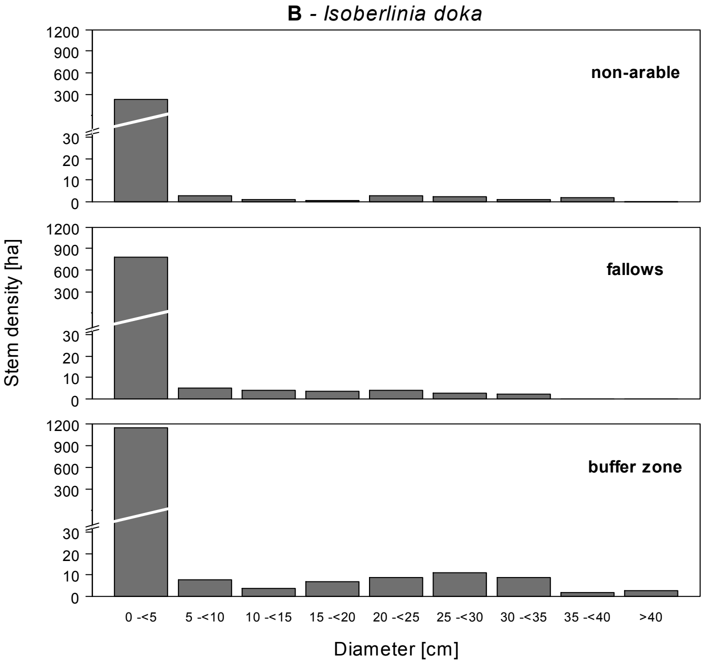

A - *Feretia apodanthera*
Stem density [ha]
1200
900
600
300
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

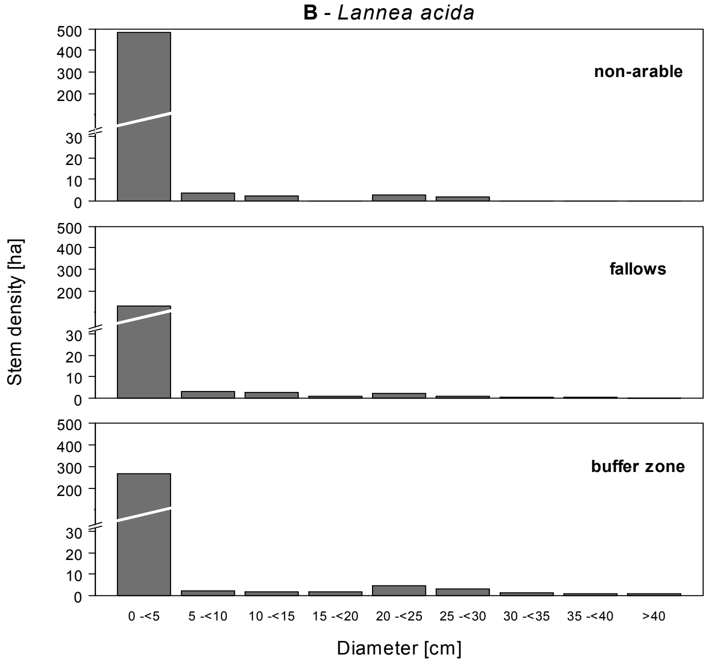

B - *Gardenia aqualla*
Stem density [ha]
250
200
150
100
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]


A - *Gardenia erubescens*
non-arable
fallows
buffer zone
Stem density [ha]
200
180
160
140
30
20
10
0
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

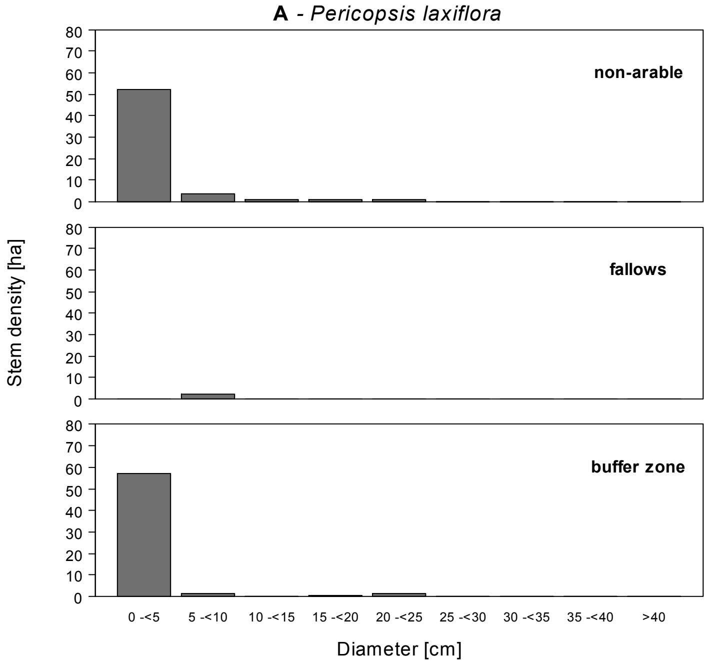

A - *Gardenia ternifolia*
non-arable
fallows
buffer zone
Stem density [ha]
400
300
200
100
30
20
10
0
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]


B - Hexalobus monopetalus
Stem density [ha]
160
140
120
100
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

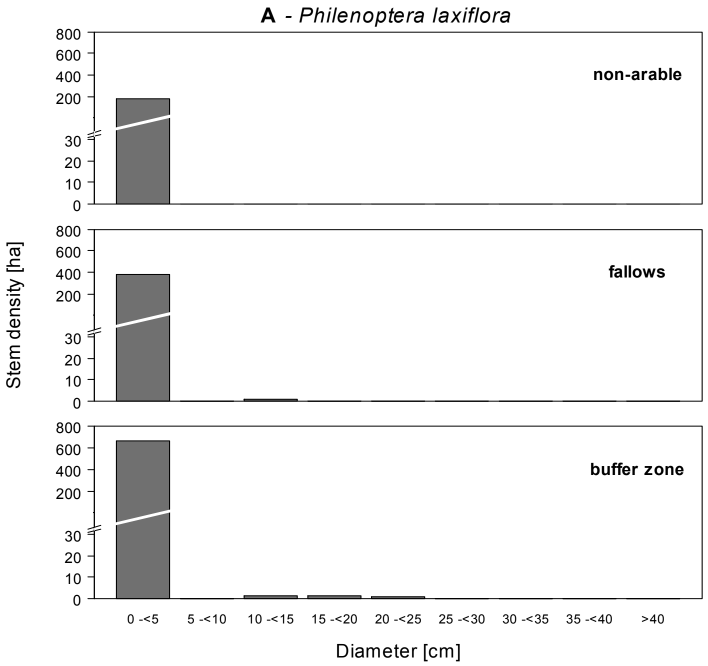

B - Isoberlinia doka
Stem density [ha]
1200
900
600
300
30
20
10
0
non-arable
fallows
buffer zone
0 -<5
5 -<10
10 -<15
15 -<20
20 -<25
25 -<30
30 -<35
35 -<40
>40
Diameter [cm]

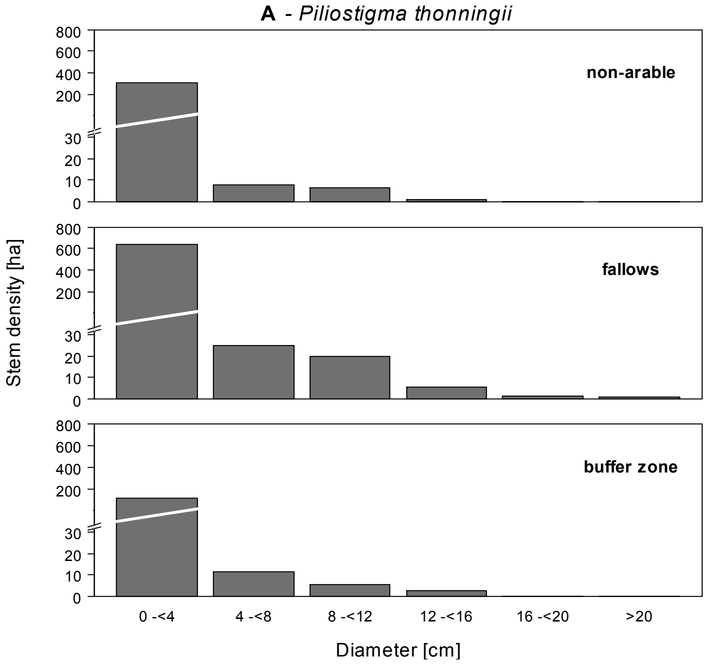


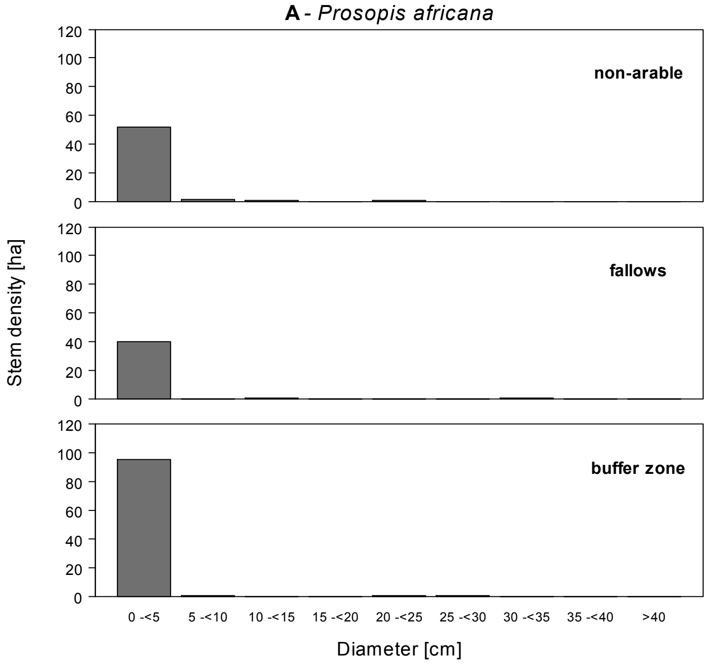
B - *Lannea acida*

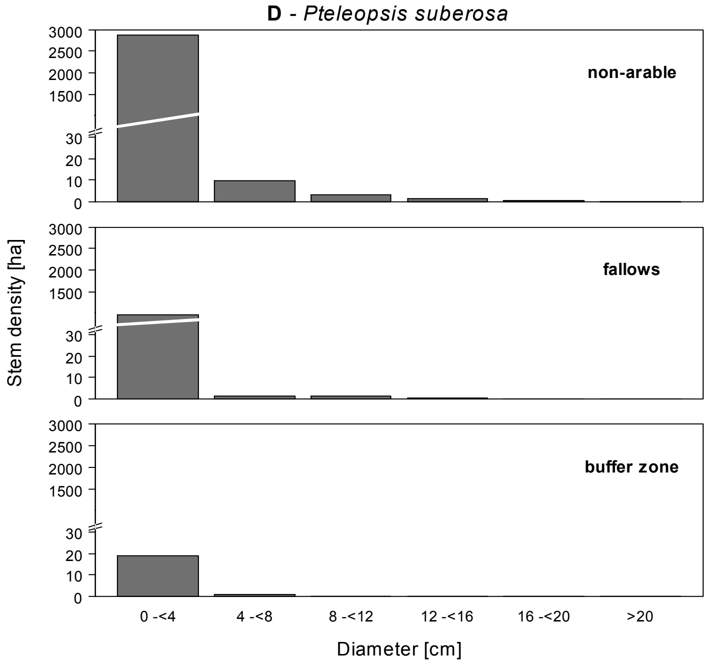


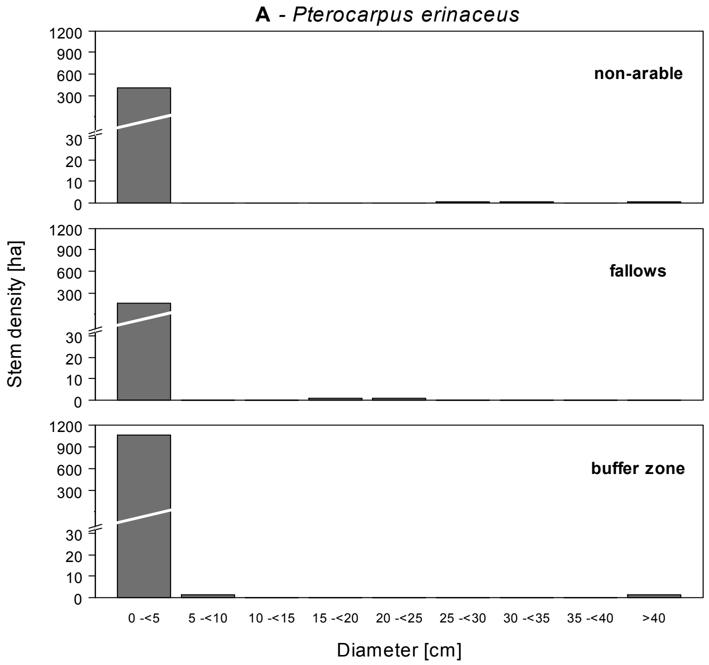
A - *Pericopsis laxiflora*

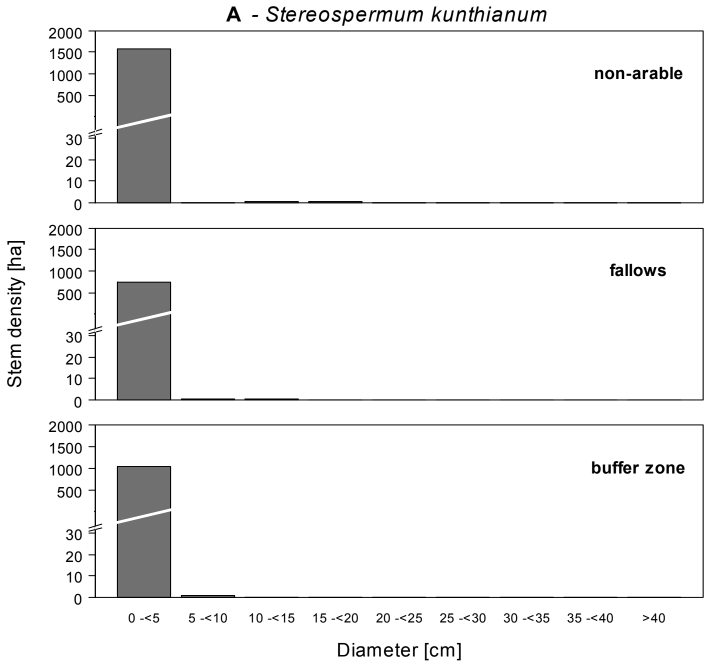

A - Philenoptera laxiflora
Stem density [ha]
800
600
400
200
30
20
10
0
non-arable
fallows
buffer zone
0 -<5
5 -<10
10 -<15
15 -<20
20 -<25
25 -<30
30 -<35
35 -<40
>40
Diameter [cm]

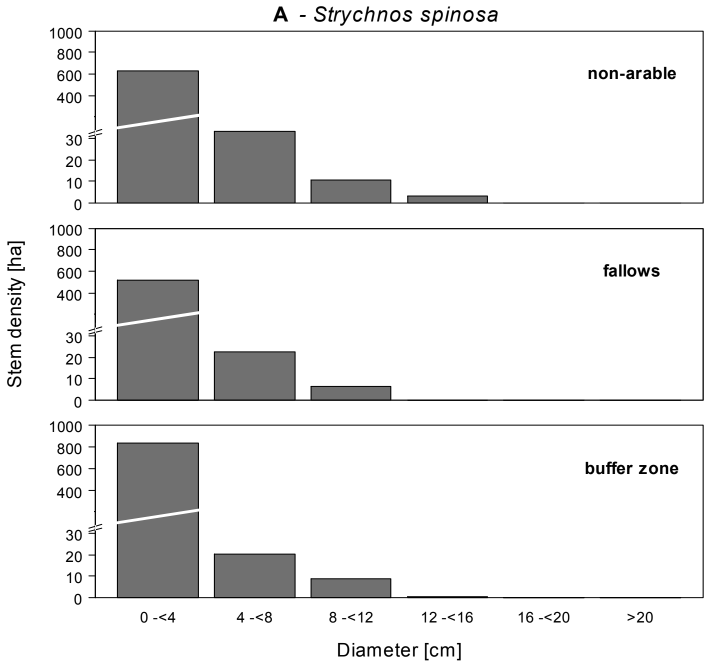

A - Piliostigma thonningii
Stem density [ha]
800
600
400
200
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]

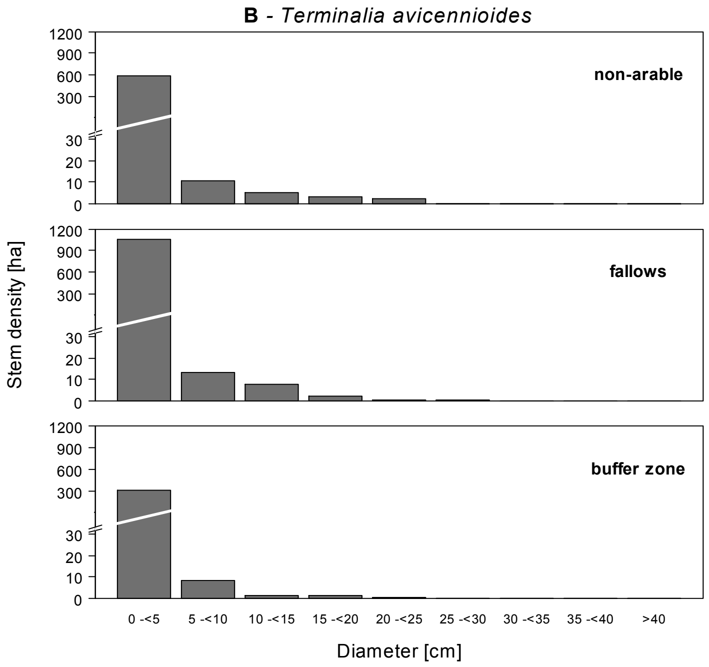

A - *Prosopis africana*
Stem density [ha]
120
100
80
60
40
20
0
non-arable
fallows
buffer zone
0 -<5
5 -<10
10 -<15
15 -<20
20 -<25
25 -<30
30 -<35
35 -<40
>40
Diameter [cm]

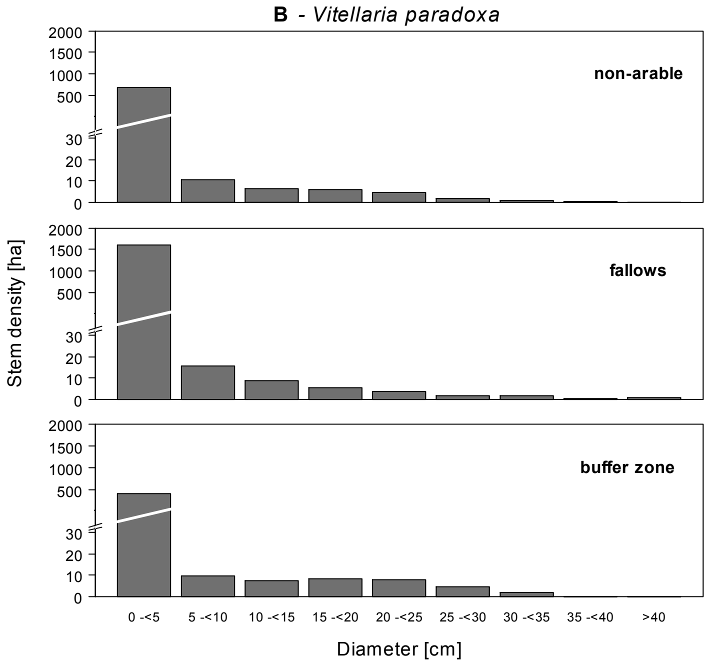

D - *Pteleopsis suberosa*
Stem density [ha]
3000
2500
2000
1500
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]


A - Pterocarpus erinaceus
Stem density [ha]
non-arable
fallows
buffer zone
1200
900
600
300
30
20
10
0
0 -<5
5 -<10
10 -<15
15 -<20
20 -<25
25 -<30
30 -<35
35 -<40
>40
Diameter [cm]


A - Stereospermum kunthianum
Stem density [ha]
non-arable
fallows
buffer zone
2000
1500
1000
500
30
20
10
0
0 -<5
5 -<10
10 -<15
15 -<20
20 -<25
25 -<30
30 -<35
35 -<40
>40
Diameter [cm]


A - Strychnos spinosa
Stem density [ha]
1000
800
600
400
30
20
10
0
non-arable
fallows
buffer zone
0 -<4
4 -<8
8 -<12
12 -<16
16 -<20
>20
Diameter [cm]


B - Terminalia avicennioides
Stem density [ha]
1200
900
600
300
30
20
10
0
non-arable
fallows
buffer zone
0 -<5
5 -<10
10 -<15
15 -<20
20 -<25
25 -<30
30 -<35
35 -<40
>40
Diameter [cm]



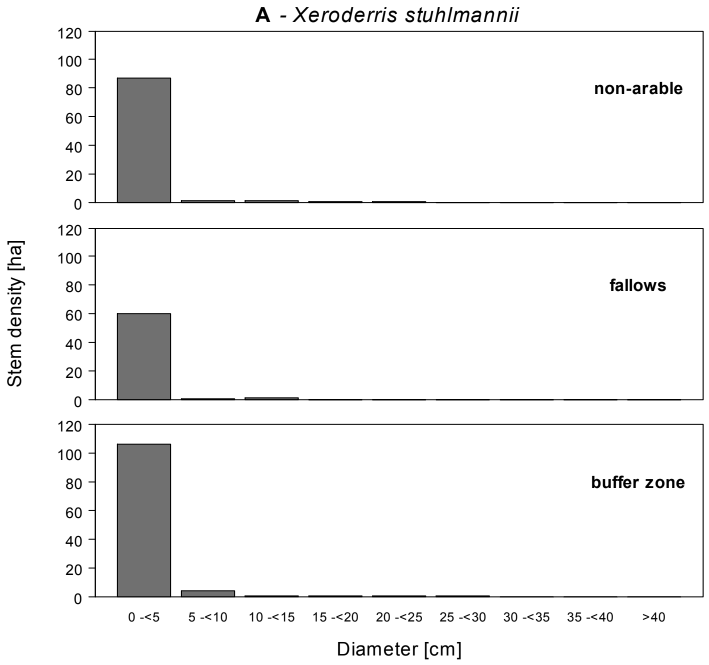


Fig. S4 Size-class distributions (stem density per ha vs. diameter class) of the analyzed tree and shrub species separated into four groups formed by species with similar distribution pattern in relation to land-cover type (compare Table 3). Species are shown in alphabetical order. **A**: non-arable&fallows&buffer zone, **B**: non-arable&fallows≠buffer zone, **C**: non-arable&buffer zone≠fallows, **D**: non-arable-fallows≠buffer zone. Similarity between land use types is marked by (&), dissimilarity by (≠).

Appendix – Chapter 3

Appendix S1 List of total number of individuals per study species, further divided according to the number of individuals per each land-cover type. Plots sampled on non-arable land: n=12, fallows: n=17 and buffer zone: n=10.

Growth forms	Family	Species	Total number of individuals	Number of individuals – non-arable	Number of individuals – fallows	Number of individuals – buffer zone
shrub	Annonaceae	*Annona senegalensis* Pers.	150	67	82	1
tree	Combretaceae	*Anogeissus leiocarpa* (DC.) Guill. & Perr.	546	145	228	173
shrub	Combretaceae	*Combretum collinum* Fresen.	191	66	99	26
shrub	Combretaceae	*Combretum molle* R.Br. ex G.Don	213	55	82	76
shrub	Combretaceae	*Combretum nigricans* Lepr. ex Guill. & Perr.	108	68	33	7
shrub	Fabaceae - Caesalpinioideae	*Detarium microcarpum* Guill. & Perr	366	343	23	0
shrub	Fabaceae - Mimosoideae	*Dichrostachys cinerea* (L.) Wight & Arn.	321	81	228	12
shrub	Ebenaceae	*Diospyros mespiliformis* Hochst. ex A.DC	60	3	56	1
shrub	Rubiaceae	*Feretia apodanthera* Delile	67	7	59	1
tree	Fabaceae - Caesalpinioideae	*Isoberlinia doka* Craib & Stapf	142	37	66	39
tree	Anacardiaceae	*Lannea acida* A.Rich.	118	43	61	14
tree	Fabaceae	*Philenoptera laxiflora* (Guill. & Perr.) Roberty	65	2	16	47
tree	Combretaceae	*Pteleopsis suberosa* Engl. & Diels	199	149	48	2
tree	Fabaceae - Faboideae	*Pterocarpus erinaceus* Poir.	62	19	9	34
tree	Bignoniaceae	*Stereospermum kunthianum* Cham.	125	57	41	27
shrub	Strychnaceae	*Strychnos spinosa* Lam.	96	35	26	35
tree	Combretaceae	*Terminalia avicennioides* Guill. & Perr.	125	46	67	12
tree	Sapotaceae	*Vitellaria paradoxa* C.F.Gaertn.	137	25	96	16

Appendix S2 Transition matrices of all study species containing the diameter-stage-specific rates of survival and transition during the rainy season. Growth forms: S: shrub, T: tree.

Species	**Non-arable**			**Fallows**				**Buffer zone**				
Anona senegalensis (S)		**0-0.8**	**> 0.8-0.95**		**0-0.4**	**> 0.4-0.6**	**> 0.6-1.23**					
	0-0.8	1.000	4.30E-07	**0-0.4**	0.9836093	0.9177282	0.000					
	> 0.8-0.95	0.0277774	1.000	**>0.4-0.6**	0.0166662	0.9999991	0.000					
				>0.6-1.23	2.15E-08	4.39E-06	0.9999792					
Anogeissus leiocarpa (T)		**0-1.0**	**> 1.0-2.9**		**0-0.8**	**> 0.8-1.87**			**0-0.1**	**> 0.1-0.36**		
	0-1.0	0.4710051	1.0734E-14	**0-0.8**	0.8358542	6.97333E-15		**0-0.1**	0.04988	0		
	> 1.0-2.98	5.0635E-14	0.9999997	**> 0.8-1.87**	0.0149223	1.00E+00		**>0.1-0.36**	0.68108	0.70769		
Combretum collinum (S)		**0-1.1**			**0-0.8**	**>0.8-1.07**			**0-0.4**	**> 0.4-0.7**	**> 0.7-0.9**	**> 0.9-1.31**
	0-1.1	0.96611		**0-0.8**	0.9894	0.89952		**0-0.4**	0.9475019	0	0	0
				>0.8-1.07	0.01084	1		**> 0.4-0.7**	0.1173691	1	0	0
								> 0.7-0.9	0.0391626	0.1721839	1	0
								> 0.9-1.31	8.77E-07	5.70E-10	4.54E-11	0.99493
Combretum molle (S)		**0-1.88**			**0-1.85**				**0-0.8**	**> 0.8-1.48**		
	0-1.88	0.937863		**0-1.85**	0.96433			**0-0.8**	0.975608	4.19E-09		
								> 0.8-148	0.050016	0.9999986		

Appendix S2 (continued)

Species	Non-arable			Fallows				Buffer zone			
Combretum nigricans (S)		**0-0.75**			**0-0.5**	**> 0.5-0.6**	**> 0.6-0.69**		**0-1.73**		
	0-0.75	0.988641		**0-0.5**	0.926833	1.28E-05	0.989194	**0-1.73**	1		
				> 0.5-0.6	0.026322	0.999999	1.28E-05				
				> 0.6-0.69	0.026322	0.989194	0.999999				
Detarium microcarpum (S)		**0-1.84**			**0-0.9**	**> 0.9-1.08**					
	0-1.84	0.982097		**0-0.9**	1	0.003271					
				> 0.9-1.08	0.031248	1					
Dichrostachys cinerea (S)		**0-0.76**			**0-1.27**				**0-0.63**		
	0-0.76	0.99115		**0-1.27**	0.950919			**0-0.63**	1		
Diospyros mespiliformis (S)		**0-0.33**			**0-1.88**				**0-0.8**	**> 0.8-1.0**	**> 1.0-1.4**
	0-0.33	0.871003		**0-1.88**	0.990363			**0-0.8**	1	1.05E-18	4.37E-14
								> 0.8-1.0	4.13E-13	1	4.37E-14
								> 1.0-1.4	1.72E-13	1	1
Feretia apodanthera (S)		**0-0.4**	**> 0.4-0.87**		**0-0.5**	**> 0.5-2.93**			**0-1.02**		
	0-0.4	1	0.00	**0-0.5**	1	0.149995		**0-1.02**	1		
	> 0.4-0.87	0.071431	1	**> 0.5-2.93**	0.065871	1					

Appendix S2 (continued)

Species | **Non-arable** | **Fallows** | **Buffer zone**

Isoberlinia doka (T)

Non-arable

	0-0.4	**> 0.4-1.8**
0-0.4	0.342854	0
> 0.4-1.8	0.020005	1

Fallows

	0-0.4	**> 0.4-0.6**	**> 0.6-0.7**	**> 0.7-2.9**
0-0.4	0.830349	0.14287	1.52E-14	0
> 0.4-0.6	0.080005	1	0.5	0
> 0.6-0.7	1.13E-11	0.28572	1	0
> 0.7-2.9	0.020005	3.01E-10	0.5	0.999998

Buffer zone

	0-0.2	**> 0.2-0.4**	**> 0.4-0.6**	**> 0.6-0.7**	**> 0.7-0.93**
0-0.2	0.545457	8.16E-10	0	0	0
> 0.2-0.4	1.94E-10	0.9374679	0.14287	1.52E-14	0
> 0.4-0.6	8.19E-11	0.0800052	0.28572	0.5	0
> 0.6-0.7	8.19E-11	1.13E-11	0.28572	1	0
> 0.7-0.93	8.19E-11	0.0200054	3.01E-10	0.5	1

Lannea acida (T)

Non-arable

	0-0.4	**> 0.4-0.52**
0-0.4	0.857181	0.999999
> 0.4-0.52	0.055557	1

Fallows

	0-1.0	**> 1.0-1.02**
0-1.0	1	2.46E-21
> 1.0-1.02	0	0.8378325

Buffer zone

	0-0.1	**> 0.1-0.17**
0-0.1	8.49E-15	1.80E-14
> 0.1-0.17	1.60E-28	2.09E-25

Philenoptera laxiflora (T)

Non-arable

	0-0.19
0-0.19	0.499983

Fallows

	0-0.1	**> 0.1-0.54**
0-0.1	0.99994	0
> 0.1-0.54	7.33E-24	1

Buffer zone

	0-0.6	**> 0.6-0.65**
0-0.6	1	1
> 0.6-0.65	0.055555	1

Pteleopsis suberosa (T)

Non-arable

	0-0.57
0-0.57	0.976112

Buffer zone

	0-0.17
0-0.17	1

Appendix S2 (continued)

Species	**Non-arable**				**Fallows**				**Buffer zone**					
Pterocarpus erinaceus (T)		**0-0.53**				**0-0.1**	**> 0.1-0.5**	**> 0.5-0.77**		**0-0.47**				
	0-0.53	1			**0-0.1**	1	0	0	**0-0.47**	0.96666				
					> 0.1-0.5	5.02E-05	1	0						
					> 0.5-0.77	5.02E-05	0.125002	1						
Stereospermum kunthianum (T)		**0-0.5**	**> 0.5-0.7**	**> 0.7-1.7**		**0-0.1**	**> 0.1-0.75**			**0-0.4**	**> 0.4-0.5**	**> 0.5-0.6**	**> 0.6-0.66**	
	0-0.5	0.984848	9.22E-09	0	**0-0.1**	1	0		**0-0.4**	0.9999999	1.50E-08	0.499964	3.40E-07	
	> 0.5-0.7	0.109403	1	0.000	**> 0.1-0.75**	0.499959	1		**> 0.4-0.5**	5.53E-07	0.999999	0.499967	1.84E-08	
	> 0.7-1.7	0.013675	0.500018	1					**> 0.5-0.6**	0.125006	1.50E-08	1	8.05E-09	
									> 0.6-0.66	0.062495	0.888888	2.14E-05	1	
Strychnos spinosa (S)		**0-0.8**	**> 0.8-0.9**	**> 0.9-0.96**		**0- 1.04**				**0-1.0**	**> 1.0-1.27**			
	0-0.8	1	1	1.84E-07	**0-1.04**	1			**0-1.0**	1	3.39E-08			
	> 0.8-0.9	7.51E-08	1	2.72E-07					**> 1.0-1.27**	0.0250015	1			
	> 0.9-0.96	0.0476181	9.35E-14	1										
Terminalia avicennioides (T)		**0-0.56**				**0-0.89**				**0-0.1**	**> 0.1-0.3**	**> 0.3-0.5**	**> 0.5-0.8**	**> 0.8-1.32**
	0-0.56	1			**0-0.89**	0.9535216			**0-0.1**	1	0.999975	0	0	0
									> 0.1-0.3	0.249691	1	2.13E-13	0	0
									> 0.3-0.5	9.72E-09	1.25E-07	1	0	0
									> 0.5-0.8	9.72E-09	1.25E-07	1	1	1.49E-05
									> 0.8-1.32	9.72E-09	1.25E-07	2.13E-13	1	1

Appendix S2 (continued)

Species	Non-arable							Fallows							Buffer zone		
Vitellaria paradoxa (T)		**0-0.1**	**> 0.1-0.2**	**> 0.2-0.3**	**> 0.3-0.4**	**> 0.4-0.7**	**> 0.7-0.78**		**0-0.1**	**> 0.1-0.3**	**> 0.3-0.5**	**> 0.5-0.7**	**> 0.7-0.9**	**> 0.9-2.78**		**0-0.1**	**> 0.1-0.35**
	0-0.1	1	0.100028	0.055055	0	0	0	**0-0.1**	1	0.021635	0	0	0	0	**0-0.1**	0.999739	0
	> 0.1-0.2	2.16E-08	1	0.08258	1.41E-07	0	0	**> 0.1-0.3**	0.589136	0.985296	5.24E-10	0	0	0	**> 0.1-0.35**	2.28E-14	1
	> 0.2-0.3	0.821775	9.25E-11	1	1.36E-07	0	0	**> 0.3-0.5**	7.29E-10	0.043269	1	4.20E-10	0	0			
	> 0.3-0.4	1.02E-09	0.099977	0.055053	1	0.0787	0	**> 0.5-0.7**	7.29E-10	5.18E-11	0.285712	1	0.99828	0			
	> 0.4-0.7	1.02E-09	0.099997	1.32E-10	0.250002	1	0.999465	**> 0.7-0.9**	7.29E-10	2.47E-10	3.22E-08	0.134311	1	4.34E-09			
	> 0.7-0.78	1.02E-09	2.80E-09	6.29E-10	1.79E-07	0.314797	1.000	**> 0.9-2.78**	7.29E-10	2.47E-10	3.22E-08	1.71E-09	2.32E-08	1			

Appendix S3 Modeling the survival probability (*S*) and transition probability (*Psi*) as a function of diameter size-class, land-cover type and season for all study species. Detection probability *p* is fixed at 0 and 1 for un-observed and aboveground plants, respectively.

Notation: diameter class, land-cover type, season, K=number of estimable parameters, AICc=small sample AICc. (+) indicates inclusion of an explanatory variable in the model (not addition); (*) indicates inclusion of explanatory variables and interactions (not multiplication) (for more details see Crawley 2007). Growth forms: S: shrub, T: tree.

Species	***S* (survival probability)**	***Psi* (transition probability)**	**K**	**AICc**
Annona senegalensis (S)	~diameter class * land-cover type * season	~diameter class + season + land-cover type + diameter class:season : land-cover type	29	26847.77
Anogeissus leiocarpa (T)	~diameter class + land-cover type + season + diameter class : land-cover type	~diameter class + season + land-cover type + diameter class : land-cover type	12	28698.82
Combretum collinum (S)	~diameter class + land-cover type + season + land-cover type : season	~diameter class + season + land-cover type + diameter class : land-cover type	28	41171.77
Combretum molle(S)	~diameter class + land-cover type + season + diameter class : season	~diameter class + season + land-cover type + diameter class : season : land-cover type	74	38394.19
Combretum nigricans (S)	~diameter class * land-cover type * season	~diameter class + season + land-cover type + diameter class : season:land-cover type	42	18579.75
Detarium microcarpum (S)	~diameter class + land-cover type + season + diameter class : season	~diameter class + season + land-cover type + diameter class : season : land-cover type)	98	83850.48
Dichrostachys cinerea (S)	~diameter class * land-cover type * season	~diameter class + season + land-cover type + diameter class : land-cover type	30	56224.02
Diospyros mespiliformis (S)	~diameter class + land-cover type + season + diameter class : season	~diameter class + season + land-cover type + diameter class : season:land-cover type	43	1846.198
Feretia apodanthera (S)	~diameter class * land-cover type * season	~diameter class * land-cover type	33	4695.434
Isoberlinia doka (T)	~diameter class * land-cover type	~diameter class * season	19	44693.86
Lannea acida (T)	~diameter class + land-cover type + season + diameter class : season	~diameter class + season + land-cover type + diameter class : season : land-cover type	34	19827.76

Appendix S3 (continued)

Species	*S* (survival probability)	*Psi* (transition probability)	K	AICc
Philenoptera laxiflora (T)	~diameter class * land-cover type * season	~diameter class + season + land-cover type + diameter class : season : land-cover type	25	19595.02
Pteleopsis suberosa (S)	~diameter class + land-cover type + season + diameter class : season	~diameter class+ season + land-cover type + diameter class : season : land-cover type	37	26071.56
Pterocarpus erinaceus (T)	~diameter class + land-cover type + season + diameter class : season	~diameter class + season + land-cover type + diameter class : season : land-cover type	24	12757.25
Stereospermum kunthianum (T)	~diameter class * land-cover type * season	~diameter class + season + land-cover type + diameter class:season:land-cover type	28	33856.43
Strychnos spinosa (S)	~diameter class + land-cover type + season + diameter class:land-cover type	~diameter class + season + land-cover type + diameter class:season:land-cover type	52	40577.86
Terminalia avicennioides (T)	~diameter class * land-cover type * season	~diameter class + season + land-cover type + diameter class:season:land-cover type	41	22669.24
Vitellaria paradoxa (T)	~diameter class * land-cover type * season	~diameter class + season + land-cover type + diameter class:season:land-cover type	25	28337.15

Appendix S4 Study species. Information on habitat requirements and species specific comments, fire sensitivity, as well as some vital parameters as defined by Noble and Slatyer (1980) are presented (Buechner & Dawkins 1961, Rietkerk et al. 1998, Bationo et al. 2001, Arbonnier 2002, Andary et al. 2005, Bellefontaine 2005, Dourma et al. 2006, Gignoux et al. 2006, Kouyaté et al. 2006, Nikiema et al. 2007, Sacande & Sanogo 2007, Cauldwell & Ziegler 2008, Dayamba et al. 2008, Duvall 2008, Orwa et al. 2009, Bognounou et al. 2010, El-Kamali 2011, CJB 2012). Growth forms: S: shrub, T: tree.

Species	**Habitat and species specific comments**	**Regeneration, survival or persistence strategy and fire sensitivity**
Annona senegalensis (S)	on gravel, fallows	seeds, root suckers, coppice, fire-sensitive
Anogeissus leiocarpa (T)	usually on loamy compact soils; tolerates temporary inundation, pioneer species	seeds, root suckers, some ability to coppice, very fire-sensitive
Combretum collinum (S)	all soil types	seeds, coppice
Combretum molle (S)	all soil types	seeds, root suckers, coppice; fire-sensitive
Combretum nigricans (S)	prefers clayey and loamy soils; also on rocky, arenaceous, sandy soils	seeds, root suckers; fire-tolerant
Detarium microcarpum (S)	arenaceous, laterite; esp. on laterite and fallows	seeds, root suckers, coppice; natural germination is hampered by bush fire
Dichrostachys cinerea (S)	heavy profound soils; invasive on fallows and overgrazed, trampled ground	seeds, root suckers; fire-sensitive
Diospyros mespiliformis (S)	gallery forest, riverbank, termite mounds, rocky hills	mainly seeds, root suckers; young trees are fire-sensitive
Feretia apodanthera (S)	termite mounds, temporary water bodies, compact soils	seeds, root suckers
Isoberlinia doka (T)	loamy and well drained soils, medium soils	seeds, root suckers; fire-sensitive
Lannea acida (T)	all soil types	seeds, root suckers, fire-tolerant
Philenoptera laxiflora (T)	all soil types	seeds
Pteleopsis suberosa (T)	silt, close to temporary water bodies, medium soils, sometimes invading in cultivated fields	seeds, root suckers, fire-tolerant
Pterocarpus erinaceus (T)	all soil types, incl. laterite	seeds, root suckers, fire-sensitive
Stereospermum kunthianum (T)	all soil types	seeds, root suckers, fire-tolerant

Appendix S4 (continued)

Species	Habitat and species specific comments	Regeneration, survival or persistence strategy and fire sensitivity
Strychnos spinosa (S)	all soil types, incl. laterite and gravel	seeds, root suckers, coppice, semi fire-tolerant
Terminalia avicennioides (T)	arenaceous soils, fallows	seeds, root suckers, fire-tolerant
Vitellaria paradoxa (T)	all soil types except, inundated soils	seeds, root suckers, fire-tolerant

Andary, C., Doumbia, B., Sauvan, N., Olivier, M. & Garcia, M. 2005. *Anogeissus leiocarpa* (DC.) Guill. & Perr. [Internet] Record from Protabase. Jansen, P.C.M. & Cardon, D. (eds.) PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, NL. URL: http://database.prota.org/search.htm. (Accessed May 2012).

Arbonnier, M. 2002. *Arbres, arbustes et lianes des zones sèches d'Afrique de l'Ouest*. 2nd ed. CIRAD, MNHN, Paris, FR.

Bationo, B.A., Ouedraogo, S.J. & Guinko, S. 2001. Stratégies de régénération naturelle de *Detarium microcarpum* Guill. et Perr. dans la forêt classée de Nazinon (Burkina Faso). *Fruits* 56: 271-285.

Bayoumi, A.A.M.S. 2001. Fire situation in Sudan. *International Forest Fire News* 25: 115-117.

Bellefontaine, R. 2005. Pour de nombreux ligneux, la reproduction sexuée n'est pas la seule voie: analyse de 875 cas - Texte introductif, tableau et bibliographie. *Sécheresse* 1 E: 1-39.

Buechner, H.K. & Dawkins, H.C. 1961. Vegetation change induced by elephants and fire in Murchison Falls National Park, Uganda. *Ecology* 42: 752-766.

Cauldwell, A.E. & Ziegler, U. 2008. A reassessment of the fire-tolerance of some miombo woody species in the Central Province, Zambia. *African Journal of Ecology* 38: 138–146.

Conservatoire et Jardin botaniques (CJB) & South African National Biodiversity Institute 2012: African Plant Database. URL: http://www.ville-ge.ch (Accessed May 2012).

Dayamba, S.D.; Tigabu, M., Sawadogo L. & Oden, P.C. 2008. Seed germination of herbaceous and woody species of the Sudanian savanna-woodland in response to heat shock and smoke. *Forest ecology and management* 256: 462-470.

Dourma, M., Guelly, K.A., Kokou, K., Batawila, K., Wala, K., Bellefontaine; R. & Akpagana, K. 2006. Multiplication par drageonnage d'*Isoberlinia doka* et *I. tomentosa* au sein des formations arborées du Nord-Togo. *Bois et forêts des tropiques* 288: 49-57.

Duvall, C.S. 2008. Pterocarpus erinaceus Poir. In: Louppe, D., Oteng-Amoako, A.A. & Brink, M. (eds.) Prota 7(1): Timbers/Bois d'œuvre 1. [CD-Rom]. PROTA, Wageningen, NL. URL: http://www.prota4u.org/search.asp. (Accessed May 2012).

El-Kamali, H.H. 2011. Diospyros mespiliformis Hochst. ex A.DC. [Internet] Record from PROTA4U. Lemmens, R.H.M.J., Louppe, D. & Oteng-Amoako, A.A. (eds.). PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, NL. URL: http://www.prota4u.org/search.asp. (Accessed 10 May 2012).

Gignoux, J., Barot, S., Menaut, J.-C. & Vuattoux, R. 2006. Structure, Long-Term Dynamics, and Demography of the Tree Community. In: Abbadie, L. [ed.]: *Lamto: structure, functioning, and dynamics of a savanna ecosystem*. Ecological Studies 179: 335-364. Springer, DE.

Kew Royal Botanical Gardens. Isoberlinia doka. [Internet] URL: http://www.kew.org/plants-fungi/Isoberlinia-doka.htm (Accessed 10 May 2012).

Kouyaté, A.M. & van Damme, P. 2006. *Detarium microcarpum* Guill. & Perr. In: Schmelzer, G.H. & Gurib-Fakim, A. (eds.) Prota 11 (1): Medicinal plants/Plantes médicinales 1. [CD-Rom]. PROTA, Wageningen, NL. URL: http://database.prota.org/search.htm. (Accessed May 2012).

Noble, I.R. & Slayter, R.O. 1980. The use if vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Plant Ecology* 43: 5-21.

Nikiema, A. & Umali, B.E. 2007. Vitellaria paradoxa C.F.Gaertn. [Internet] Record from Protabase. van der Vossen, H.A.M. & Mkamilo, G.S. (eds.) PROTA (Plant Resources of Tropical Africa / Ressources végétales de l'Afrique tropicale), Wageningen, NL. URL: http://database.prota.org/search.htm. (Accessed May 2012).

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

Rietkerk, M., Blijdorp, R. & Slingerland, M. (1998) Cutting and resprouting of *Detarium microcarpum* and herbaceous forage availability in a semiarid environment in Burkina Faso. *Agroforestry Systems* 41: 201-211.

Appendix – Chapter 4

Appendix 1 Pearson correlation coefficients (r) between physical and chemical characteristics of soil from 39 study sites, those variables with a strong intercorrelation (r >±0.7) are in bold type.

Parameter 1	**Parameter 2**	***r***	***F*-value**	***P*-value**
Height herb layer [cm]	Cover tree/shrub layer [%]	-0.4345	-2.932	0.006
Height herb layer [cm]	Cover herb layer [%]	0.560	4.115	0.000
Height herb layer [cm]	pH	0.382	2.513	0.016
Height herb layer [cm]	K^+ [mmolc/kg]	0.433	2.923	0.006
Height herb layer [cm]	H-value	-0.476	-3.296	0.002
Height herb layer [cm]	BS-value	0.547	3.973	0.000
Height herb layer [cm]	Coarse silt [%]	0.526	3.760	0.000
Height herb layer [cm]	Medium silt [%]	-0.055	-0.337	0.738
Height herb layer [cm]	Clay < 2µm [%]	-0.641	-5.075	1.12E-05
Height herb layer [cm]	K_2O [mg/100g]	0.038	0.231	0.819
Cover tree/shrub layer [%]	Cover herb layer [%]	-0.440	-2.980	0.005
Cover tree/shrub layer [%]	pH	-0.300	-1.904	0.065
Cover tree/shrub layer [%]	K^+ [mmolc/kg]	-0.354	-2.303	0.0270
Cover tree/shrub layer [%]	H-value	0.610	4.682	3.75E-05
Cover tree/shrub layer [%]	BS-value	-0.549	-3.995	0.000
Cover tree/shrub layer [%]	Coarse silt [%]	-0.329	-2.118	0.041
Cover tree/shrub layer [%]	Medium silt [%]	0.040	0.242	0.810
Cover tree/shrub layer [%]	Clay < 2µm [%]	0.523	3.734	0.000
Cover tree/shrub layer [%]	K_2O [mg/100g]	-0.191	-1.181	0.245
Cove herb layer [%]	pH	0.326	2.096	0.043
Cove herb layer [%]	K^+ [mmolc/kg]	0.297	1.894	0.066
Cove herb layer [%]	H-value	-0.637	-5.029	1.29E-05
Cove herb layer [%]	BS-value	0.598	4.540	5.78E-05
Cove herb layer [%]	Coarse silt [%]	0.473	3.270	0.002
Cove herb layer [%]	Medium silt [%]	-0.155	-0.957	0.345
Cove herb layer [%]	Clay < 2µm [%]	-0.609	-4.668	3.92E-05
Cove herb layer [%]	K_2O [mg/100g]	0.021	0.130	0.897
pH	K^+ [mmolc/kg]	0.536	3.867	0.000
pH	H-value	-0.208	-1.293	0.204
pH	BS-value	0.610	4.679	3.78E-05
pH	Coarse silt [%]	-0.128	-0.785	0.438
pH	Medium silt [%]	-0.237	-1.486	0.146
pH	Clay < 2µm [%]	-0.245	-1.539	0.132
pH	K_2O [mg/100g]	0.442	2.996	0.005

Appendix 1 (continued)

Parameter 1	**Parameter 2**	***r***	***F*-value**	***P*-value**
K^+ [mmolc/kg]	H-value	-0.209	-1.303	0.201
K^+ [mmolc/kg]	BS-value	0.559	4.103	0.000
K^+ [mmolc/kg]	Coarse silt [%]	-0.182	-1.129	0.266
K^+ [mmolc/kg]	Medium silt [%]	-0.139	-0.853	0.399
K^+ [mmolc/kg]	Clay < 2µm [%]	-0.0689	-0.413	0.682
K^+ [mmolc/kg]	**K_2O [mg/100g]**	**0.785**	**7.709**	**3.29E-09**
H-value	**BS-value**	**-0.783**	**-7.663**	**3.77E-09**
H-value	Coarse silt [%]	-0.426	-2.861	0.007
H-value	Medium silt [%]	0.316	2.024	0.050
H-value	Clay < 2µm [%]	0.574	4.269	0.000
H-value	K_2O [mg/100g]	0.013	0.082	0.935
BS-value	Coarse silt [%]	0.152	0.939	0.354
BS-value	Medium silt [%]	-0.319	-2.045	0.048
BS-value	Clay < 2µm [%]	-0.424	-2.851	0.007
BS-value	K_2O [mg/100g]	0.330	2.052	0.047
Coarse silt [%]	Medium silt [%]	0.235	1.468	0.151
Coarse silt [%]	Clay < 2µm [%]	-0.500	-3.509	0.001
Coarse silt [%]	K_2O [mg/100g]	-0.415	-2.776	0.009
Medium silt [%]	Clay < 2µm [%]	0.249	1.567	0.126
Medium silt [%]	K_2O [mg/100g]	-0.237	-1.486	0.146
Clay < 2µm [%]	Clay < 2µm [%]	0.141	0.868	0.391

Appendix 2 Juvenile densities [100 m^2] of the 25 analyzed woody species. Densities are presented according to species group affiliation, land-cover type and census (plots sampled on non-arable land: n=12, fallow: n=17 and buffer zone: n=10). Similarity between land-cover types is marked by (&), dissimilarity by (≠).

			May 2008			**Oct 2008**			**May 2009**			**Oct 2009**			**May 2010**		
Life form	**Family**	**Species**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**
group A: non-arable ≠ fallows ≠ buffer zone																	
tree	Fabaceae	*Pterocarpus erinaceus*.	24	24	32	36	32	60	44	24	80	52	36	92	52	36	72
group B: non-arable & fallows ≠ buffer zone																	
shrub	Annonaceae	*Annona senegalensis*.	40	148	0	64	160	0	68	164	0	84	204	4	140	252	0
shrub	Rubiaceae	*Crossopteryx febrifuga*	28	36	40	28	28	40	28	28	40	28	28	40	28	24	40
tree	Anacardiaceae	*Lannea acida* A.Rich.	24	48	0	24	52	0	48	104	8	64	148	0	76	184	8
tree	Combretaceae	*Terminalia avicennioides*	28	120	8	52	128	8	76	132	20	88	152	28	88	200	28
group C: non-arable & buffer zone ≠ fallows																	
shrub	Mimosaceae	*Acacia hockii*	0	36	4	0	36	4	0	40	4	0	48	4	0	36	4
tree	Combretaceae	*Anogeissus leiocarpa*.	8	52	8	8	68	8	76	292	20	56	272	36	104	496	36
shrub	Combretaceae	*Combretum collinum*	72	360	40	76	376	56	72	384	52	92	444	64	104	424	64
shrub	Mimosaceae	*Dichrostachys cinerea*	184	696	20	228	732	20	240	648	20	256	668	28	252	608	32
shrub	Ebenaceae	*Diospyros mespiliformis*	0	124	4	0	132	4	4	172	4	4	188	4	4	196	4
shrub	Rubiaceae	*Feretia apodanthera*	8	180	4	8	180	4	16	216	4	16	228	4	16	220	4
shrub	Rubiaceae	*Gardenia ternifolia*	36	44	20	44	36	28	36	40	24	44	36	28	44	36	24
shrub	Caesalpiniaceae	*Piliostigma thonningii*.	16	120	4	20	128	8	28	112	8	28	132	8	24	148	8
shrub	Strychnaceae	*Strychnos spinosa*.	32	38	72	68	80	96	60	56	96	92	88	120	72	88	120
tree	Sapotaceae	*Vitellaria paradoxa*	56	168	12	62	224	24	80	268	20	84	82	328	80	292	32
group D: fallows & buffer zone ≠ non-arable																	
shrub	Combretaceae	*Combretum glutinosum*	36	16	4	44	12	4	40	12	8	48	12	8	44	12	8
shrub	Combretaceae	*Combretum nigricans*.	144	92	16	156	84	16	164	108	20	192	108	20	204	112	20
shrub	Caesalpiniaceae	*Detarium microcarpum*	628	128	0	816	128	0	824	132	0	1028	136	0	948	152	0
tree	Caesalpiniaceae	*Isoberlinia doka*	8	88	32	12	104	60	12	120	64	36	176	96	44	156	56
tree	Fabaceae	*Philenoptera laxiflora*	4	56	24	0	60	28	0	52	40	4	64	96	0	60	76
shrub	Combretaceae	*Pteleopsis suberosa*	408	212	0	416	204	4	384	200	4	424	224	4	8	220	8
tree	Bignoniaceae	*Stereospermum kunthianum*	136	136	20	192	128	52	164	116	48	188	140	76	192	144	68

Appendix 2 (continued)

			May 2008			Oct 2008			May 2009			Oct 2009			May 2010		
Life form	**Family**	**Species**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**	**Non-arable**	**Fallows**	**Buffer zone**
group E: non-arable & fallows & buffer zone																	
tree	Bombacaceae	*Bombax costatum*	4	20	12	8	20	12	12	16	8	32	36	24	20	44	12
shrub	Combretaceae	*Combretum molle*	84	124	76	112	144	92	136	212	88	156	232	136	140	268	212
shrub	Rubiaceae	*Gardenia aqualla*	8	16	16	4	28	12	8	28	12	8	32	16	8	32	16

Appendix 3 Results of Linear mixed effect model (LME) for each study species (n=25). The maximum model was fitted with number of individuals as dependent variable, census (numerical) and land-cover type (factor) as explanatory variables, and census (numerical) as random variable. Additionally, results of multiple comparisons of means of land-cover types are presented (Tukey Contrasts)

Species are shown in alphabetical order. Land-cover type A: non-arable, land-cover type B: fallows, land-cover type C: buffer zone.

Acacia hockii De Wild.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_C	19.05	38.24	0.498
Land-cover type B	198.73	56.28	3.531

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	198.73	56.28	3.531	0.000414***

Annona senegalensis Pers.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_C	850.76	76.93	11.059
Land-cover type B	-842.76	151.92	-5.547

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type C - A&B == 0	-842.8	151.9	-5.547	2.90E-08***

Anogeissus leiocarpa (DC.) Guill. & Perr.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_C	339.8	269.1	1.263
Land-cover type B	926	300.7	3.079

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	926	300.7	3.079	0.00208**

Bombax costatum Pellegr. & Vuill.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_B	121.931	19.199	6.351
Land-cover type B	2.869	37.915	0.076

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type C - A&B == 0	2.869	37.915	0.076	0.94

Combretum collinum Fresen.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_C	611	240.9	2.536
Land-cover type B	1530.3	354.7	4.315

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	1530.3	354.7	4.315	1.60E-05***

Combretum glutinosum Perr. ex DC.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	356.36	35.23	10.115
Land-cover type B_C	-296.36	41.58	-7.128

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type A - B&C == 0	-296.36	41.58	-7.128	1.02E-12***

Combretum molle R.Br. ex G.Don

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	1050.2	215.5	4.873
Land-cover type B	23.6	255	0.093
Land-cover type C	137	291.1	0.471

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
B-A == 0	23.6	255	0.093	0.995
C-A == 0	137	291.1	0.471	0.885
C-B == 0	113.4	262.8	0.432	0.902

Combretum nigricans Lepr. ex Guill. & Perr.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	1458.9	212.9	6.853
Land-cover type B_C	-1051.5	251.3	-4.185

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type A - B&C == 0	-1051.5	251.3	-4.185	2.85E-05***

Crossopteryx febrifuga (Afzel. ex G.Don) Benth.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_B	187.59	33.6	5.583
Land-cover type C	140.41	66.35	2.116

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type C - A&B == 0	140.41	66.35	2.116	0.0343*

Detarium microcarpum Guill. & Perr.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	7339.6	558.6	13.14
Land-cover type B_C	-6893.9	659.3	-10.46

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type A - B&C == 0	-6893.9	659.3	-10.46	<2e-16***

Dichrostachys cinerea (L.) Wight & Arn.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	2091.6	573.7	3.646
Land-cover type B	1576.8	728.2	2.165
Land-cover type C	-1862.8	831.4	-2.241

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
B-A == 0	1576.8	728.2	2.165	0.0768
C-A == 0	-1862.8	831.4	-2.241	0.0642
C-B == 0	-3439.6	750.5	-4.583	<0.001***

Diospyros mespiliformis Hochst. ex A.DC.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_C	26.67	112.94	0.236
Land-cover type B	866.67	166.24	5.213

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	866.7	166.2	5.213	1.85E-07***

Feretia apodanthera Delile

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_C	73.9	141.3	0.523
Land-cover type B	1053.2	208	5.064

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	1053	208	5.064	4.11E-07***

Gardenia aqualla Stapf & Hutch.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	65.45	62.08	1.054
Land-cover type B_C	75.12	73.26	1.025

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type A - B&C == 0	75.12	73.26	1.025	0.305

Gardenia ternifolia Schumach. & Thonn

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_C	297.14	44.65	6.655
Land-cover type B	-97.14	65.72	-1.478

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	-97.14	65.72	-1.478	0.139

Isoberlinia doka Craib & Stapf

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	202.2	106.6	1.897
Land-cover type B_C	416.7	115.4	3.612

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type A - B&C == 0	416.7	115.4	3.612	0.000304***

Lannea acida A.Rich.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_B	513.66	86.56	5.934
Land-cover type C	-481.66	90.51	-5.322

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type C - A&B == 0	-481.66	90.51	-5.322	1.03E-07***

Philenoptera laxiflora (Guill. & Perr.) Roberty

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	13.09	86.24	0.152
Land-cover type B_C	351.48	101.78	3.453

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type A - B&C == 0	351.5	101.8	3.453	0.000554***

Piliostigma thonningii (Schumach.) Milne-Redh.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A_C	135.62	54.34	2.496
Land-cover type B	547.94	79.99	6.85

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	547.94	79.99	6.85	7.36E-12***

Pteleopsis suberosa Engl. & Diels

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	3645.1	483.4	7.541
Land-cover type B_C	-2930.2	570.5	-5.136

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type A - B&C == 0	-2930.2	570.5	-5.136	2.80E-07***

Pterocarpus erinaceus Poir.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	370.91	63.14	5.874
Land-cover type B	-220.69	80.14	-2.754
Land-cover type C	232.29	91.5	2.539

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
B-A == 0	-220.69	80.14	-2.754	0.0161*
C-A == 0	232.29	91.5	2.539	0.0298*
C-B == 0	452.98	82.59	5.484	<0.001***

Stereospermum kunthianum Cham.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type A	1490.9	148.8	10.02
Land-cover type B_C	-896.6	175.6	-5.106

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type A - B&C == 0	-896.6	175.6	-5.106	3.29E-07***

Strychnos spinosa Lam.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover-type B	706.29	79.24	8.914
Land-cover type A_C	-300.06	116.63	-2.573

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	-300.1	116.6	-2.573	0.0101*

Terminalia avicennioides Guill. & Perr.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover type A_B	710.62	78.78	9.02
Land-cover type C	-545.82	155.59	-3.508

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type C - A&B == 0	-545.8	155.6	-3.508	0.000451***

Vitellaria paradoxa C.F.Gaertn.

Linear mixed effect model	Estimate	S.E.	*t* value
Land-cover type A_C	454.1	200.1	2.269
Land-cover type B	938.8	294.5	3.187

Tukey Contrasts	Estimate	S.E.	*z* value	Pr (>|z|)
Land-cover type B - A&C == 0	938.8	294.5	3.187	0.00144**

Appendix 4 Mean (± S.E.) of the density [ha] of adult individuals per species. For shrubs, adult individuals have a diameter in breast height (dbh) > 12cm and trees: dbh> 15 cm. For group details see Table 1.

Life form	Species	Adults		
		Non-arable	**Fallows**	**Buffer zone**
group A: non-arable ≠ fallows ≠ buffer zone				
tree	*Pterocarpus erinaceus* Poir.	0.2 ± 0.1	0.5 ± 0.2	0.2 ± 0.1
group B: non-arable & fallows ≠ buffer zone				
shrub	*Annona senegalensis* Pers.	1.2 ± 0.4	0.5 ± 0.3	0.0 ± 0.0
shrub	*Crossopteryx febrifuga* (Afzel. ex G.Don) Benth.	6.6 ± 1.4	0.9 ± 0.3	5.0 ± 1.0
tree	*Lannea acida* A.Rich.	1.2 ± 0.3	0.9 ± 0.2	2.1 ± 0.5
tree	*Terminalia avicennioides* Guill. & Perr.	1.2 ± 0.5	0.4 ± 0.1	0.3 ± 0.2
group C: non-arable & buffer zone ≠ fallows				
shrub	*Acacia hockii* De Wild.	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
tree	*Anogeissus leiocarpa* (DC.) Guill. & Perr.	0.1 ± 0.1	0.8 ± 0.3	0.8 ± 0.3
shrub	*Combretum collinum* Fresen.	0.8 ± 0.5	1.4 ± 0.4	0.4 ± 0.3
shrub	*Dichrostachys cinerea* (L.) Wight & Arn.	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0
shrub	*Diospyros mespiliformis* Hochst. ex A.DC.	0.2 ± 0.2	0.4 ± 0.3	0.0 ± 0.0
shrub	*Feretia apodanthera* Delile	0.3 ± 0.2	0.3 ± 0.2	0.4 ± 0.3
shrub	*Piliostigma thonningii* (Schumach.) Milne-Redh.	0.3 ± 0.2	3.0 ± 0.8	0.4 ± 0.3
shrub	*Strychnos spinosa* Lam.	0.6 ± 0.4	0.1 ± 0.1	0.4 ± 0.3
tree	*Vitellaria paradoxa* C.F.Gaertn.	2.5 ± 0.5	2.5 ± 0.5	4.0 ± 1.1
group D: non-arable ≠ fallows & buffer zone				
shrub	*Combretum glutinosum* Perr. ex DC.	2.9 ± 0.7	0.8 ± 0.3	0.7 ± 0.4
shrub	*Combretum nigricans* Lepr. ex Guill. & Perr.	1.2 ± 0.6	2.0 ± 0.8	0.0 ± 0.0
shrub	*Detarium microcarpum* Guill. & Perr.	14.2 ± 4.3	0.7 ± 0.3	1.1 ± 0.6
shrub	*Gardenia ternifolia* Schumach. & Thonn.	0.2 ± 0.2	0.2 ± 0.2	0.0 ± 0.0
tree	*Isoberlinia do*ka Craib & Stapf	1.5 ± 0.4	2.3 ± 0.5	4.3 ± 1.1
tree	*Philenoptera laxiflora* (Guill. & Perr.) Roberty	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 0.3
shrub	*Pteleopsis suberosa* Engl. & Diels	1.4 ± 0.6	0.1 ± 0.1	0.0 ± 0.0
tree	*Stereospermum kunthianum* Cham.	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0
group E: non-arable & fallows & buffer zone				
tree	*Bombax costatum* Pellegr. & Vuill.	0.0 ± 0.0	0.1 ± 0.1	0.1 ± 0.1
shrub	*Combretum molle* R.Br. ex G.Don	2.0 ± 0.5	3.2 ± 1.0	2.5 ± 0.6
shrub	*Gardenia aqualla* Stapf & Hutch.	0.0 ± 0.0	0.0 ± 0.0	0.7 ± 0.6