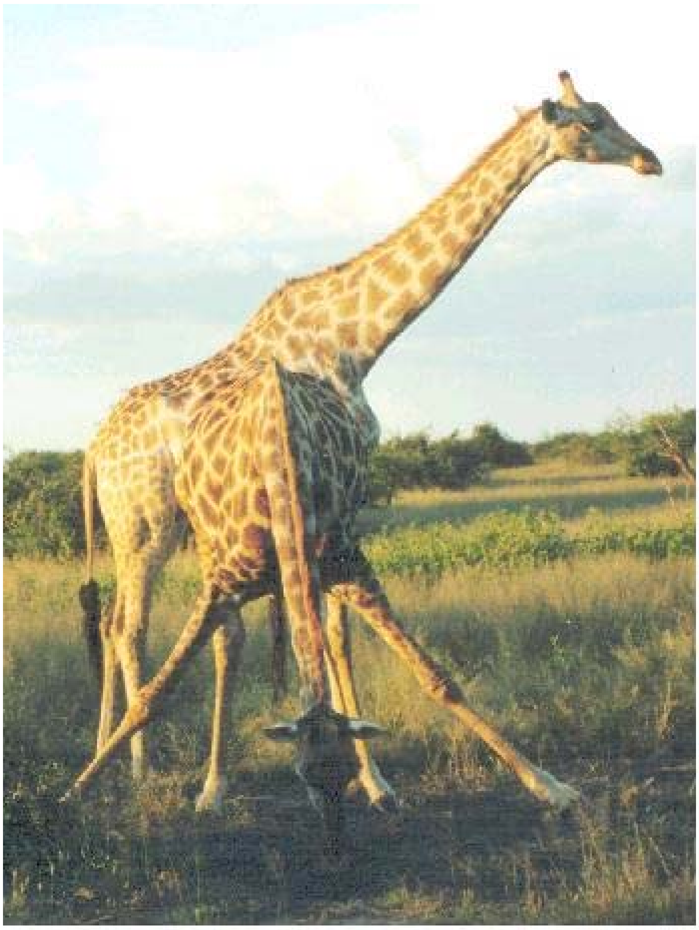
Growth pattern and reproduction of woody vegetation in a semi-arid savanna in southern Botswana



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Growth pattern and reproduction of woody vegetation in a semi-arid savanna in southern Botswana

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Abstract

In 1997 the woody vegetation in an area of semi-arid savanna in Botswana was subject to a baseline study prior to an exclosure experiment. Six plots were surveyed and after the survey was finished three of the plots where fenced to keep large herbivores out, and three plots where left as controls. In 2001 the same area was surveyed with emphasis on seedlings. The survey was carried out in transects laid out in the plots, and all seedlings found were measured and various data was collected. In this study only part of the data collected in one of the control plots (plot no. 2) was used.

Data from both surveys were used in this paper in order to describe the woody vegetation in terms of plant number, species diversity, height structure and spatial distribution. Also results from another seedling study, made in the same study area, were used to study a possible “window of opportunity” created by rainfall.

The study area was found to host a variety of woody species. In total 43 species were identified, and out of them 15 were also found as seedlings. Species with a high frequency of mature individuals were the ones that also were present as seedlings.

The majority of woody species was found to have an aggregated spatial distribution. Also seedlings grew aggregated and were found to grow relatively close to their potential mother plants.

Ground cover (herbs and standing litter) was shown to influence seedling establishment at both a large and a small scale, with most pronounced effects on the smaller scale. Different species were affected in different ways by ground cover, some benefited from the protection of ground cover and others were out competed by the herbs.

The seedling density found during the seedling survey was unexpectedly high. This indicated a ”window of opportunity” explained by the rain-rich year giving rise to a greater success in seedling recruitment than normal years.

Keywords: ground cover, tree height, savanna, spatial distribution, species diversity, “window of opportunity”, woody vegetation.

Introduction

General

Tropical savannas cover approximately 40 % of Africa and the biome is an important element in southern Africa. The distinguishing feature of savannas is the co-dominance of trees and grasses, and one of the central questions in savanna ecology is the mechanism of their coexistence (Scholes & Walker, 1993, Stuart-Hill & Tainton, 1989).

The woody species, trees and shrubs, play a major role in the savanna biome and the population dynamics of the savanna trees and shrubs are of utmost importance for the savanna structure and function (Belsky 1994). Woody species are important to the dry savanna ecology as they give shade, alter evapo-transpiration and affect nutrient status of the soil. These species are also food for a great number of wild herbivores. The woody species of the savanna are also directly important to people living in these arid areas as they, for example, provide fodder for domestic animals, fruits, fuelwood and material for construction and handy-craft.

Species diversity and spatial distribution

Species diversity in the savanna biome is considered to be lower than in the moist tropical forests, but richer than in temperate forests. However, such patterns may vary between different types of savannas and areas. α-diversity, also commonly referred to as species richness, is the number of species in a small area of more or less uniform habitat (Ricklefs, 1996). It can be estimated by simply using the total number of species found within an area, or more commonly the average number of species found per sample plot (Økland, 1990).

A species distribution pattern depends on the many different factors affecting the species. If one or a few factors have a greater effect on performance or survival of a species, the distribution of that species will be determined by those factors. Spatial distribution among woody species can be of three main types; random, regular or aggregated (Greig-Smith 1983). Random distribution may occur when no factor has a stronger influence than any other factor on a species' spatial distribution, or when many factors together influence the species distribution pattern. A regular or aggregated distribution indicates that one or a few factors determine the distribution of the species.

Determinants

The dynamics of dry savannas are often explained by competitive relations between the grass-dominated herbaceous layer and the layer of woody plants. Impact on one of these layers may cause considerable changes in the other and shift the savanna vegetation between different stages with widely different tree/grass ratio (Walker & Noy-Meir, 1982, Stuart-Hill & Tainton, 1989, Skarpe, 1992). The savanna net primary productivity, and thus value for human land use, is regulated by different tree/grass ratios (Archer et al. 1992, Skarpe, 1990, 1992). The literature describes four main factors that determine the tree/grass ratio and, thereby, shape savannas (Flyman, 1999, Scholes & Walker, 1993, Skarpe, 1992):

- Moisture (Plant Available Moisture = PAM)
- Nutrients (Plant Available Nutrients = PAN)
- Fire
- Herbivores

Soil moisture (PAM) and nutrient availability (PAN) are closely linked since they both depend on rainfall regime and soil type. Different soil types retain water more or less strongly, something that both affect the amount of PAM and the amount of nutrient leakage and rate of decomposition, which in turn determines PAN. The heterogeneity of the savanna system is increased by a rainfall regime, which varies in both time and space. Fire and herbivory on the other hand are factors disturbing and modifying the savanna structure created by climate and soil type (Sjögren 2000, Flyman 1999, Skarpe 1992).

Fire occurs with different intervals in different savanna types (dry-moist) and its intensity depends on the amount of dry grass and herbs present. Together with PAM and PAN, fire determines the density of woody species in savannas. Fire may also promote an aggregated distribution pattern and is important in controlling the establishment of woody seedlings and young trees. Fire and herbivory also interact in several ways. For example herbivory may reduce the amount of grass and herbs and hence the fire frequency and/or intensity (Skarpe 1992). On the other hand, fire may keep the woody layer within browsing height.

Although relatively few studies have been conducted on the subject of browse utilization in African savannas, available evidence indicates that browse constitutes a significant part of the total fodder for large herbivores, both wild and domestic. Most woody species have some form of adaptation to defend themselves from browsers, or to compensate for browsing impact. But, when high herbivore density is coupled with severe drought, savanna structure may be altered (Bergström 1992, Skarpe 1992).

Many factors indicate that the savanna as a biome might not exist in its present form if humans had not influenced it. Fires have great impact on the savanna dynamics, and are often started by man. Bush encroachment has been attributed to human activities, mainly in the form of heavy grazing by livestock. Hence the question weather savannas are climatic or anthropogenic has been raised (Skarpe, 1990, Skoglund, 1992).

Recruitment and establishment of woody plants; ”Window of opportunity”

Seed banks in tropical biomes, as savannas, have been concluded to be smaller than those in temperate ecosystems. This has been thought to be a consequence of the disturbance by fire and herbivory, which both may affect the mortality risk of seeds. Especially in dry savannas, rainfall during the dry season may also trigger seeds to germinate at unfavourable times and the seedlings will die (Skoglund, 1992).

In dry savannas, many woody species mainly regenerate vegetatively by root suckers and basal shoots. Sexual reproduction is promoted by favourable sequences of for example rainfall and fires, which can provide a ”window of opportunity” for seedlings to germinate and establish (van der Valk, 1992, Veenendaal et al. 1996). Thus, the success in short-term recruitment in the savanna environment is to a great extent dependent on chance, or as expressed by Flyman (1999) ”a function of being at the right place at the right time”.

Regeneration from seeds is important as a long-term strategy for almost all species but may in the short time-scale be insignificant for many savanna woody species. Seedlings may germinate and establish in considerable numbers, but most of them die due to different causes, one important factor being drought (Gerhardt 1993, Flyman 1999). There are also many other factors that may influence the survival of seedlings, like, for example, large and small mammalian herbivores, and insects. These herbivores may directly kill a seedling, but they may also change the field layer vegetation and, thus, the competitive situation for seedlings (Bergström et al. 2000, Gerhardt 1993, Flyman 1999, Linzey & Kesner 1997).

Objectives

Specifically, the intention with the present study was to investigate and describe the regeneration and distribution patterns of woody savanna species in a dry savanna. To do so the following factors were considered:

- woody species diversity
- tree height distribution
- spatial distribution of woody species
- seedling occurrence in relation to cover of herbs and standing litter
- seedling distribution in relation to large trees/shrubs
- seedling recruitment and the influence of ”window of opportunity”

To relate my data on number, height and distribution of seedlings I analysed an earlier collected data set, from the same study area. An earlier seedling study by Flyman (1999) was also performed in the same study area. Since the Flyman study was performed during the ”bad” rainy season of 1997/1998, while the present seedling study followed the exceptionally wet rainy season of 2000, it was possible to discuss the existence of a ”window of opportunity” for seedling establishment.

Study area

This study was performed at Mokolodi Nature Reserve (24° 45’ S, 25° 55’ E), about 15 km southwest of Gaborone, Botswana. The reserve is a former cattle ranch and encompasses, after a recent extension, approximately 4 500 ha. The cattle keeping stopped in 1986 and today the reserve is fenced to keep domestic animals out and wild animals in.

Since the area was turned into a reserve, eight species of large herbivores, which all occurred naturally in the area before it was used for cattle grazing, have been re-introduced to the area. The introductions were carried out between 1992 and 1994 (Bråten, 1997). In total there are 16 large herbivore species in the reserve, and out of these eight species are grazers, five are browsers and three are mixed feeders (Table 1).

The topography of southeast Botswana, where the study area was situated, is undulating and hilly. This contrasts with the rest of the country, which is flat and sand covered. The study area was located at an altitude of approximately 1050 metres. The soils belong to the eutric regosols with a dominant lithic phase. The colour is yellowish red, yellow and greyish brown. The soil varies between shallow to very shallow, excessively drained to moderately drained and coarse sands to clay loams (de Wit & Nachtergaele, 1990).

Table 1. Large herbivores at Mokolodi Nature Reserve. Each species is presented with English name, scientific name, type of feeder; grazer=g, browser=b and if introduced to the reserve 1992-1994 indicated with a ”y” (Bråten, 1997).

English name	Scientific name	Type of feeder	Introduced
Impala	Aepyceros melampus	g + b	
Hartebeest	Alcelaphus buselaphus	g	y
Grey duiker	Sylvicapra grimmia	b	
White rhinoceros	Ceratotherium simum	g	y
Blue wildebeest	Connochaetes taurinus	g	y
Giraffe	Giraffa camelopardalis	b	y
Burchell’s zebra	Equus burchelli	g	y
Common waterbuck	Kobus ellipsiprymnus	g	y
Klippspringer	Oreotragus oreotragus	b	
Gemsbok	Oryx gazella	g	y
Warthog	Phacochoerus aethiopicus	g	
Steenbok	Raphicerus campestris	g + b	
Mountain reedbuck	Redunca fulvorufula	g	
Eland	Taurotragus oryx	g + b	y
Bushbuck	Tragelaphus scriptus	b	
Greater kudu	Tragelaphus strepsiceros	b	

The climate is semi-arid with an average annual precipitation of 538 mm (in Gaborone, 30 years mean; Botswana Weather Bureau, unpublished). Rainfall is strongly seasonal and mostly occurs during the summer months November to February. Rainfall data collected at the Mokolodi Nature Reserve during 2000 and fist half of 2001 is shown in figure 1. The hottest month is December when the highest mean maximum temperature of 32.6° C occurs. June and July are the coldest months with a mean minimum of 3° C (Tolsma et al. 1987).

In the study area, three broad vegetation zones have been described (Skarpe et al. 2000): The combretum-zone on the upper hill slopes, dominated by *Combretum apiculatum*, the acacia-zone on the lower hill slopes, characterised by species like *Acacia tortilis* and the spirostachys-zone along drainage lines, defined by dominance of *Spirostachys africana*.

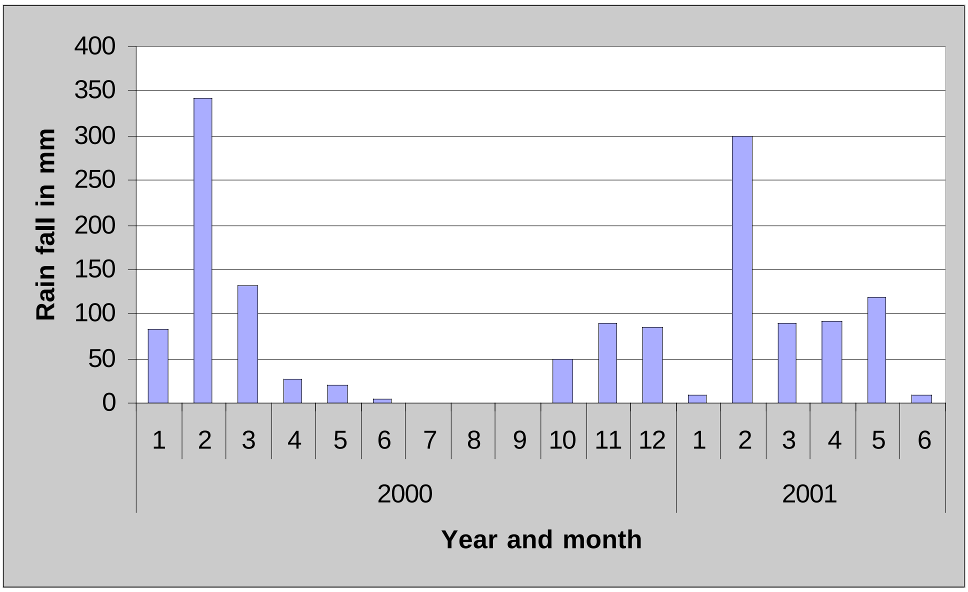

Figure 1. Rainfall the year 2000 and the first half of 2001, Mokolodi Nature Reserve.

Methods

Inventories

Two different inventories at the same study area were used in this study of woody vegetation in semi-arid savanna.

Base-line study
A project to study herbivore impact on semi-arid savanna was started in 1997 by NORAD (Norweigan Agency for Development Cooperation) in cooperation with the University of Botswana. The project is centred around three pairs of 140×140 m permanent plots, subjectively placed within representative parts of the acacia-zone in the Mokolodi Nature Reserve. Each pair of plots was placed in as similar vegetation as possible and one plot per pair was fenced (fenced area 150×150 m, i.e. a buffer zone of 5 m between fence and plot) to exclude animals larger than the size of a scrub hare. The unfenced plot in each pair serves as a control. Each 140×140 m plot, referred to as main plot, was divided into 196 subplots of 10×10 metres. The corners of the subplots were marked with metal pegs. Before and during the fencing of the three main plots, a baseline study of vegetation was conducted.

As described by Sjögren (2000), the baseline study was conducted in 1997, during the end of the wet season, from last week January till end of March. Each subplot was analysed individually and all dead and alive woody plants 0.2 m and higher, (hereafter called trees) were mapped by recording coordinates using measuring tapes and rulers. A tree was defined as one or more stems of the same species emerging from the ground less than 0.5 m apart. When a tree consisted of more than one stem, coordinates were set to the estimated centre point. For each tree, species was recorded according to Coates-Palgrave (1983). Coordinates and plant height, i.e. vertical height from ground to highest living shoot, with plant in natural position, were measured to the closest 0.1 meters. For each tree, signs of browsing by large herbivores were recorded as present or absent (Sjögren, 2000). During the same inventory the canopy cover of important herbaceous species and the total field layer cover was recorded as percentage for each subplot. The base-line survey was conducted in all six main plots as described above, but in this paper only data from plot no. 2 is used.

Seedling study
After the start of the project in Mokolodi in 1997, several inventories and experiments, concerning plants, small rodents and insects, have been conducted in the permanent plots. In spring 2001 another inventory was carried out. The main goal this time was to study tree seedlings and how they were affected by browsing**,** trampling etc. of large herbivores. The survey was carried out during the same period of the year as the base-line study, from the last week of January till the end of March, but with different methods.

The 2001 inventory of seedlings did not include the main plots as a whole but used transects of 4×100 metres, placed along the lines of pegs marking the corners of subplots. Transects were re-surveyed approximately four weeks after the first inventory to follow up on the performance of the found seedlings. Two transects were done per main plot, which gives a surveyed area of 800 m^2 per main plot. Each transect was marked with measure tapes placed between the pegs, which marked the middle of transect. To record coordinates for all live woody seedlings rulers were used. In this study we focused on tree seedlings having started their growth the current or last rainy season. Suckers from stumps or dead or living trees were excluded when the original plant could be identified at the base of the seedling.

For each seedling found several variables were recorded. In this paper, the following variables were used;

- species, (nomenclature according to Wyk & Wyk 1997, Coates-Palgrave 1983, and Smit 1999)
- estimated age of the seedling, given as germinated during current (1) or last (2) wet season
- plant length, measured in centimetres with the plant stretched out as far as was feasible without damaging it
- total cover of the field layer, the combined cover of live and dead plant material less than 50 cm high. Cover was estimated as percentage of a circular plot of 0.5 m^2 with the seedling in the centre.
- cover of live field layer vegetation, estimated as percentage of total cover
- height of the field layer, recorded as an average of the height in cm of the field layer in the circular plot.
- tree canopy cover, vertically above the seedling, recorded with the species name, alternatively ”not present”. This was recorded independent of the height of the tree.
- distance (in dm) to nearest mature individual (= individual that have reached reproductive height, see Table 4) of the same species as the seedling.

The inventory was conducted in all six main plots as described above, but in this paper only data from plot no. 2 is used. This facilitated comparisons with data from the base-line study.

Calculations and statistical analyses

All data treatment and statistical work were carried out in Excel. The different correlations in the present study were made by means of Pearson correlation.

Linear regression and polynomial regression were used to illustrate possible connections between herbaceous cover and number of woody seedlings and saplings.

In the literature, several different tests are available to test whether a specific spatial distribution diverge or not from the theoretical random distribution. In this study the ”variance to mean ratio” (t-test) by Greig-Smith (1983) was used. The test uses the frequency distribution of quadrates compared to a Poisson distribution to measure the degree of dispersion or aggregation of individuals. If the ratio of variance to mean is less than one, a regular distribution can be assumed, if greater than one an aggregated distribution is indicated. Only species with seven or more individuals present were used in this test.

The significance of divergence from one was tested with a t-test based on the ratio and its standard error. The standard error was calculated as suggested by Bartlett (quoted in Greig-Smith 1983);

$$s = \sqrt{[2/(N-1)]}$$

and the t-value as follows;

$$t = [(V/M)-1] / s$$

Species inventories are almost always made through sampling and there are several methods developed to estimate the total number of species in an area. In this study, first order Jack knife method was used. The method is based on the distribution of species in the samples. First order Jack knife estimate of total species richness (Burnham & Overton, 1979), was calculated using the following formula:

$$S_{j1} = S_{obs} + Q_1\left(\frac{m-1}{m}\right),$$

where S_{j1} = the estimated total number of species in an area, S_{obs} = total number of observed species, Q_1 = number of species occurring in one sample and m = number of samples.

The mean of several different cumulative observed species curves, where the order of the sample plots is randomised, is used to calculate the species-area relationship. Therefore the observed values can be non-integers, which not is expected from observed number of species.

Results

Species diversity and abundance

Baseline study

In the base-line study of plot 2, 6788 live tree individuals were found of 43 identified species (Table 2). First order Jack Knife value for total number of species in the investigation area was 48.97, which is approximately 6 more species than found in the survey. Unidentified species were not considered in this paper; however only 16 individuals found during the survey could not be identified. *Euclea* spp. was noted as one group.

As it was not possible to separate seedlings of a certain age in the baseline study, I have in the present analyses split the trees into two classes based on height: ”small trees” (0.2-1.0 m) and ”big trees” (> 1 m). Out of the 6788 individuals found, 3065 were ”small trees”, and they were of 37 identified species, all found also as ”big trees”. Maximum number of species found in one subplot (10x10 m) was 19 and maximum number of species of small trees represented in one subplot was 15 (it was not the same subplot that had both maximums). Minimum number of species found in one subplot was 3 and minimum number of species with small trees represented in one subplot was 1. Mean number of species per subplot was 10.1 (±standard deviation: ±3.1). Mean number of species with small trees represented was 6.2 (±2.5) (Figure 2).

Ranked in descending order, the most numerous species in the baseline study were *Combretum apiculatum, Grewia bicolor, Dichrostachys cinerea, Euclea* spp. *Rhus leptodictya, Acacia tortilis* and *Spirostachys africana* (Table 2). These five species made up nearly 70 % of all registered stems. Almost the same species were the most numerous when considering only small trees (0.2-1.0 m), but, they were slightly differently ordered: *Combretum apiculatum, Grewia bicolor, Rhus leptodictya, Euclea* spp., *Acacia tortilis* and *Dichrostachys cinerea* (Table 3).

Maximum number of tree individuals found in one subplot was 87 and maximum number of small trees in one subplot was 41 (it was not the same subplot that had both maximums). Minimum number of tree individuals found in one subplot was 6 and minimum number of small trees in one subplot was 1 (it was not the same subplots that had the minimums). Mean number of tree individuals per subplot was 34.6 (±15.2) and mean number of small trees (0.2-1.0 m) was 15.7 (±7.9) (Figure 3). Table 2 also reveals that five species were represented by only one individual in the whole data-set and that 13 species never had more than one stem in an individual subplot.

The frequency, that is percentage of subplots where a specific species occurs, was high for all numerous species mentioned above, except for *Spirostachys africana.* The most numerous species mentioned above were all present in more than 60 % of all subplots, except for *Spirostachys africana* that only was present in 16% of the plots. The highest frequency had *Combretum apiculatum* with 95.9 % (Table 2). Considering only small trees the frequency was slightly lower, the most numerous species were all present in more than 40 % of the subplots. Also here, *Combretum apiculatum* had the highest frequency, 91.3 % (Table 3).

Species represented by few individuals also naturally have a low frequency. Nine species were present in only 1 % or less of the subplots, and the corresponding number for small trees was eight. However, some species represented by fewer individuals than *Spirostachys africana* had a higher frequency than *Spirostachys africana,* for example *Grewia flava* with 142 individuals present and a frequency of 41.3 % (Table 2).

Table 2. Total number of individuals per species, mean number of individuals per species and subplot, standard deviation (sd), maximum number of individuals per species and subplot and frequency (percentage of subplots with the species present).

Species	No. of trees	mean	sd	max	% of plots
Acacia caffra	116	0.59	1.00	7	38.3
Acacia erubescens	64	0.33	0.79	5	20.4
Acacia fleckii	1	0.01	0.07	1	0.5
Acacia mellifera	49	0.25	0.94	10	13.8
Acacia nilotica	161	0.82	1.28	8	45.4
Acacia robusta	14	0.07	0.33	3	5.6
Acacia tortilis	350	1.79	2.07	12	64.8
Boscia albitrunca	2	0.01	0.10	1	1.0
Boscia foetida	7	0.04	0.21	2	3.1
Bridelia mollis	2	0.01	0.10	1	1.0
Berchemia zeyheri	29	0.15	0.37	2	14.3
Carissa bispinosa	2	0.01	0.14	2	0.5
Combretum apiculatum	2225	11.35	9.04	45	95.9
Combretum hereroense	26	0.13	0.41	2	10.7
Combretum imberbe	22	0.11	0.35	2	10.2
Combretum molle	2	0.01	0.10	1	1.0
Combretum zeyheri	3	0.02	0.12	1	1.5
Commiphora schimperi	20	0.10	0.34	2	9.2
Dichrostachys cinerea	569	2.90	2.91	17	82.7
Dombeya rotundifolia	102	0.52	0.89	4	33.2
Ehretia rigida	139	0.71	0.96	5	44.4
Euclea spp.	466	2.38	2.41	15	80.1
Flueggia virosa	3	0.02	0.12	1	1.5
Gardenia volkensii	7	0.04	0.26	3	2.6
Grewia bicolor	952	4.86	3.48	16	93.4
Grewia flava	142	0.72	1.18	9	41.3
Grewia flavescens	56	0.29	0.76	6	18.4
Grewia monticola	56	0.29	0.61	3	21.4
Maytenus senegalensis	148	0.76	1.18	6	42.3
Olea europaea	1	0.01	0.07	1	0.5
Ozoroa paniculosa	2	0.01	0.10	1	1.0
Pappea capensis	165	0.84	1.23	6	43.9
Peltophorum africanum	48	0.24	0.52	3	20.9
Rhigozum brevispinosum	1	0.01	0.07	1	0.5
Rhus leptodictya	443	2.26	2.58	22	77.6
Sclerocarya birrea	3	0.02	0.12	1	1.5
Spirostachys africana	245	1.25	4.33	28	16.3
Tarchonanthus camphoratus	77	0.39	1.74	23	19.4
Vangueria infausta	1	0.01	0.07	1	0.5
Vitex zeyheri	34	0.17	0.58	5	11.7
Ximenia americana	3	0.02	0.12	1	1.5
Ximenia caffra	10	0.05	0.22	1	5.1
Ziziphus mucronata	20	0.10	0.32	2	9.7
Total	6788	34.63	15.16	87	100

Table 3. Total number of individuals (0.2-1.0 m high) per species, mean number of individuals (0.2-1.0 m) per species and subplot, standard deviation (sd), maximum number of individuals (0.2-1.0 m) per species and subplot and frequency (percentage of subplots with the species present).

Species	No. of trees	mean	sd	max	% of plots
Acacia caffra	53	0.27	0.60	3	20.9
Acacia erubescens	22	0.11	0.40	3	8.7
Acacia fleckii	1	0.01	0.07	1	0.5
Acacia mellifera	23	0.12	0.70	8	5.1
Acacia nilotica	56	0.29	0.66	6	21.9
Acacia robusta	2	0.01	0.10	1	1.0
Acacia tortilis	182	0.93	1.51	8	43.9
Berchemia zeyheri	8	0.04	0.20	1	4.1
Boscia albitrunca	2	0.01	0.10	1	1.0
Boscia foetida	7	0.04	0.21	2	3.1
Carissa bispinosa	1	0.01	0.07	1	0.5
Combretum apiculatum	1166	5.95	5.45	31	91.3
Combretum hereroense	9	0.05	0.21	1	4.6
Combretum imberbe	6	0.03	0.17	1	3.1
Combretum zeyheri	2	0.01	0.10	1	1.0
Commiphora schimperi	16	0.08	0.29	2	7.7
Dichrostachys cinerea	142	0.72	1.10	8	44.9
Dombeya rotundifolia	21	0.11	0.34	2	9.7
Ehretia rigida	78	0.40	0.73	4	28.1
Euclea spp.	201	1.03	1.54	12	51.0
Flueggia virosa	1	0.01	0.07	1	0.5
Gardenia volkensii	3	0.02	0.12	1	1.5
Grewia bicolor	375	1.91	1.82	9	76.0
Grewia flava	90	0.46	0.87	5	31.1
Grewia flavescens	21	0.11	0.36	2	9.2
Grewia monticola	9	0.05	0.21	1	4.6
Maytenus senegalensis	76	0.39	0.82	5	25.0
Pappea capensis	81	0.41	0.83	6	27.6
Peltophorum africanum	19	0.10	0.36	3	8.2
Rhus leptodictya	323	1.65	2.22	18	63.8
Sclerocarya birrea	1	0.01	0.07	1	0.5
Spirostachys africana	35	0.18	0.74	6	8.2
Tarchonanthus camphoratus	13	0.07	0.32	3	5.1
Vangueria infausta	1	0.01	0.07	1	0.5
Vitex zeyheri	8	0.04	0.20	1	4.1
Ximenia caffra	3	0.02	0.12	1	1.5
Ziziphus mucronata	8	0.04	0.20	1	4.1
Total	3065	15.6	7.9	41	100

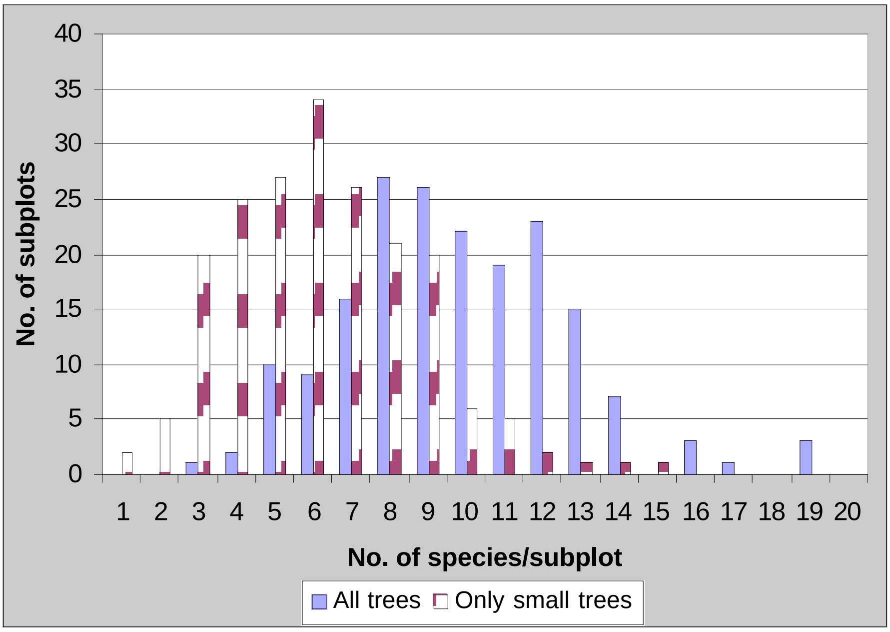

Figure 2. Distribution of number of species per subplot, split into all trees and only small trees.

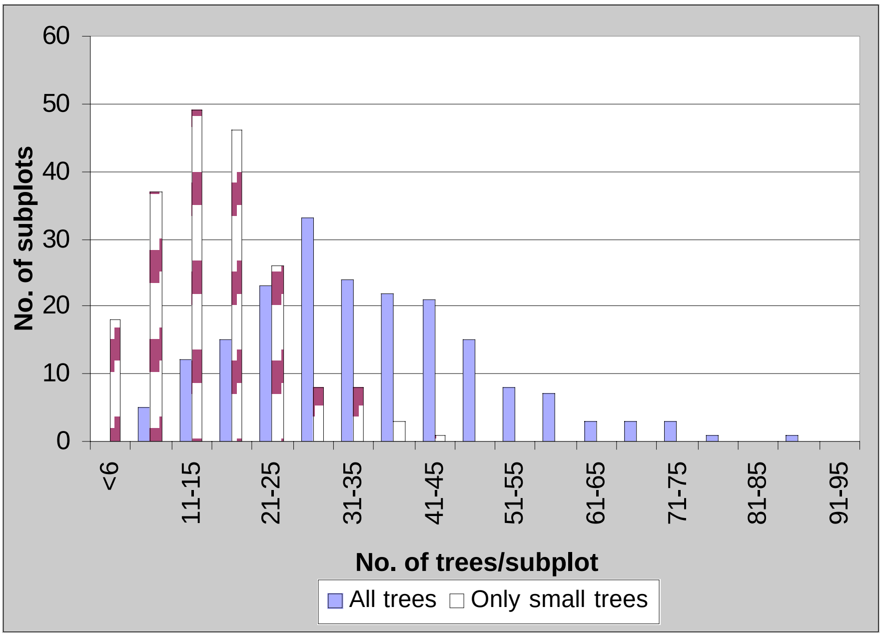

Figure 3. Distribution of number of tree individuals per subplot, split into all trees and only small trees.

Seedling study
In the seedling study, a total of 269 seedlings were found in the studied main plot 2. This corresponds to 33.6 seedlings per 100 m^2. The seedlings were identified to 15 species, of which *Grewia* spp. was noted as one group, and so was *Acacia* spp. except for *A. nilotica* and *A. erubescens* that could be identified with certainty (Table 4).

The most numerous species in the seedling study were, in descending order, *Grewia* spp., *Euclea* spp., *Dichrostachys cinerea*, *Combretum apiculatum*, and *Spirostachys africana*.

Totally 197 of the individuals found had established in 2000, which was almost three times as many as the 72 that had established in 2001 (Table 4).

Table 4. Species found, total number of seedling per species and age class (1 season or 2 seasons = established during present or preceding season), also showing definition of reproduction height (m) for the different species.

Species	No. of seedlings	1 season	2 seasons	Rep. height (m)
Acacia erubescens	4	0	4	1
Acacia nilotica	3	1	2	2
Acacia spp.	9	5	4	2
Combretum apiculatum	27	8	19	2
Combretum hereroense	4	0	4	2
Dichrostachys cinerea	36	6	30	1
Euclea spp.	62	37	25	1
Flueggia virosa	1	0	1	1
Grewia spp.	79	7	72	1
Maytenus senegalensis	3	2	1	1
Pappea capensis	5	2	3	2
Peltophorum africanum	2	0	2	2
Rhus leptodictya	9	2	7	1
Spirostachys africana	24	1	23	2
Ximenia americana	1	1	0	1
Total	269	72	197	

Height distribution

Baseline study

Considering all tree individuals found, the mean tree height was 1.5 m and most trees (>400 trees) were found in the height categories 0.4 m, 0.5 m, 0.6 m and 0.7 m (Fig. 4). Using only the same 15 species that were found in the seedling study, to enable later comparison between the two studies, the mean tree height was still 1.5 m and the most common height categories (>400 trees) were 0.5 m, 0.6 m and 0.7 m (Fig. 5). It can also be seen that trees in the study plot rarely exceed 5-6 m.

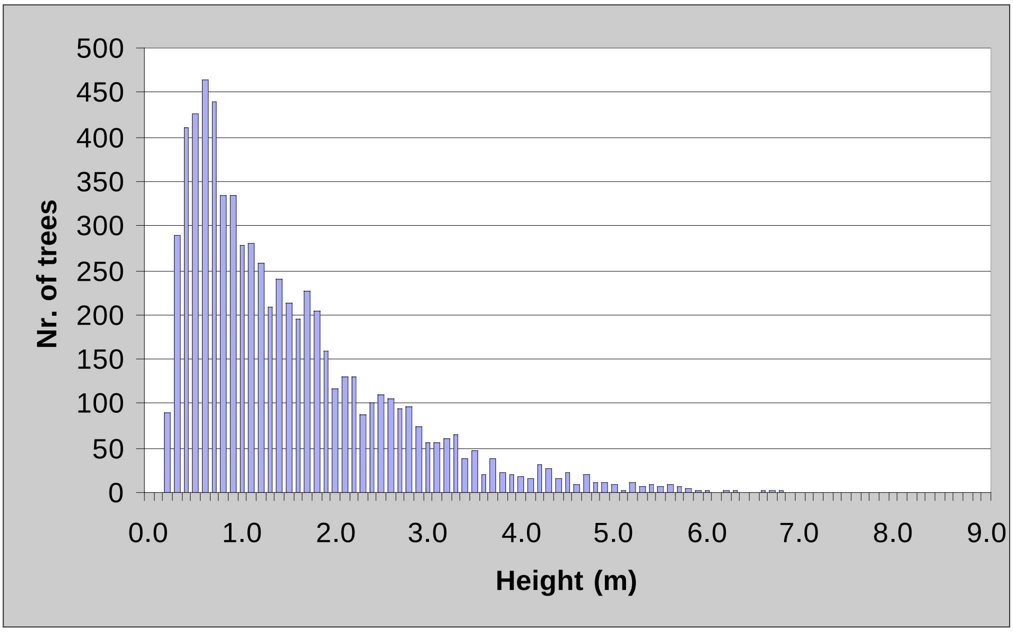

Figure 4. Height distribution of all trees.

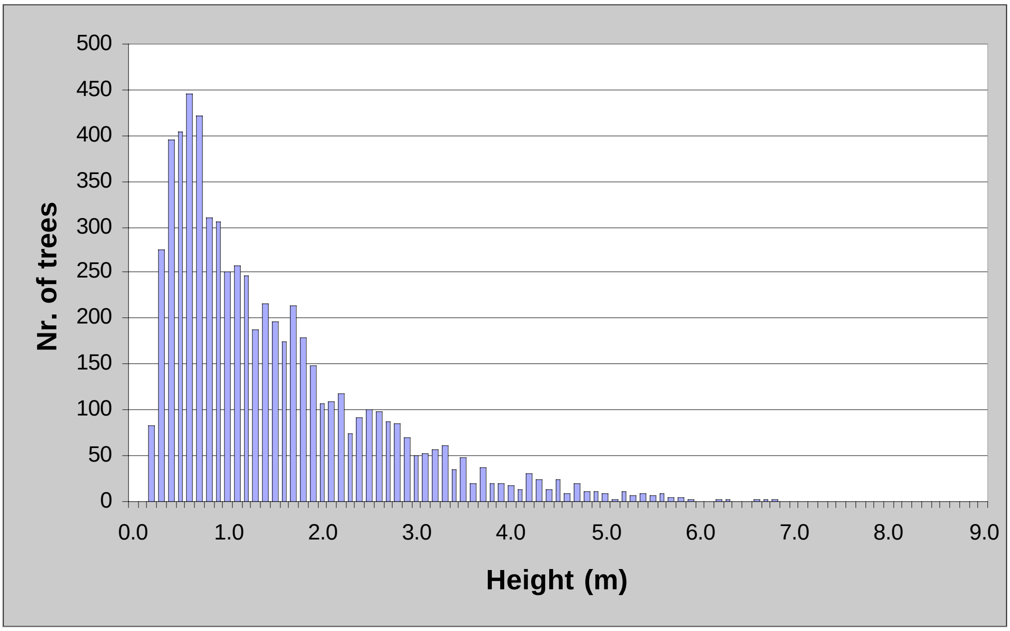

Figure 5. Height distribution of all trees of the same species as found in the seedling study.

Seedling study

The mean seedling length was 0.095 m. The dominating length class was the one comprising the lengths of 0.01-0.10 m and 93 % of all seedlings were lower than 0.2 m, i.e. the lowest registered trees in the base-line study. The smallest seedling was 0.01 m, the longest was 0.74 m and only 6 individuals were longer than 0.35 m (Fig. 6).

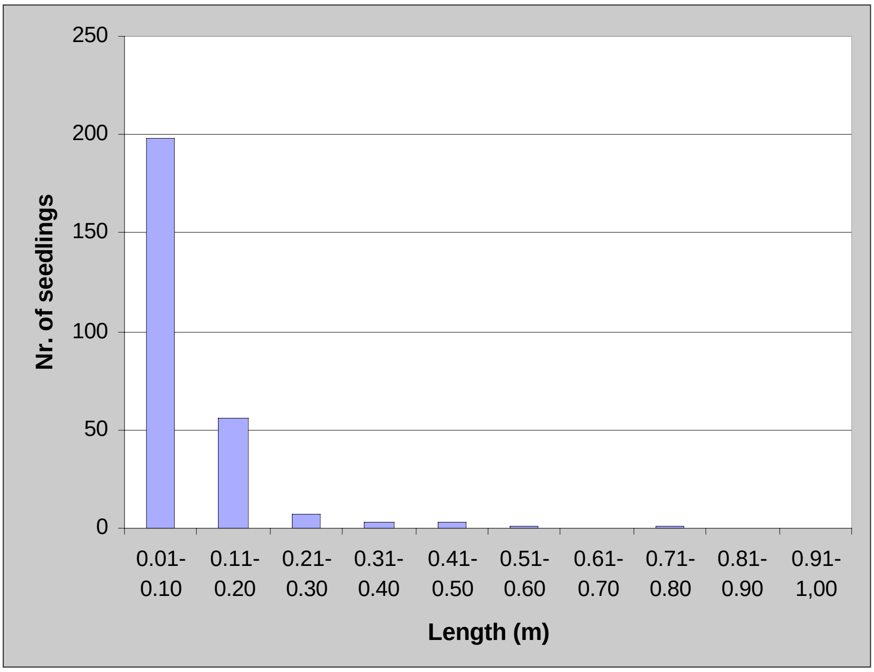

Figure 6. Seedling length distribution.

Spatial distribution

Baseline study

As presented earlier, the mean total number of trees per subplot was 34.6, which corresponds to 34.6 trees/100 m^2 or 0.35 trees/m^2. The mean number of small trees/m^2 was 0.16.

When using the variance to mean ratio, and t-test, as suggested by Greig-Smith (1983), to test spatial distribution pattern in the data set, it can be seen that most species show an aggregated distribution pattern. Six species, for example *Combretum imberbe* and *Peltophorum africanum*, however, show a distribution pattern that was not significantly different from random (table 5).

Table 5. Results of t-test of the variance to mean ratio for all species found, with seven or more individuals present, in the baseline study. (196 squares of 100 m^2)

Species	No. of individuals	V/M	t-value	Significance
Acacia caffra	116	1.67	6.58	***
Acacia erubescens	64	1.92	9.12	***
Acacia mellifera	49	3.48	24.54	***
Acacia nilotica	161	1.99	9.80	***
Acacia robusta	14	1.50	4.94	***
Acacia tortilis	350	2.39	13.68	***
Boscia foetida	7	1.25	2.47	**
Berchemia zeyheri	29	0.92	-0.78	n.s.
Combretum apiculatum	2225	7.16	60.84	***
Combretum hereroense	26	1.25	2.49	**
Combretum imberbe	22	1.07	0.69	n.s.
Commiphora schimperi	20	1.10	0.97	n.s.
Dichrostachys cinerea	569	2.90	18.75	***
Dombeya rotundifolia	102	1.50	4.93	***
Ehretia rigida	139	1.30	2.94	**
Euclea spp.	466	2.43	14.16	***
Gardenia volkensii	7	1.82	8.11	***
Grewia bicolor	952	2.48	14.58	***
Grewia flava	142	1.92	9.12	***
Grewia flavescens	56	2.04	10.23	***
Grewia monticola	56	1.29	2.82	**
Maytenus senegalensis	148	1.84	8.29	***
Pappea capensis	165	1.79	7.85	***
Peltophorum africanum	48	1.09	0.87	n.s.
Rhus leptodictya	443	2.94	19.14	***
Spirostachys africana	245	14.90	137.27	***
Tarchonanthus camphoratus	77	7.70	66.14	***
Vitex zeyheri	34	1.94	9.32	***
Ximenia caffra	10	0.95	-0.50	n.s.
Ziziphus mucronata	20	1.00	-0.02	n.s.

Seedling study

Mean number of seedlings per square metre was found to be 0.34, which means that there was a mean of 34 seedlings per 100 m^2 (subplot size = 100 m^2).

To use the variance to mean ratio, and t-test, as suggested by Greig-Smith (1983), on the data from the seedling study, transects were divided into plots of 4 x 4 m. Note that, due to difficulties in identifying small seedlings, at some occasions the tests have been done on the genus level. All species or species groups in the seedling study, represented by more than 7 individuals, showed an aggregated spatial distribution. Except for *Acacia* spp, all species or group of species had roughly the same variance/mean ratio (Table 6).

Table 6. Results of t-test of the variance to mean ratio for seedlings, only considering species or species groups with more than 7 individuals present. (50 squares of $16m^2$)

Species	No. of individuals	V/M	t-value	Significance
Acacia spp.	9	1.04	0.21	*
Combretum apiculatum	27	5.72	23.36	***
Dichrostachys cinerea	36	8.28	36.03	***
Euclea spp.	62	9.02	39.69	***
Grewia spp.	79	6.86	29.02	***
Rhus leptodictya	9	7.04	29.91	***
Spirostachys africana	24	5.19	20.72	***

Seedling occurrence in relation to cover of herbs and standing litter

Baseline study

To test the relationship between herb cover and number of small trees/shrubs, Pearson correlation was used (Table 7). Regression was also used to visualise a possible relation between the two variables (Fig. 7).

Four of the six species tested were significantly correlated to herb cover. *Acacia tortilis* and *Euclea* spp. were negatively correlated to herb cover, while *Combretum apiculatum* and *Grewia bicolor* were positively correlated to herb cover.

For *Acacia tortilis* (Fig. 7), *Combretum apiculatum*, *Dichrostachys cinerea* and *Rhus leptodictya* polynomial regression turned out to fit better to the plotted values than did the straight-line regression. However, the improvements were small for all species except *Acacia tortilis*.

Table 7. Correlations of grass cover and number of small trees/shrubs per subplot. Only the six most numerous species were tested.

Species	df	Slope	Correlation coefficient	P
Acacia tortilis	194	-	0.39	**
Combretum apiculatum	194	+	0.28	**
Dichrostachys cinerea	194	-	0.10	n.s.
Euclea spp.	194	-	0.21	**
Grewia bicolor	194	+	0.15	*
Rhus leptodictya	194	-	0.02	n.s.

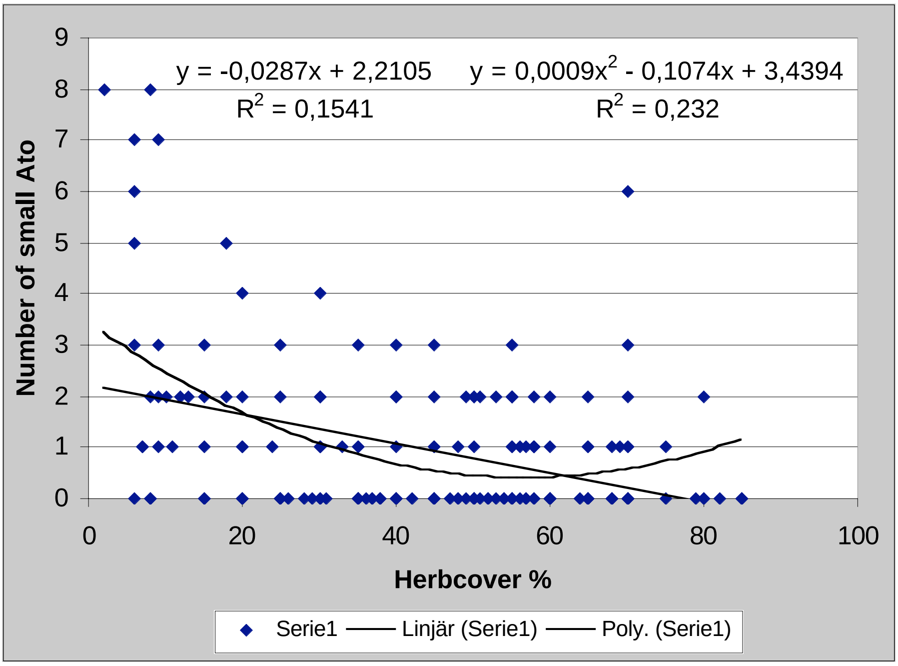

Figure 7. Herb cover plotted against number of seedlings of *Acacia tortilis*.

Seedling study

Favourable growth condition for the seedlings in terms of cover of herbs and standing litter was measured by means of percentage of ground cover (herbs and standing litter) surrounding each seedling. Mean percentage ground cover and live ground cover is shown in Table 8.

Generally herbs and standing litter covered approximately 50 % of the area closest to the seedlings. *Euclea* spp. and *Combretum apiculatum* had the highest percentage ground cover around the seedlings and *Dichrostachys cinerea* the lowest.

Table 8. Total cover of herbs and standing litter measured as percentage cover of a circular plot of 0.5 m^2 with the seedling in the centre, and live plant biomass measured as percentage of total cover. Here showing mean total cover, standard deviation, maximum and minimum cover, mean percentage live plant cover, and result (p-value) of Kolmogorov-Smirnov normality test for mean total cover.

Species	Mean % total cover	SD	Max	Min	Mean % live cover	P
Combretum apiculatum	73.7	11.3	95	40	26.5	0.149
Dichrostachys cinerea	45.8	21.6	80	0	47.4	>0.15
Euclea spp.	74.0	18.0	100	10	17.1	0.054
Grewia spp.	56.5	20.5	95	20	32.9	>0.15
Spirostachys africana	61.7	8.8	80	50	12.3	>0.15

Mean percentage of ground cover, total and live, was found to vary to a certain extent between species of seedlings and was tested (t-test) for possible significant differences between the five most numerous species (Table 9a and 9b). All species showed significant differences except for *Combretum apiculatum* and *Euclea* spp. that had almost identical mean ground cover.

Table 9a. Results of statistical t-test of difference between species in mean percentages of total cover. n.s. = not significant = p>0,05, * = p<0,05; ** = p<0,01 and *** = p<0,001.

Species	Mean cover	Tested against	Mean cover	P	Sign.
Combretum apiculatum	73.7	*Dichrostachys cinerea*	45.8	0.0000	***
		Euclea spp.	74.0	0.4688	n.s.
		Grewia spp.	56.5	0.0000	***
		Spirostachys africana	61.7	0.0000	***
Dichrostachys cinerea	45.8	*Euclea* spp.	74.0	0.0000	***
		Grewia spp.	56.5	0.0072	**
		Spirostachys africana	61.7	0.0001	***
Euclea spp.	74.0	*Grewia* spp.	56.5	0.0000	***
		Spirostachys africana	61.7	0.0000	***
Grewia spp.	56.5	*Spirostachys africana*	61.7	0.0407	*

Table 9b. Results of statistical T-test of difference between species in mean percentage of live biomass cover. n.s. = not significant (p>0.05), * = significant (p<0.05), ** = significant (p<0.01) and *** = highly significant (p<0.001)

Species	Mean % live cover	Tested against	Mean % live cover	P	Sign.
Combretum apiculatum	26.5	*Dichrostachys cinerea*	47.4	0.0000	***
		Euclea spp.	17.1	0.0008	***
		Grewia spp.	32.9	0.0253	*
		Spirostachys africana	12.3	0.0000	***
Dichrostachys cinerea	47.4	*Euclea* spp.	17.1	0.0000	***
		Grewia spp.	32.9	0.0003	***
		Spirostachys africana	12.3	0.0000	***
Euclea spp.	17.1	*Grewia* spp.	32.9	0.0000	***
		Spirostachys africana	12.3	0.0119	*
Grewia spp.	32.9	*Spirostachys africana*	12.3	0.0000	***

Seedling distribution in relation to large trees

Seedling study

The number of seedlings growing under the canopy cover of another tree (independent of height) was 249, while the remaining 20 grew in the open (Table 10). Out of these 249 seedlings 82 (i.e. about 30 % of total number of seedlings) grew under a conspecific tree. All species are presented in the table although many of them occur in low numbers. A variation between species could be seen, for example *D. cineria* with 50 % of the seedlings growing under another *D. cineria* and *Grewia* spp. with 20 % (Table 10).

Table 10. Number of seedlings that grew under the canopy of another tree, number and percentage of seedlings that grew under the canopy of a conspecific tree.

Species	Total	No. under canopy	No. under conspecific	% under conspecific
Acacia erubescens	4	3	0	0
Acacia nilotica	3	2	0	0
Acacia spp.	9	4	1	11
Combretum apiculatum	27	27	13	48
Combretum hereroense	4	4	0	0
Dichrostachys cinerea	36	27	18	50
Euclea spp.	62	62	26	42
Flueggia virosa	1	1	0	0
Grewia spp.	79	75	16	20
Maytenus senegalensis	3	3	2	67
Pappea capensis	5	5	1	20
Peltophorum africanum	2	2	0	0
Rhus leptodictya	9	9	1	11
Spirostachys africana	24	24	4	17
Ximenia americana	1	1	0	0
Total	269		82	30

Considering all seedlings of all species 77.6 % of the seedlings were found closer than 3 m from nearest mature conspecific tree (Fig. 8) and the mean distance was 2.25 m (standard deviation ±2.81). (A mature conspecific tree has to be large enough to be considered capable to produce seeds, for height definitions per species see Table 4.) Considering the five most numerous species the mean distances varied and were tested (t-test) for significant differences. The most apparent difference found was that *Dichrostachys cinerea* grew significantly further away from nearest adult conspecific than all the other four species (Table 11).

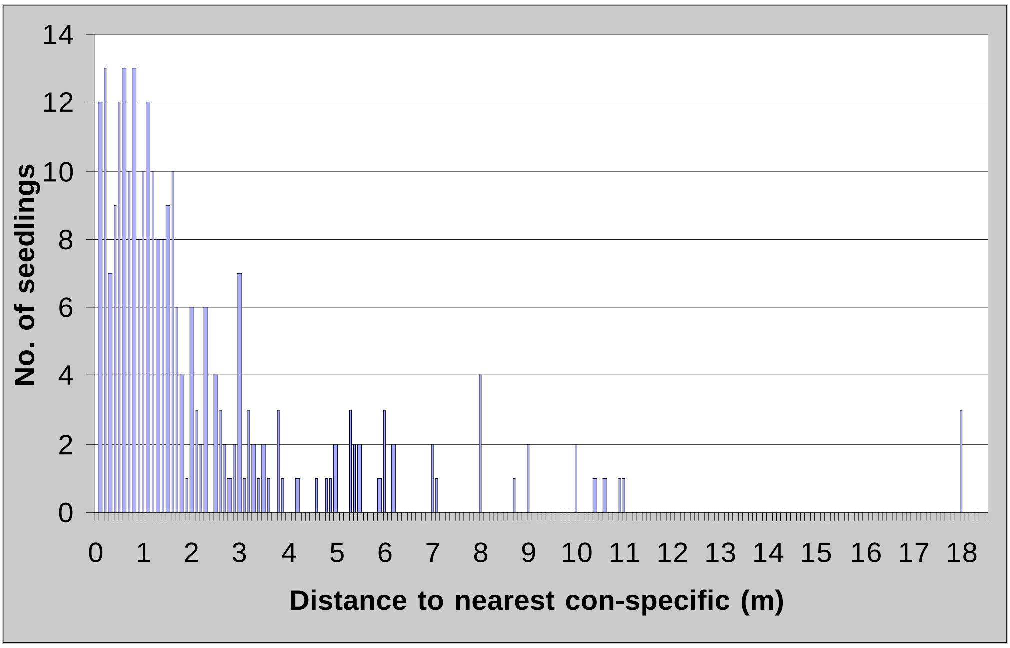

Figure 8. The distribution of distances from seedlings to nearest mature conspecific tree.

Table 11. Mean distances (in metres) from seedlings of the five most numerous species to their nearest mature conspecific tree. T-test of differences (mean distances) between species. n.s. = not significant = p>0,05, * = p<0,05, ** = p<0,01 and *** = p<0,001.

Species	Mean distance	Tested against	Mean distance	P	Sign.
Combretum apiculatum	1.26	*Dichrostachys cinerea*	4.06	0.0005	***
		Euclea spp.	1.85	0.0860	n.s.
		Grewia spp.	1.78	0.0210	*
		Spirostachys africana	1.55	0.1989	n.s.
Dichrostachys cinerea	4.06	*Euclea* spp.	1.85	0.0065	**
		Grewia spp.	1.78	0.0032	**
		Spirostachys africana	1.55	0.0019	**
Euclea spp.	1.85	*Grewia* spp.	1.78	0.4406	n.s.
		Spirostachys africana	1.55	0.2709	n.s.
Grewia spp.	1.78	*Spirostachys africana*	1.55	0.2531	n.s.

Discussion

Species diversity

Baseline study

The full inventory of the main plot appears to have captured a wide spectrum of the woody species in the area. Apart from the common species, many less frequent species were found, and considering the result of the Jack Knife test, which indicated that approximately 6 more species could be expected to exist in the study area, it could be assumed that most species in the study area were found.

The study area is quite species rich with its 43 identified woody species in an area of nearly 2 ha. The area contain fewer species than the really species rich biomes, such as the rainforests or the Mediterranean biomes (Crawley 1997), but considerably more than many areas at higher latitudes.

Seedling study

Approximately 35% of the species found in the baseline study were also found in the smaller scale seedling study. Species with high frequency in the baseline study are the ones also found in the seedling study. There may be several explanations to this. The observed pattern indicates, for example, that there are few rare species, which establish a high number of seedlings, or that seedlings of rare species have a higher mortality rate than more common species. One strongly influencing factor in this case is thought to be difference in inventory method and scale, e.g. the whole plot (1.96 ha) was surveyed in the baseline study while transects (total area 0.08 ha) were surveyed in the seedling study.

Identification problems have to be mentioned as one factor that could give raise to differences between the base-line study and the seedling study. Uncertainty regarding species exists in the seedling study for all four individuals called *Combretum hereroense*, and four of the *Acacia* spp. individuals, since they had just started to develop when found after the rains in March.

Height distribution

As the two surveys used in the present study did not consider the same height classes, it is difficult to compare the data sets. However, it is obvious that the base-line study, with a lowest registered tree height of 0.2 m, missed most of the young seedlings, as 93 % of the registered seedlings in the seedling study never reached that height during the time of the survey.

The obtained seedling density in the seedling study was 33.6 seedlings per 100 m^2, and if this figure is used to estimate the total number of seedlings in the main plot, the estimate will be 6586 seedlings. This corresponds to the total number of trees above 0.2 m in the base-line study on the whole main plot. The number of trees below 0.8 m (=highest seedling in seedling study) in the base-line study was 2119. The estimated total number of seedlings is more than twice as much as the number of trees between 0.2 - 0.8 m found during the base-line study. This difference may depend on that seedlings generally are smaller than 0.2 m when they are younger than 2 years. Hence, many seedlings were most likely not registered during the base-line study. Also to consider is the influence of a ”window of opportunity”, as might be seen when comparing the results of the seedling study with the results of Flyman’s study from 1999, which will be discussed later.

Spatial distribution

Baseline study

Both in the present study of main plot 2 and an earlier study of main plot 1 made by Sjögren (2000), an aggregated spatial pattern was dominant amongst the species found. In the present study six species were found not to differ from a random distribution pattern while Sjögren (2000) only found one species to be randomly distributed.

In his study, Sjögren (2000) found *Boscia foetida* being the only species with a random distribution, while in the present study *Boscia foetida* was found to grow significantly aggregated. This result may appear just because *B. foetida* occurs with few individuals. However, it cannot be ruled out that these results indicate that the factor/s influencing the distribution pattern of *Boscia foetida* and some other species vary between main plot 1 and 2 at Mokolodi Nature Reserve. It is not possible to say which these factors may be, since the studies are separated in time, and factors, such as rainfall, also vary with time.

Seedling study

All species and groups of species tested for spatial pattern grew aggregated within the surveyed transect. This aggregated pattern might be explained by the fact that seedlings tend to establish most successfully under or close to their adult parents, see further discussion under ”Seedling distribution in relation to large trees”. But of course also environmental factors such as water and nutrient availability, cover of field layer, trees and shrubs and competition with the herbaceous layer influence establishment of seedlings.

Seedling occurrence in relation to cover of herbs and standing litter

Woody seedlings and herbs may compete for the same resources (Belsky 1994, Scholes & Walker 1993, Stuart-Hill & Tainton, 1989), which, in turn, may affect seedling establishment in herb-covered areas. Stuart-Hill and Tainton (1989) showed that a healthy grass sward has a suppressive effect on woody plants. Standing litter as well as herbs and other woody species may also protect the seedlings from desiccation and high temperatures, while at the same time reduce light availability. Hence, cover of herbs and standing litter may act as a favourable factor as well as a suppressive factor.

Baseline study

In the baseline study, the occurrence of *Acacia tortilis* and *Euclea* spp. were negatively correlated to herb cover, which indicates that these species prefer to grow where there is less herb cover. This could imply that these species get out-competed by herbs, or that they manage to survive in more exposed locations than herbs, or that they have higher light requirement. *Combretum apiculatum* and *Grewia bicolor* were positively correlated to herb cover, which indicates that they prefer to grow where there are plenty of herbs. Maybe it is more profitable for them to grow with herbs because herbs give them shelter from harmful sunlight or hide them from herbivores, or it might simply depend on that they are as strong competitors as the herbs.

Seedling study

When looking at the five most numerous species in the seedling study there are significant differences in ground cover surrounding seedlings of different species. Both *Combretum apiculatum* and *Euclea* spp. grew surrounded by significantly more herbs and standing litter than the other three species. However, *Euclea* spp. was surrounded by significantly less live biomass than three of the four other species, and may hence be less competitive when it comes to the soil resources water and nutrients. *Dichrostachys cinerea* grew on spots with the lowest cover, as indicated by mean cover being significantly lower than that of the other species. But considering percentage of live biomass *Dichrostachys cinerea* was surrounded by a significantly higher percentage live biomass than any of the other four species. The cover around the remaining two species, *Grewia* spp. and *Spirostachys africana,* had intermediate values i.e. lower than *Combretum apiculatum* and *Euclea* spp., but higher than *Dichrostachys cinerea*. *Spirostachys africana* was surrounded by significantly less live biomass than all the other species and appears to have a similar strategy as *Euclea* spp.

Comparing the two studies

In the baseline study herb cover was measured as percentage coverage of subplots of 100 m^2, while in the seedling study ground cover (both herbs and standing litter) was measured as percentage of a circle of 0.5 m^2 with the seedling in the centre. The baseline study represents ground cover at a larger scale than the seedling study. Different types of tests were also used on data from the two studies, but with the same purpose, to find if cover influences the establishment and occurrence of woody species.

The results indicate that ground cover, of herbs and standing litter, is a factor affecting seedling establishment both at the large and the small scale. In some cases the two studies show similar results, for example *Euclea* spp. is shown to prefer little herb cover in both studies. In other cases the cover factor appears to affect species differently at the two scales. For example, *Dichrostachys cinerea* was surrounded by significantly higher percentage live biomass than the other species in the seedling study, but results of the baseline study show no correlation at all between herb cover and presence of the species. Hence, the results indicate a stronger influence of cover on the smaller scale than on the larger scale. This could depend on the fact that seedlings mainly are influenced by herbs and standing litter in the near surroundings. A healthy grass sward covering 50 % of an area of 100 m^2 may have no influence on seedlings/saplings growing in the other half of that area. Such effects of scale will to a large extent be depending on the spatial patterns of the vegetation.

Seedling distribution in relation to large trees

Seedling study

The mean distance to nearest mature conspecific was slightly longer in the present seedling study than in the similar study in 1999 by Flyman. Flyman reported the majority of the seedlings were found at a distance of 2 metres from nearest mature conspecific. In the present study the mean distance was 2.25 metres. It seems like the majority of seedlings that manage to establish grows in the near surrounding of its (possible) mother plant.

Also looking at mean distances per species, most species grew at a similar distance from nearest mature conspecific. Amongst the five most numerous species only *Dichrostachys cinerea* (4.06 m) showed a different pattern by growing significantly further away from nearest mature conspecific than all the others. Why this species grew further from potential mother plants cannot be explained by this study.

The conclusion that seedlings grow relatively close to its potential mother plant can partly be explained by the way different species disperse their seeds. Seeds may fall directly on the ground under the mother plant. Seed may be spread by means of animals that eat them. These animals, birds and mammals, often rest in or under the trees where they drop their dung, which is why seeds spread by animals also often end up under trees and bushes (Guevara et al. 1986). Trees/bushes also enhance the nutrient status of the soil surrounding their growth place (Vetaas, 1992). The richer nutrient content in soils surrounding large trees/bushes may be one of the reasons that seedlings have a tendency to grow near large trees/bushes. Two of the genus (Euclea and Grewia) that was studied in terms of distance to conspecific trees carry berries (Coates-Palgrave, 1983) and this indicates a seed dispersal facilitated by animals. This is true also for Dichrostachys cinerea, a species that has a cluster of pods, which are known to be eaten by animals. The other two species, Combretum apiculatum with a winged fruit and Spirostachys africana with a lobed capsule, have characteristics not indicative of animal seed dispersal. However, no clear patterns can be observed in the results in relation to type of seed dispersal and further studies are needed to properly evaluate the observed results.

Stuart-Hill and Tainton (1989) concluded that 1 m tall *A. karoo* trees influenced grass to a distance of approximately nine times their height. Considering that seedlings grow under the same conditions as grasses and herbs it might be assumed that the influence would act in a similar way on seedlings.

Seedling recruitment and the ”window of opportunity”

Seedling study

In the seedling study, number of seedlings per surface unit was unexpectedly high. In earlier studies number of seedlings in arid savannas have been reported to be generally low (Kiyiapi 1994, Flyman 1999). In the Flyman study, which was conducted in the same study area as the present study, a total of 58 seedlings of 10 species were found, including seedling sprouts and suckers. The average number of plants per surface area was reported to be 0.15 plants per m^2, i.e. 15 plants per 100 m^2. If only true seedlings are considered the number is approximately 5.7 seedlings per 100 m^2, as a total of 22 true seedlings were found. In the present study 33.6 seedlings per 100 m^2 were found, which is nearly six times as many as in the Flyman study.

Comparing the amount of rain during the different years, rainfall was higher in 2000/2001 than 1997/1998. Approximately 190 mm of rain fell during December 1997 - February 1998 (rainfall data in Flyman 1999), while February 2000 alone had as much as 341 mm of rain. The total annual rainfall of 1997 was 670 mm and in 1998 it was 588 mm, while 2000 had 823 mm and 2001 as much as 1084 mm (Mokolodi Newsletter, 2002). Additionally, compared to the long-term mean for the area, 538 mm, 2000/2001 was a period with unusually rich rainfall.

The difference in number of seedlings and the difference in amount of rain correspond. During the years with rich rainfalls, seedlings appear to germinate and establish easier and therefore in greater amounts than during the less rainy years. From these facts it is possible to confirm what was earlier stated by for example van der Valk (1992) and Veenendaal et al. (1996), i.e. that favorable sequences of rainfall actually creates ”windows of opportunity” for seedling recruitment.

Interestingly, seedlings found during the seedlings survey had an uneven age distribution, almost three times as many seedlings had established in 2000 as in 2001. However, this could simply depend on that the rainy period of 2001 had not ended when the survey took place. Since 2001 also turned out to be a year with a lot of rain, it is suspected that the effect of a ”window of opportunity” on seedling establishment described here would have been even more obvious if the survey would have stretched to the end of the rainy season of 2001 or early growing season the same year. A contributing reason could be that the heavy rains 2000 may have triggered germination in older seeds in a soil seed bank, which, subsequently, were not available the following year.

Comparing with the baseline study

The same conclusion as above might be assumed from a comparison to the baseline study. If considering small trees in the baseline study comparable to young trees/saplings, and then comparing the number of individuals per square metre found in that study with the same parameter in the seedling study, it is found to be twice as many individuals per square metre in the seedling study than in the baseline study.

Even though older trees are represented amongst the small trees found in the baseline study they present fewer individuals per square metre than found in the seedling study. This can, however, have different explanations. One might be that in the base-line study no individuals less than 0.2 m were included in the survey, but if also smaller plants would have been counted the number of saplings/young trees could hypothetically have reached the same numbers as in the seedling study. Despite this circumstance, it is still possible to associate the difference in number of seedlings/young trees to the rainy ”window of opportunity” of 2000.

Conclusions

This study showed that several factors affect regeneration and distribution pattern of woody savanna species. The distribution of seedlings and the habitat of their choice were found to vary between species. However, most species seems to have a growth pattern that is determined by one or a few key factors, of which one is suspected to be distance to mother plant or other large plant. This could be due to both regeneration strategies of the species and the protection and extra nutrients offered by the larger plants, or on the combination of these factors. When it comes to other physical factors, such as herbs and standing litter, the species have different strategies. Some species seems to benefit from the protection offered by herbs and litter while others seemingly cannot compete with the herbs and therefore grow where there are fewer herbs.

There appears to be a clear connection between the amount of rain and the amount of seedlings establishing and surviving in the dry savanna of Mokolodi Nature Reserve. As seen when comparing with both the base-line study and the earlier study by Flyman a lot more seedlings were found during the survey in 2001. Also the years of 2000 and 2001 had larger amounts of rain than did the years of the earlier studies. Sexual reproduction amongst woody savanna species may hence be said to be more successful during years with a lot of rain.

As savanna ecology is a very complex issue it is impossible, in a study like this, to sort out which factors influence different species and which factor is the most important one in determining establishment of woody plants. To better understand the mechanisms, more experimental work is needed.

Skoglund (1992) concluded that few studies have been made on the importance and function of sexual reproduction of plants in dry savannas, compared to similar studies in the temperate region. Considering the overall importance of sexual reproduction for species development and survival and the fact that it is difficult for woody species in dry savanna to reproduce sexually, there is much to study to get ”the whole picture” of this part of the savanna ecology.

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