

Impact of land use on juvenile densities of woody plants in a West African savanna

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Summary: In West African savannas, human land use affects the density of woody species seedlings and saplings (juveniles) by altering the state of the physical, chemical, and biological characteristics of the land resulting in different land-cover types. We determined juvenile densities of 25 characteristic woody savanna species on non-arable sites, in fallows and in a protected area (in total 39 plots), and analyzed the influence of land use on juvenile densities. We further related the influence of land use on juvenile densities to 23 environmental parameters describing soil properties and vegetation structure. Soil acidity, particle size distribution of the soil, and 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, their direct effects on juvenile densities are less pronounced than their 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.

Key words: abundance, Benin, human impact, soil conditions, vegetation cover, vegetation height

IMPACT DE L'UTILISATION DES TERRES SUR LES DENSITÉS JUVÉNILES DE PLANTES LIGNEUSES DANS UNE SAVANE D'AFRIQUE DE L'OUEST

Résumé: Dans les savanes de l'Afrique de l'Ouest, l'occupation des sols affecte la densité des semis et des jeunes plants des espèces ligneuses par son influence sur les caractéristiques physiques, chimiques et biologiques des terres, ce qui entraîne de différents types de couvert végétal. Nous avons déterminé la densité juvénile de 25 espèces caractéristiques de savane ligneuse sur des sites non arables, en jachère et dans une aire protégée (au total 39 parcelles), et nous avons analysé l'influence de l'utilisation des terres sur les densités juvéniles. Nous avons également mis en rapport l'influence de l'utilisation des terres sur les densités juvéniles avec 23 paramètres environnementaux décrivant les propriétés du sol et la structure de la végétation. L'acidité du sol, la répartition granulométrique du sol et la structure de la végétation différaient selon les types de couvert végétal. En termes d'impact humain, nous avons détecté cinq groupes d'espèces répondant de manière similaire à l'utilisation des terres. Bien que nous ayons détecté des différences significatives dans les propriétés du sol, leurs effets directs sur les densités juvéniles sont moins prononcés que leurs effets indirects. En modifiant la disponibilité des ressources, les propriétés du sol affectent la hauteur et la couverture de toutes les plantes qui poussent à l'entour d'une jeune plante ligneuse, augmentant la concurrence pour la lumière, l'eau et les nutriments pendant l'établissement et la croissance initiale. Ces effets sont intensifiés par l'utilisation des sols et varient selon les types de couvert végétal.

Mots clés: abondance, Bénin, impact humain, conditions du sol, couverture végétale, hauteur de végétation

AUSWIRKUNGEN DER LANDNUTZUNG AUF DAS VORKOMMEN VON GEHÖLZJUNGWUCHS IN EINER WESTAFRIKANISCHEN SAVANNE

Zusammenfassung: In den westafrikanischen Savannen beeinflusst die Landnutzung die Dichte der Gehölzkeimlinge und Jungpflanzen, indem sie physikalische, chemische und biologische Eigenschaften der Flächen verändert und zu unterschiedlichen Landnutzungstypen führt. Es wurde der Einfluss der Landnutzung auf die Individuendichte von Keimlingen und Jungpflanzen von 25 charakteristischen Savannengehölzarten auf nicht kultivierten Flächen, in Brachen und in einem Schutzgebiet (insgesamt 39 Parzellen) untersucht. Darüber hinaus haben wir den Einfluss der Landnutzung auf die Individuendichte mit 23 Umweltparameter in Beziehung gesetzt, die die Bodeneigenschaften und die Vegetationsstruktur beschreiben. Die Bodensäure, die Korngrößenzusammensetzung des Bodens und die Vegetationsstruktur unterscheiden sich zwischen den Landnutzungstypen. In Bezug auf den menschlichen Einfluss, ließen sich fünf Artengruppen unterscheiden, die jeweils ähnlich auf die Landnutzung reagieren. Obwohl wir signifikante Unterschiede in den Bodeneigenschaften festgestellt haben, sind ihre direkten Auswirkungen auf die Individuendichte der Gehölzkeimlinge und Jungpflanzen weniger ausgeprägt als ihre indirekten Effekte. Die Bodeneigenschaften verändern die Verfügbarkeit von Ressourcen und beeinflussen darüber die Höhe und Bedeckung der Pflanzen, die im Umfeld des Gehölzjungwuchses wachsen. Dadurch erhöht sich die Konkurrenz um Licht, Wasser und Nährstoffe für den Jungwuchs in seiner Etablierungs- und anfänglichen Wachstumsphase. Diese Effekte werden durch die Landnutzung verstärkt und variieren zwischen Landnutzungstypen.

Schlagworte: Abundanz, Benin, menschlicher Einfluss, Bodenbedingungen, Vegetationsbedeckung, Vegetationshöhe

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 (see, e.g., WITTIG et al. 2002). During recent decades, social and economic conditions have changed dramatically (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 of trees and shrubs (e.g. by harvesting of non-timber forest products). JURISCH et al. (2012) showed that the population structure of some woody plant populations, especially tree populations, is strongly affected by human-induced disturbances, while others perform quite well under the current land use system, mainly shrub species. For many tree species, reproductive individuals of the sub-adult and adult stage were missing. This can reduce the availability of their seeds and may thereby lead to a lack of regeneration and a low density of their juveniles (young, immature individuals) (PLUMPTRE 1995, MAKANA & THOMAS 2004, McLAREN et al. 2005). This development becomes more pronounced as due to increased human pressure, habitats suitable for juvenile establishment are becoming fewer. In the long run, the observed results may have implications for local woody species composition.

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 interspecific plant competition) is very high (ABRAHAMSON 1980, BOND 2008, JURISCH et al. 2012, 2013; PRIOR et al. 2010, ZIDA 2007). Habitats like less disturbed termite mounds show a consistently higher species richness and diversity of juvenile woody plants than their surrounding savannas (ERPENBACH et al. 2014). 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). In situ experimental studies from semi-arid South Africa have revealed that herbaceous competition was intensified under nutrient-rich conditions by enhancing growth rates of grasses. This may lead to a decrease in seedling densities, as well as to 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).

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 (DJOSSA et al. 2008, PARE et al. 2009, SCHUMANN et al. 2011) and in relation to management practices (DHILLON & GUSTAD 2004, KOUAMI et al. 2009, KY-DEMBELE et al. 2007).

These studies generally report higher seedling and sapling densities in non-protected areas with moderate human disturbance compared to protected sites. 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 interspecific plant competition for light, water and nutrients (DHILLON & GUSTAD 2004, DJOSSA et al. 2008, KELLY et al. 2004, WALKER et al. 1981). By contrast, some 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 greater 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). Aside from the direct damage of the plant, grazing can reduce fire frequency and intensity due to the reduction of the amount of inflammable biomass (WALKER et al. 1981, JEFFREY 1987, ARCHER 1995) and may change the availability of soil nutrients and structural properties of soil by deposition of dung and the impact of trampling (BRESHEARS et al. 1997, DAVENPORT et al. 1998, POSSE et al. 2000, SAVADOGO et al. 2007, VAN DER WAAL 2010). Fires have chemical and physical consequences, such as the mineralization of nutrients stimulating the growth of surviving species, the increase in soil compaction, soil temperature and a decrease in organic material in turn leading to lowered soil-water content (JEFFREY 1987, SNYMAN 1994). All these factors influence growing conditions for plants (MWAVU & WITKOWSKI 2008) and may facilitate or hinder the development of individuals.

Summarizing 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 and biological characteristics of the land-cover types caused by human impact. Therefore, we expect to observe a significant effect of human land use on the density of seedlings and saplings by affecting population structure of woody plants and altering abiotic and biotic habitat conditions (SWAINE 1996). We further assume that the strength of this effect is related to species' ecological preferences, which refer to the environmental conditions under which the species is most likely to occur. Within this study, we investigated patterns of population densities 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 stages of woody species. We aim to answer the following questions:

- How are juvenile densities affected by land use?
- Can we identify specific environmental conditions, soil conditions and vegetation structure, determining juvenile densities?
- Does the density of reproductive adults have an effect on juvenile densities?

2 METHODS

2.1. Study site

The study was carried out around Sampeto village (11°40'-12°23' N, 2°04'-3°05' E) located in the northern part of Benin at the periphery of the W Transborder Park (Parc National du W), one of the largest protected areas in West Africa. Sampeto had 3725 inhabitants in 2013 (KNOEMA 2013), although this number has most likely increased since the last census. The area belongs to the North-Sudanian vegetation zone which is characterized by an average annual precipitation of 700-1000 mm and a 6 month lasting rainy season from May to October (BONOU 2008).

All field data were collected in the surroundings of Sampeto (within 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. The most common agricultural system is shifting cultivation where almost all land is used for agriculture excluding protected areas or areas ill-suited due to their relief conditions or where we find crusted soils or soils containing a high amount of gravel (RUTHENBERG 1980, FAO 1983, OKIGBO 1985, ALEXANDRE & KAÏRÉ 2001). Because the location is at the periphery of a national park (W National Park), we were also able to consider sites which are less altered by human impact – the buffer zone of the national park - and represent semi-natural conditions.

Harvesting of NTFPs for firewood, medical purposes or livestock forage is common in the settlement area, thus fallow areas and non-arable areas are equally exposed to harvesting activities. In the buffer zone, these activities are limited by law, but still some illegal timber extraction occurs. 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 mainly grazed 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 and during a period of about six weeks (from 2004 to 2009, GRÉGOIRE & SIMONETTI 2010). The fire activity tends to increase and clearly indicates an increased overall anthropogenic pressure on the protected areas. 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 nutrient poor-to-medium, previously cultivated soils (at least 10 y ago, with differ-

ent 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*; *Penisetum polystachion*, *Desmodium velutinum* and *Chasmodium caudatum* (hereafter referred to as 'fallow'). (3) Semi-natural tree and shrub savanna on medium soils covered with tall grasses, such as *Hyparrhenia involucreta* 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. The studied land-cover types were comparable with respect to their adult vegetation composition (Appendix 1). Fallows and non-arable land are exposed to similar disturbance intensities (fire, grazing, harvesting) and are freely accessible. As a result of the stepwise land-use change, the landscape becomes fragmented and consists of patches of more or less native vegetation embedded into a matrix of different land-cover types, including non-arable sites and fallows (STOATE et al. 2001, GREEN et al. 2005, ABDULLAH & NAKAGOSHI 2006).

2.2 Vegetation data

Within each of the three land-cover types we randomly chose plots for vegetation sampling. The minimal distance between chosen plots was 100 m. The woody layer was investigated in 900 m² plots and the herb layer in 100 m² plots. The herb layer plots were randomly located inside the corresponding woody layer plots. Percentage canopy coverage of all vascular plant species, separately for the tree, shrub and herb layer, was estimated visually on each plot (NACOLMA et al. 2011).

To examine the density of juveniles and adults adequately, squared plots of two sizes were established at each study site. Adult individuals were sampled on 1800 m² plots, while juveniles were determined on four sub-plots (each with a size of 6.25 m²) nested in the 1800 m² plots. In total, 39 of these 1800 m² plots were investigated, 12 on non-arable sites, 17 on fallows, and 10 in the buffer zone. On each of the 6.25-m² subplots, numbers of juveniles were counted, comprising all young, immature individuals of the seedling and sapling stage smaller than 1 m. 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 adults with diameter at breast height (dbh) of more than 5 cm were collected, measuring dbh (cm) and height (m). 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.

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). The plant species nomenclature followed the African Plants Database (<http://www.ville-ge.ch/musinfo/bd/cjb/africa>).

2.3. Environmental data

Environmental conditions were characterised 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 m²) and the herbaceous layer (on one subplot of 100 m²) in September/October 2007. Measurements were performed for the tree and shrub layer (woody plants > 5 m) and the herbaceous layer (all plants up to 0.5 m in height).

On each of the 1800-m² plots, we took three randomly placed soil samples of the upper 0-20 cm layer in May 2009. These three samples were pooled and subsequently analysed for plant-available phosphorus, potassium, nitrogen, organic and inorganic carbon, cation exchange capacity (CEC, with ion concentrations of sodium, potassium, calcium, and magnesium), particle size distribution (PSD), and pH. Plant-available phosphorus (phosphorus pentoxide, P₂O₅) and potassium (potassium oxide, K₂O) 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 CaCl₂ 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 BaCl₂ 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).

2.4 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 2).

2.5 Influence of land use and environment on juvenile densities

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. In total, we considered 16 shrub and seven tree species (for density values see Appendix 3). To analyze if a population has good regeneration relative to the number of adult trees, we determined the mean of the density per hectare of adult individuals (trees: dbh > 15 cm. shrubs: dbh > 12 cm) per species.

The statistical analyses addressed two different issues for each species: (1) to determine the influence of land use on juvenile densities, and (2) to determine which environmental conditions affect juvenile densities additional to the influence of land use.

To answer the first issue, we calculated a linear mixed-effect model (LME) with number of juveniles as response variable and land-cover type (factor) 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 particular 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 were grouped together even though the juvenile density of two species differed.

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 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) using the quasi-Poisson model, as this model described the distribution of the residuals for count data, e.g. the juvenile densities, best. We performed a model simplification by omitting non-significant parameters until only significant parameters remained (CRAWLEY 2007).

All statistical analyses were done using the software package R (version 2.13.2) with the additional package *vegan* (version 2.0-5), "lme4" (version 0.999999-0) and "multcomp" (version 1.2-15).

3 RESULTS

3.1. 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 characterising the vegetation structure and eight soil parameters (Table 1).

Table 1: Mean (\pm SE) of 23 environmental parameters (soil parameters and vegetation structural data) per land-cover type. The samples were taken at 39 plots (12 on non-arable sites, 17 in fallows, 10 in the buffer zone), different letters (a, b and c) indicate significant differences ($P < 0.05$, highlighted with *). BS-value: percentage base saturation, S-value: Quantity of basic interchangeable Ions / Moyenne (\pm SE) de 23 paramètres environnementaux (paramètres du sol et données structurales de la végétation) par type de couvert végétal. Les échantillons ont été prélevés sur 39 parcelles (12 sur les sites non arables, 17 dans les jachères, 10 dans la zone tampon), différentes lettres (a, b et c) indiquent des différences significatives ($P < 0,05$, accentué avec *). Valeur BS: pourcentage de saturation de base, valeur S: Quantité d'ions interchangeables de

Environmental parameter	Non-arable (n = 12)	Fallows (n = 17)	Buffer zone (n = 10)
Cover tree/shrub layer (%)*	29.8 \pm 4.71 a	19.7 \pm 1.29 ab	13.3 \pm 2.1 b
Height herb layer (cm) *	50.2 \pm 12.46 a	42.8 \pm 6.32 a	184 \pm 5.42 b
Cover herb layer (%)*	48.6 \pm 3.68 a	62.4 \pm 4.25 b	71.9 \pm 2.61 b
CECpot (cmolc/kg) *	73.2 \pm 9.12 a	49.5 \pm 4.29 b	38.1 \pm 5.14 b
Medium silt (%)*	9.3 \pm 0.52 a	8.1 \pm 0.3 b	8.6 \pm 0.47 ab
Clay < 2 μ m (%)*	21.1 \pm 1.34 a	18.6 \pm 1.04 a	13.4 \pm 0.6 b
K ₂ O (mg/100g) *	6.0 \pm 0.36 a	8.4 \pm 0.73 b	7.8 \pm 0.77 ab
Coarse silt (%)*	32.4 \pm 1.35 ab	31.2 \pm 1.69 a	38.6 \pm 1.78 b
pH*	4.8 \pm 3.07 a	5.4 \pm 2.83 b	5.6 \pm 3.85 b
K ⁺ (mmolc/kg) *	0.8 \pm 0.05 a	1.1 \pm 0.11 ab	1.4 \pm 0.16 b
BS-value*	34 \pm 3.27 a	48.3 \pm 2.07 b	54.9 \pm 2.78 b
C/N-ratio	20.1 \pm 2.08 a	22 \pm 2.18 a	20.4 \pm 2.51 a
Ca ²⁺ (mmolc/kg)	25.9 \pm 1.17 a	35.4 \pm 3.89 a	34.6 \pm 5.21 a
Coarse sand (%)	7.9 \pm 1.54 a	8.6 \pm 1.89 a	6.4 \pm 2.22 a
C-organic (%)	1.8 \pm 0.16 a	1.7 \pm 0.18 a	1.5 \pm 0.16 a
Fine sand (%)	18.2 \pm 1.2 a	21.4 \pm 1.45 a	22.7 \pm 1.15 a
Fine silt (%)	4.1 \pm 0.22 a	3.8 \pm 0.23 a	3.9 \pm 0.15 a
Medium sand (%)	7.1 \pm 0.61 a	7.9 \pm 0.65 a	6.5 \pm 0.36 a
Mg ²⁺ (mmolc/kg)	7.7 \pm 0.78 a	10.5 \pm 0.85 a	10.7 \pm 1.2 a
Na ⁺ (mmolc/kg)	0.4 \pm 0.07 a	0.3 \pm 0.03 a	0.3 \pm 0.04 a
N-total (%)	0.1 \pm 0.01 a	0.1 \pm 0 a	0.1 \pm 0.01 a
P ₂ O ₅ (mg/100g)	0.3 \pm 0.05 a	0.3 \pm 0.02 a	0.3 \pm 0.03 a
S-value	34.8 \pm 1.36a	47.4 \pm 4.6 a	47 \pm 6.31 a

On non-arable sites, we detected the highest amount of acid exchangeable cations (CECpot), 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 from 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 subsurface 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).

3.2 Influence of land use and environment on juvenile densities

The 16 shrub and seven tree species were assigned to five groups (A-E). Each group comprises species responding similar to land use (Table 2). 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. Highest juvenile density of this species was found in the buffer zone whereas the highest number of adults was found on fallows. 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. All species had high juvenile densities in the communal area, especially on fallows: Only *C. febrifuga* showed more juveniles in the buffer zone compared to the communal area. 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 shrub 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 (CECpot) 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

Table 2: Juvenile densities, sampled on one subplot of 100 m², of the 25 analyzed woody species. Densities are presented per land-cover type (non-arable land: n=12, fallow: n=17 and buffer zone: n=10). Similarity between land-cover types concerning the juvenile densities, calculated by a linear-mixed-effect model and a subsequent Tukey's multiple comparison test, is marked by (&), dissimilarity by (≠). Growth form: S: shrub, T: tree. / Densités juvéniles, échantillonnées sur une sous-parcelle de 100 m², des 25 espèces ligneuses analysées. Les densités sont présentées par type de couvert végétal (terres non arables: n = 12, jachère: n = 17 et zone tampon: n = 10). La similitude entre les types de couverture concernant les densités juvéniles, calculée par un modèle à effet mixte linéaire et un test de comparaison multiple de Tukey subséquent, est indiquée par (&), dissimilarité par (≠). Forme de croissance: S: arbuste, T: arbre.

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

sites, were assigned to group D. Some species (*Combretum glutinosum*, *Detarium microcarpum*, *Pteleopsis suberosa* and *Stereospermum kunthianum*) had the highest juvenile densities on those non-arable sites where we also found a high number of adult individuals of this species (Table 4). In the case of *Combretum nigricans*, we found the highest recruitment rates on non-arable site but less adult individuals compared to fallows. Differences in the percentage cover of the herb layer, pH, CECpot 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 (*Bombax costatum*, *Combretum molle*, *Gardenia aqualla*) showed no influence of land use on juvenile abundances (Tables 2, 3). For *B. costatum*, juvenile densities were low in all land cover types similar

as the number of adults. The shrub species *C. molle* showed high recruitment rates in all land cover types which corresponded well to similarly high number of adults (Table 4).

4 DISCUSSION

4.1 Differences in environmental facts between land-cover types

The detected differences between different land-cover types due to chemical and physical soil properties as well as characteristics of the vegetation structure were in line with observations by HAHN (1996) that physical soil properties determined the occurrence of vegetation types in West African savannas. However, as also found by ORTHMANN (2005), we

Table 3: Influence of environmental factors on juvenile densities by species affiliation groups A-E. The GLMs (quasi-Poisson model) were fitted using juvenile densities as dependent variable, and environmental variables (numerical) as explanatory variables. / Influence des facteurs environnementaux sur les densités juvéniles selon les groupes d'affiliation des espèces A-E. Les GLM (quasi-Poisson model) ont été ajustés en utilisant la densité juvénile comme variable dépendante et les variables environnementales (numériques) comme variables explicatives.

	Estimate	SE	t value	Pr (> t)
group A: non-arable ≠ fallows ≠ buffer zone				
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				
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				
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*
CECpot (cmolc/kg)	-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				
(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**
CECpot (cmolc/kg)	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				
(Intercept)	6.10	0.20	30.4	<0.001***

additionally detected soil acidity and alkalinity indicated by pH and percentage base saturation (BS-Value) as important factors differing between land-cover types; in our case the values were increased in the communal area (non-arable sites and fallows) compared to the buffer zone.

4.2 Influence of land use and environment on juvenile densities

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 *Pterocarpus 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. HOUËSSOU, 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 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, GAOUË

& 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, DUVAL 2008, GLELE KAKAÏ et al. 2009).

The lower juvenile density of *Crossopteryx febrifuga* in the communal area compared to the buffer zone may be linked to the high grazing pressure in the communal area that 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. These observations are supported by our results of a previous study where we detected many reproductive trees in the communal area, especially on non-arable sites (JURISCH et al. 2012). 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

Table 4: Mean (\pm 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. / Moyenne (\pm S.E.) de la densité (ha) d'individus adultes par espèce. Pour les arbustes, les individus adultes ont un diamètre en hauteur de poitrine (dbh) > 12cm et arbres: dbh > 15 cm. Pour les détails du groupe, voir le tableau 1.

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

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* (NACOUUMA 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). The competitive strength of these species is expressed by their healthy population structure, showing well-shaped size-class distributions with high numbers of juveniles and a gradual decline with increasing stem diameter (JURISCH et al. 2012). In this study, we also detected a high juvenile density and a large number of adult trees for *P. thonningii*. 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 favoured on fallows compared to sites with a dense vegetation cover (BOGNOUNOU et al. 2010, SACANDE & SANOGO 2007). We also suppose

that the facilitation of some species by traditionally managed agroforestry systems can affect woody plant populations by altering the relationship between juveniles and adult trees (JURISCH et al. 2012, PARE et al. 2009). *Vitellaria paradoxa*, the shea tree, has a high socioeconomic importance and in particular, individuals with a high fruit yield are spared when woodland is cleared for agriculture (LOVETT & HAQ 2000). Once the land becomes inadequate for crop production, it is abandoned and a few trees producing high numbers of off-springs are left. This may explain the high number of juveniles for *V. paradoxa* in fallows and a low number of adults compared to the buffer zone, where we found significantly less juveniles.

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 CECpot and low pH); nevertheless, the soils were only slightly acidic which promotes nutrient availability and plant growth. However, for two species, *Isobertinia 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. 2012). 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. HOUSSOU, pers. comm.), which may limit the number of juveniles and reduce the population viability as well (DHILLION & GUSTAD 2004, GAOUE & TICKTIN 2008, HALL & BAWA 1993). 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). Habitat loss and accelerated mortality of adults may have a great impact on juvenile densities of such species where the larger mother tree shelters the smaller, fire and drought sensitive seedlings. The species *P. laxiflora* mainly reproduces by seeds, 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 was highest on non-arable sites compared to fallows and the buffer zone. The ability of vegetative reproduction can also be important for explaining differences between adult and juveniles densities, such as in the case of *S. kunthianum*. For this species, a low number of adults or even the lack of adults, such as in fallows and in the buffer zone, does not necessarily have implications for the number of observed juveniles. For *S. kunthianum* it is known, for example, that once established, juveniles develop extensive and widespread root systems under the soil surface, enabling them to set up offspring through vegetative repro-

duction, building a net of connected juveniles (HOFFMAN et al. 2004; OUEDRAOGO 2006; GROSSNICKLE 2005; WIGLEY et al. 2009).

Juvenile densities of *Combretum molle* were high in all land-cover types what is consistent with findings of a former study, where we detected a similar pattern for sub-adult and adult individuals of *C. molle*, in relation to land use (JURISCH et al. 2012). This species is not site-specific and shows 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 (BOND & MIDGLEY 2001, DEVINEAU & FOURNIER 2005, DROBNIK et al. 2011, LAVOREL et al. 1997). However, *Gardenia 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. *Gardenia aqualla* is characteristic for sites with low vegetation cover (SCHMIDT & ZIZKA 2014). 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 usable as lumber and its fibers are mainly used for stuffing, 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 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, SCHUMANN et al. 2011, TICKTIN 2004). Furthermore, its leaves are highly digestible and eaten by livestock, further reducing the number of young individuals.

5 CONCLUSION

Land use was shown to significantly affect juvenile densities of almost all studied woody species, as demonstrated by a grouping of species according to their observed densities. Almost all species (20 out of 25 species) showed higher juvenile densities in the communal area compared to the buffer zone. For those species, we also expect a positive development of the population in the long-run as many woody species showed high survival and growth rates in the communal area (survival probability $> 1 \cdot 10^{-6}$, JURISCH et al. 2013). We have shown that many species regenerate well despite low numbers of adult individuals. Thus, it seems that dispersal limitation is not the major factor controlling juvenile densities (see also PARE et al. 2009).

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 esta-

blishment 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 (BOND 2008, SANKARAN et al. 2008, SCHOLLES & 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 enhance 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 of non-timber forest products), causing removal and impairment of the vitality of reproductive individuals. This can reduce the availability of seeds and may thereby lead to a lack of regeneration (MAKANA & THOMAS 2006, MCLAREN et al. 2005, PLUMPTRE 1995).

Both processes, loss of established individuals as a potential seed source and lack of regeneration due to high juvenile mortality by environmental factors, may result in a total loss of recruitment in an area. 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. Those studies should also investigate ecological characteristics such as dispersal ability, as the exchange of individuals between suitable habitats becomes important in fragmented landscapes and in areas where domestic animals and humans play a significant role in seed dispersal.

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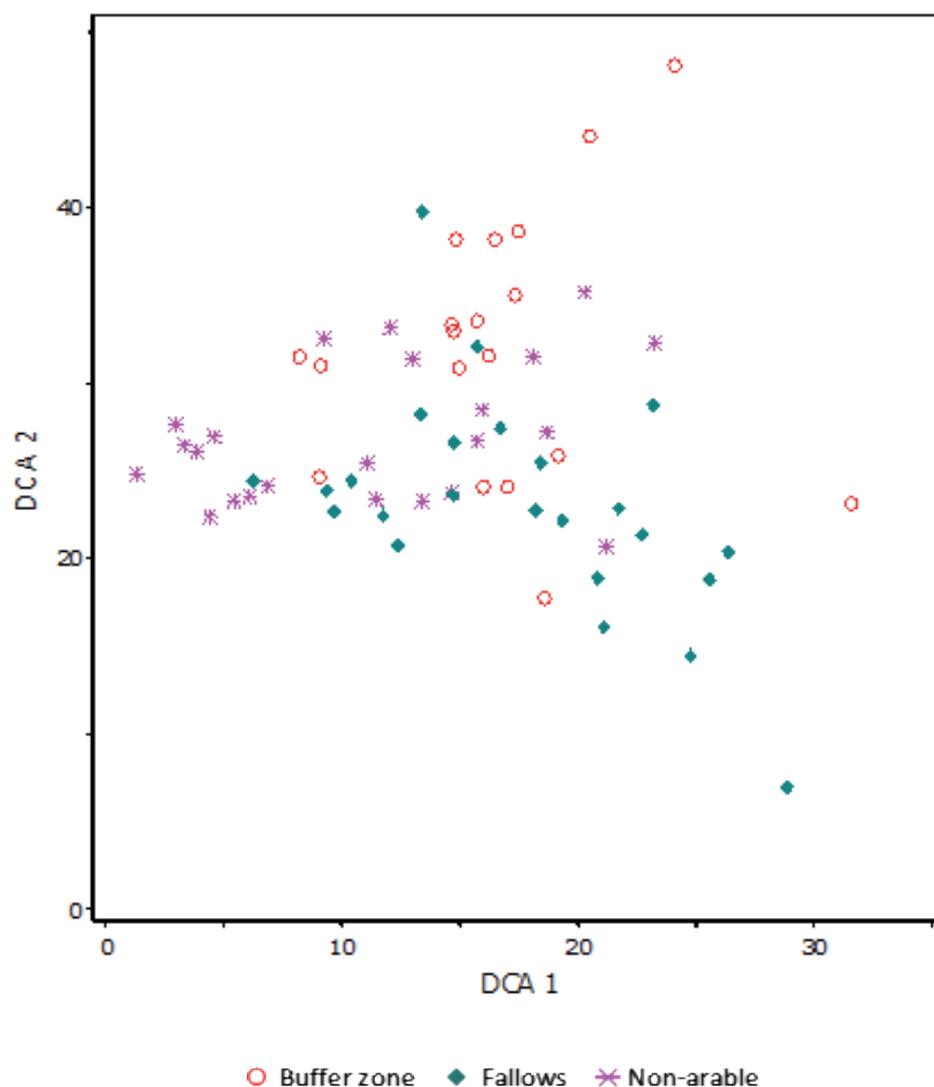
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Appendix



Appendix 1: DCA plot of the vegetation of non-arable sites, fallows and the buffer zone, based on the species cover of woody plants of the woody layers. The ordination was based on 130 species in 66 plots (23 on non-arable sites, 24 in fallows, 19 in the buffer zone), length of first axis 2.5, explained variance: 9.3%, second axis: 6.8% explained variance.

In order to reveal similarities or differences in vegetation composition between the three land-cover types, we used detrended correspondence analysis (DCA), as this technique provides eigenvalues that allow estimation of gradient length as a measure of variation between samples (HILL & GAUCH 1980). Prior to analyses, vegetation data were arcsine-squareroot-transformed. The results of this analysis are presented in Appendix 3 and clearly show that the studied land-cover types were comparable with respect to their vegetation composition. / DCA plot de la végétation des sites non arables, des jachères et la zone tampon, sur la base de la couverture des espèces de plantes ligneuses des couches ligneuses. L'ordination était basée sur 130 espèces réparties sur 66 parcelles (23 sur les terres non arables, 24 sur les jachères, 19 dans la zone tampon), longueur du premier axe 2.5, variance expliquée: 9.3%, deuxième axe: 6.8% de la variance expliquée.

Afin de révéler des similitudes ou des différences de composition végétale entre les trois types de couvert végétal, nous avons utilisé l'analyse de correspondance détreuillée (DCA), car cette technique fournit des valeurs propres qui permettent d'estimer la longueur du gradient comme mesure de variation entre les échantillons (HILL ET GAUCH 1980). Avant les analyses, les données sur la végétation étaient transformées en arcsine-squareroot. Les résultats de cette analyse sont présentés dans l'annexe 3 et montrent clairement que les types de couvert végétal étudiés étaient comparables par rapport à leur composition végétale.

Appendix 2: Pearson correlation coefficients (r) between physical and chemical characteristics of soil from 39 study sites, those variables with a strong intercorrelation ($r \geq \pm 0.7$) were highlighted a star. / Coefficients de corrélation de Pearson (r) entre les caractéristiques physiques et chimiques du sol des 39 sites d'étude, les variables ayant une forte corrélation ($r \geq \pm 0,7$) ont été mises en évidence par une étoile.

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)	CECpot (cmolc/kg)	-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	1.12*10 ⁻⁵
Height herb layer (cm)	K ₂ O (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 (%)	CECpot (cmolc/kg)	0.610	4.682	3.75*10 ⁻⁵
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 ₂ O (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 (%)	CECpot (cmolc/kg)	-0.637	-5.029	1.29*10 ⁻⁵
Cove herb layer (%)	BS-value	0.598	4.540	5.78*10 ⁻⁵
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	3.92*10 ⁻⁵
Cove herb layer (%)	K ₂ O (mg/100g)	0.021	0.130	0.897
pH	K ⁺ (mmolc/kg)	0.536	3.867	0.000
pH	CECpot (cmolc/kg)	-0.208	-1.293	0.204
pH	BS-value	0.610	4.679	3.78*10 ⁻⁵
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 ₂ O (mg/100g)	0.442	2.996	0.005
K ⁺ (mmolc/kg)	CECpot (cmolc/kg)	-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 ₂ O (mg/100g)	0.785	7.709	3.29*10 ⁻⁹
CECpot (cmolc/kg)*	BS-value	-0.783	-7.663	3.77*10 ⁻⁹
CECpot (cmolc/kg)	Coarse silt (%)	-0.426	-2.861	0.007
CECpot (cmolc/kg)	Medium silt (%)	0.316	2.024	0.050
CECpot (cmolc/kg)	Clay < 2µm (%)	0.574	4.269	0.000
CECpot (cmolc/kg)	K ₂ O (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 ₂ O (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 ₂ O (mg/100g)	-0.415	-2.776	0.009
Medium silt (%)	Clay < 2µm (%)	0.249	1.567	0.126
Medium silt (%)	K ₂ O (mg/100g)	-0.237	-1.486	0.146
Clay < 2µm (%)	Clay < 2µm (%)	0.141	0.868	0.391

Appendix 3: Juvenile densities (100 m²) 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 concerning the juvenile densities, calculated by a linear-mixed-effect model and a subsequent Tukey's multiple comparison test, is marked by (&), dissimilarity by (≠). / Densités juvéniles (100 m²) des 25 espèces ligneuses analysées. Les densités sont présentées selon l'appartenance au groupe d'espèces, le type de couverture et le recensement (parcelles échantillonnées sur les terres non arables: n = 12, jachère: n = 17 et zone tampon: n = 10). La similarité entre les types de couvert végétal concernant les densités juvéniles, calculée par un modèle à effet mixte linéaire et un essai de comparaison multiple de Tukey subséquent, est indiquée par (&), dissimilarité par (≠).

Life form	Family	Species	May 2008			Oct 2008		
			non-arable	fallows	buffer zone	non-arable	fallows	buffer zone
Group A: non-arable ≠ fallows ≠ buffer zone								
tree	Fabaceae	<i>Pterocarpus erinaceus</i> .	24	24	32	36	32	60
Group B: non-arable & fallows ≠ buffer zone								
shrub	Annonaceae	<i>Annona senegalensis</i> .	40	148	0	64	160	0
shrub	Rubiaceae	<i>Crossopteryx febrifuga</i>	28	36	40	28	28	40
tree	Anacardiaceae	<i>Lannea acida</i> A.Rich.	24	48	0	24	52	0
tree	Combretaceae	<i>Terminalia avicennioides</i>	28	120	8	52	128	8
Group C: non-arable & buffer zone ≠ fallows								
shrub	Mimosaceae	<i>Acacia hockii</i>	0	36	4	0	36	4
tree	Combretaceae	<i>Anogeissus leiocarpa</i>	8	52	8	8	68	8
shrub	Combretaceae	<i>Combretum collinum</i>	72	360	40	76	376	56
shrub	Mimosaceae	<i>Dichrostachys cinerea</i>	184	696	20	228	732	20
shrub	Ebenaceae	<i>Diospyros mespiliformis</i>	0	124	4	0	132	4
shrub	Rubiaceae	<i>Feretia apodanthera</i>	8	180	4	8	180	4
shrub	Rubiaceae	<i>Gardenia ternifolia</i>	36	44	20	44	36	28
shrub	Caesalpiniaceae	<i>Piliostigma thonningii</i>	16	120	4	20	128	8
shrub	Strychnaceae	<i>Strychnos spinosa</i>	32	38	72	68	80	96
tree	Sapotaceae	<i>Vitellaria paradoxa</i>	56	168	12	62	224	24
Group D: fallows & buffer zone ≠ non-arable								
shrub	Combretaceae	<i>Combretum glutinosum</i>	36	16	4	44	12	4
shrub	Combretaceae	<i>Combretum nigricans</i>	144	92	16	156	84	16
shrub	Caesalpiniaceae	<i>Detarium microcarpum</i>	628	128	0	816	128	0
tree	Caesalpiniaceae	<i>Isoberlinia doka</i>	8	88	32	12	104	60
tree	Fabaceae	<i>Philenoptera laxiflora</i>	4	56	24	0	60	28
shrub	Combretaceae	<i>Pteleopsis suberosa</i>	408	212	0	416	204	4
tree	Bignoniaceae	<i>Stereospermum kunthianum</i>	136	136	20	192	128	52
Group E: non-arable & fallows & buffer zone								
tree	Bombacaceae	<i>Bombax costatum</i>	4	20	12	8	20	12
shrub	Combretaceae	<i>Combretum molle</i>	84	124	76	112	144	92
shrub	Rubiaceae	<i>Gardenia aqualla</i>	8	16	16	4	28	12

Appendix 3 (continued).

Life form	Family	Species	May 2009			Oct 2009			May 2010		
			non-arable	fallows	buffer zone	non-arable	fallows	buffer zone	non-arable	fallows	buffer zone
Group A: non-arable ≠ fallows ≠ buffer zone											
tree	Fabaceae	<i>Pterocarpus erinaceus</i>	44	24	80	52	36	92	52	36	72
group B: non-arable & fallows ≠ buffer zone											
shrub	Annonaceae	<i>Annona senegalensis</i>	68	164	0	84	204	4	140	252	0
shrub	Rubiaceae	<i>Crossopteryx febrifuga</i>	28	28	40	28	28	40	28	24	40
tree	Anacardiaceae	<i>Lannea acida</i> A.Rich.	48	104	8	64	148	0	76	184	8
tree	Combretaceae	<i>Terminalia avicennioides</i>	76	132	20	88	152	28	88	200	28
Group C: non-arable & buffer zone ≠ fallows											
shrub	Mimosaceae	<i>Acacia hockii</i>	0	40	4	0	48	4	0	36	4
tree	Combretaceae	<i>Anogeissus leiocarpa</i>	76	292	20	56	272	36	104	496	36
shrub	Combretaceae	<i>Combretum collinum</i>	72	384	52	92	444	64	104	424	64
shrub	Mimosaceae	<i>Dichrostachys cinerea</i>	240	648	20	256	668	28	252	608	32
shrub	Ebenaceae	<i>Diospyros mespiliformis</i>	4	172	4	4	188	4	4	196	4
shrub	Rubiaceae	<i>Feretia apodanthera</i>	16	216	4	16	228	4	16	220	4
shrub	Rubiaceae	<i>Gardenia ternifolia</i>	36	40	24	44	36	28	44	36	24
shrub	Caesalpinaceae	<i>Piliostigma thonningii</i>	28	112	8	28	132	8	24	148	8
shrub	Strychnaceae	<i>Strychnos spinosa</i>	60	56	96	92	88	120	72	88	120
tree	Sapotaceae	<i>Vitellaria paradoxa</i>	80	268	20	84	82	328	80	292	32
Group D: fallows & buffer zone ≠ non-arable											
shrub	Combretaceae	<i>Combretum glutinosum</i>	40	12	8	48	12	8	44	12	8
shrub	Combretaceae	<i>Combretum nigricans.</i>	164	108	20	192	108	20	204	112	20
shrub	Caesalpinaceae	<i>Detarium microcarpum</i>	824	132	0	1028	136	0	948	152	0
tree	Caesalpinaceae	<i>Isobertinia doka</i>	12	120	64	36	176	96	44	156	56
tree	Fabaceae	<i>Philenoptera laxiflora</i>	0	52	40	4	64	96	0	60	76
shrub	Combretaceae	<i>Pteleopsis suberosa</i>	384	200	4	424	224	4	8	220	8
tree	Bignoniaceae	<i>Stereospermum kunthianum</i>	164	116	48	188	140	76	192	144	68
Group E: non-arable & fallows & buffer zone											
tree	Bombacaceae	<i>Bombax costatum</i>	12	16	8	32	36	24	20	44	12
shrub	Combretaceae	<i>Combretum molle</i>	136	212	88	156	232	136	140	268	212
shrub	Rubiaceae	<i>Gardenia aqualla</i>	8	28	12	8	32	16	8	32	16