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Multi-scale patterns and bush encroachment in an arid savanna with a shallow soil layer

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Abstract

Question: Bush encroachment (i.e. an increase in density of woody plants often unpalatable to domestic livestock) is a serious problem in many savannas and threatens the livelihood of many pastoralists. Can we derive a better understanding of the factors causing bush encroachment by investigating the scale dependency of patterns and processes in savannas?
Location: An arid savanna in the Khomas Hochland, Namibia.
Methods: Patterns of bush, grass, and soil nutrient distribution were surveyed on several scales along a rainfall gradient, with emphasis on intraspecific interactions within the dominant woody species, *Acacia reficiens*.
Results: Savannas can be interpreted as patch-dynamic systems where landscapes are composed of many patches (a few ha in size) in different states of transition between grassy and woody dominance.
Conclusions: In arid savannas, this patchiness is driven both by rainfall that is highly variable in space and time and by inter-tree competition. Within the paradigm of patch-dynamic savannas, bush encroachment is part of a cyclical succession between open savanna and woody dominance. The conversion from a patch of open savanna to a bush-encroached area is initiated by the spatial and temporal overlap of several (localized) rainfall events sufficient for *Acacia* germination and establishment. With time, growth and self-thinning will transform the bush-encroached area into a mature *Acacia* stand and eventually into open savanna again. Patchiness is sustained due to the local rarity (and patchiness) of rainfall sufficient for germination of woody plants as well as by plant-soil interactions.

Keywords: *Acacia*; Cyclic succession; Namibia; Patch-dynamics; Size-frequency distribution.

Nomenclature: Dyer (1975, 1976); Ross (1979); Gibbs-Russell et al. (1991).

Introduction

Bush encroachment is the proliferation of typically unpalatable woody plants, which suppress herbaceous production and, thus, grazing capacity (Smit et al. 1996). The causes of this widespread phenomenon (Archer et al. 2001) are poorly understood. The most widely accepted theory explaining bush encroachment is the two-layer soil-water hypothesis. Here, water is the limiting factor and it is assumed that grasses use only topsoil moisture and nutrients, while woody plants use subsoil resources (Walker et al. 1981). If grasses are removed by heavy grazing, grass roots will extract less water from the topsoil layer, allowing more water to percolate into the subsoil where it becomes available for woody plant growth. The predicted increase of shrub or tree abundance under heavy grazing has been observed in some studies (van Vegten 1983; Skarpe 1990; Perkins & Thomas 1993) but not all (Brown & Archer 1999). Two further observations suggest that soil partitioning and heavy grazing cannot be the sole cause of bush encroachment. First, Andersson (1856) reported bush encroachment during the 19th century in areas in Namibia that, according to historical records, had not been heavily grazed. Second, bush encroachment also occurs on soils too shallow to allow for root separation (e.g., this study). Overall, the causes of bush encroachment are poorly understood (Midgley & Bond 2001; Ward in press).

We hypothesize that bush encroachment is an emergence of a spatial pattern in vegetation distribution driven by natural conditions. In spatial savanna models, spatial patterns are typically created by fire or heterogeneous distribution of tree seeds (e.g. Jeltsch et al. 1996; Higgins et al. 2000), suggesting that tree-grass coexistence is mediated by spatial heterogeneity (see also Jeltsch et al. 1998). A first step in addressing this hypothesis is to assess the degree of heterogeneity in the spatial distribution of savanna vegetation. Once the spatial patterns in plant distribution have been revealed, the processes causing these patterns need to be identified and tested for their potential to promote tree-grass coexistence.

We describe vegetation and soil nutrient patterns in an arid savanna dominated by one woody species, with grass fuel loads too low to sustain fire and with a homogeneous, very shallow soil layer. We investigated patterns of tree distribution, grass distribution and, as a link between tree and grass patterns, soil nutrient distribution. Based on the spatial pattern of tree distribution, we deduced (spatio-) temporal tree dynamics using space-for-time substitution (Pickett 1989). Our study may serve as a starting point for understanding more complex systems.

In the following, we summarize the hypotheses underlying our investigations. Based on previous observations that trees appeared to be distributed in patches consisting of one or two tree sizes, we hypothesized that tree size-frequency distributions in small areas exhibit uni- and bimodality and are independent of average annual rainfall, within the limits set by our study area (80-170 mm/year: Ward et al. 2004). At the landscape scale, we expected the tree size-frequency distribution to follow a negative-exponentially declining function as it would be caused by temporally continuous recruitment, continuous growth (resulting in a close size-age relationship), and a constant mortality rate (cf. Adler 1998). Such a landscape pattern would be in agreement with a savanna (tree population) at equilibrium in the sense of constancy of the relative proportions of age classes on the landscape (Turner et al. 1993). For patches with unimodal, and possibly also for patches with bimodal tree size frequencies, the combination of the assumptions of continuous growth and constant mortality rate leads to the additional hypothesis that local density of trees decreases with increasing average tree size resulting from mortality due to interspecific competition (cf. Kenkel et al. 1997).

Patchiness in soil nutrient distribution is known to influence grass productivity (Belsky 1994). In grasslands with a homogeneous soil layer, soil nutrients and carbon are relatively evenly distributed (Schlesinger et al. 1996). However, woody plants in deserts and savannas accumulate nutrients and build 'islands of fertility' (Belsky 1994; Schlesinger et al. 1996). Thus, if soil nutrient distribution is patchy, we expect grasses to grow patchily as well. Furthermore, we were interested in determining if increased patchiness in soil nutrient distribution is a cyclic or a one-way process in our study system.

Methods

Study site

The study was conducted west of Windhoek on the western edge of the Khomas Hochland, Namibia, on three adjacent ranches: Quabis (7000 ha), Tweespruit (5000 ha) and Changans (20 000 ha) situated between two parallel mountain ranges. There is a shallow layer of sandy soil overlying Swakop schist from the Damara sequence (Van der Merwe 1983). Thus, roots of both woody and grassy plants are confined to a thin soil layer (< 5 – 15 cm deep).

The most abundant grasses are *Stipagrostis uniplumis*, *S. obtusa*, *S. ciliata*, *Eragrostis nindesis*, *E. annulata*, *E. desvauxii* and *Entoplocamia aristulata*. Woody plants in the area are restricted to *Acacia reficiens*, *A. senegal* and *Boscia foetida*, with *A. reficiens* being by far the most abundant and forming bush-encroached patches. As indices of tree size, we use tree height and canopy diameter.

Rainfall, longitude, latitude, altitude

To be able to analyse the influence of rainfall on tree distribution, rainfall was measured over three years (October 1995 - September 1998) in 14 rain gauges across the study site on a monthly basis (see Ward et al. 2004 for a map). Rain falls in summer (January - April) and is very patchy (Ward et al. 2004). There is no significant correlation between similarity in rainfall and distance between pairs of rain gauges (distances ranging from about 1.5 km to ca. 25 km). There is a north-south rainfall gradient across the three ranches from 80 mm/year on Changans to 170 mm/year on Quabis. In order to determine the best proxy variable for rainfall, we conducted a best subsets regression of the mean annual rainfall vs. longitude, latitude, and altitude using the magnitude of r^2 as the best criterion.

Size frequency distributions

Acacias in our study area commonly appear in patches. We measured tree sizes along line transects in 53 patches distributed across the three ranches in areas with bush encroachment. On each transect, the height and species of up to 60 trees transecting the line were measured. Tree heights were measured to the nearest 0.1 m and trees taller than 3 m were classified as 3 m in height. Trees were mainly *A. reficiens* (88%) and *A. senegal* (11%). To investigate the influence of average rainfall on central tendency in tree height, we calculated average and modal tree height for each transect. For the calculation of the mode, the cumulative size 'class' 3.0 m was excluded. This did not introduce a bias as the nine cases in which size class 3.0 m was the most commonly occurring value were spread out over the entire range of latitudes.

To test the hypothesis that tree size distributions in small areas are uni- and bimodal, we analysed the tree size-frequency distributions of the transects with incremental polynomial regression using polynomials from the second to the fourth order. For this purpose, we divided our data into classes of a roughly logarithmic scale with the following class boundaries: 0, 0.2, 0.4, 0.6, 0.8, 1, 1.4, 1.8, 2.5, 3 and ≥ 3 m. We chose these intervals to minimize the distribution of even-aged plants into several size classes, assuming that variance in tree size is greater for older plants. Two further classes, that always contained zero trees, were added at both ends. Due to these empty classes, we found that bimodal distributions were best described by fourth-order polynomials, while second- or third-order polynomials better described unimodal distributions. Agreement of this automated classification method with visual classification was very good (results not shown).

As a non-parametric measure of variability (or inequality) in tree sizes, we used the Gini coefficient (Glasser 1962), which equals 0 when all trees are equal in size and approaches unity when the tree size hierarchy is strongly unequal. We complemented the Gini coefficient with the Lorenz Asymmetry Coefficient (Damgaard & Weiner 2000). If the coefficient is greater (or smaller) than 1, the inequality is due to many small (some large) individuals. In this case, we consider the distribution ‘asymmetric due to small trees’ (or ‘asymmetric due to large trees’).

We also report the overall size frequency distribution of a different study laid out to measure tree density. Two transects, one on Quabis and one on Changans, were investigated using the point-centred quarter distance sampling method (Krebs 1989). A point was laid out every 25 m along a 400 m-long transect. Two randomly-selected transects were run. The mean canopy diameter of the nearest tree in each of four quadrants was measured at each point.

Tree size and nearest neighbour distance

Plants in semi-arid and arid areas are often water-limited and therefore, we expect inter-tree competition to be severe. If this is true, inter-tree competition should determine density and pattern of woody plant distribution across savanna landscapes. For example, trees in patches with even-sized stands will exhibit increasing nearest-neighbour distances with increasing tree size. To test this idea, the canopy diameter and the distance to the nearest neighbour was measured on Quabis for *A. reficiens* trees in 16 even-sized stands (5 trees in each stand), 8 with small trees (< 1.5 m in canopy diameter) and 8 with large trees (> 3.5 m).

Neighbour removal

To investigate the effect of inter-tree competition in bush-encroached plots on tree growth, we conducted a neighbour removal experiment with *A. reficiens* on Quabis in March 1997: Nine different bush-encroached patches were selected. In each patch, two similar-sized bushes were selected within 5 m of each other. For one of these, we removed all the neighbouring *Acacia* trees within a 1.5 m radius. We measured height and canopy size of the focal trees in March 1997, September 1998, and April 2000.

Density and size distribution of bushes in encroached patches

To measure how densely small bushes are packed and thus get an idea of the intensity of competition among them, we selected 12 plots, each 10 m × 10 m in size, that were densely encroached by small *A. reficiens*. In September 1995, we measured the canopy diameter of all bushes to obtain size distribution and overall density in each plot. The plots incorporated six pairs with similar tree size and densities. One plot in each pair was cut down for a different experiment. Trees in the remaining six plots were re-measured in April 2000. Given the unknown identity of the plants, all woody plants were included in our analyses (*A. reficiens* constituted 92.5% and 96.2% of all woody plants in 1995 and 2000).

Spatial extent of patches

Trees appeared to be distributed in patches consisting of one or two tree sizes. In order to obtain a qualitative estimate of the spatial extent of these patches, we measured patch size as the diameter of the patch to the nearest 100 m from a vehicle. For each patch, we estimated by eye the one or two typical heights of the trees to the nearest 50 cm.

Acacia germination after grass clearing

Reducing the competitive ability of the grass layer (e.g. by heavy grazing) is thought to lead to germination of woody plants (e.g. Skarpe 1992). Therefore, starting in September 1995, we removed all grass in eight blocks of three 100 m^2 plots without woody plants across the entire study area on a seasonal basis (one plot in each block was cut near the end of the dry season, i.e. September, and one was cut in the wet season, March), for three years. Over this period, we determined the number of newly germinated woody seedlings in March.

Patchiness in soil nutrients

In 1997, we measured the amount of soil organic carbon and used a bioassay with *Raphanus sativa* to measure overall nutrient value of the soils (see Ward et al. 1998) beneath 15 live trees, 15 dead trees, and in 15 ‘open’ areas between trees. ‘Open’ areas were at least twice the diameter of a canopy of a large tree. *R. sativa* was chosen for the bioassay because of its wide tolerance and preference for soil type. Thus, differences in growth are unlikely to be due to specific preferences but to lower overall soil nutrient availability. The bioassay was performed in the greenhouse with soils from woody patches (under live and dead trees) and the open. Soil sample depth was 5 - 10 cm and all trees were ca. 2 m in height. The dead trees had been cut down by one of the ranchers in the mid-1970s (and left *in situ*) in an attempt at bush clearing. Furthermore, to test whether soil nutrients increase with time under trees, we compared total nitrogen, organic carbon, and phosphorus in soils beneath 15 large trees (ca. 3 m in height) and 15 small trees (less than 1 m in height). Finally, we measured the spatial distribution of organic carbon in 112 adjacent plots arranged in a 9 m × 12 m rectangle in an encroached and a non-encroached area on Quabis, following Schlesinger et al. (1996). We scraped away the top 5 cm of soil and took three random samples in each plot and lumped them. Organic carbon was measured by standard Walkley-Black protocol (Nelson & Sommers 1996). As a measure of patchiness, we used Green's index of patchiness, where G.I. = ((variance/mean) – 1) / (N – 1) (Ludwig & Reynolds 1988).

Grass patchiness

To investigate our hypothesis that grass productivity is patchy, in April 1998 we measured grass height in 12 unencroached plots throughout the study area using a linear point-frequency frame with 10 pins equally spaced in 10 cm intervals (Ward et al. 2004). In each plot, we randomly placed the frame 10 times and calculated the coefficient of variation in grass height.

Furthermore, we compared the coefficient of variation in grass height at 50 randomly selected points each in a non-encroached valley (Zebra Post) and in three bush-encroached areas on Quabis. In March 1998, we measured the coefficient of variation in grass height in six bush-cleared and six bush-encroached control plots (cf. Density and size distribution of bushes in encroached patches).

Table 1. Indices describing tree density (*Density*) and distribution of tree heights along 53 transects across the study area. *Mean*, *c.v.*, *Skew*, *Gini*, *Lorenz*: Mean tree height, coefficient of variation, skewness, kurtosis, Gini coefficient, and Lorenz asymmetry of tree heights. All indices are given for the overall size frequency distribution of all tree species observed (*All trees*), for the overall distribution of *Acacia reficiens* only, and for the 1st., 2nd., and 3rd. quartile of the separate size distributions along the transects (considering *A. reficiens* only).

	Density	Mean	C.V.	Skew	Gini	Lorenz
All trees	0.16 /m	0.83 m	98.7	1.56	0.49	1.03
A. reficiens	0.14 /m	0.80m	100.6	1.63	0.49	1.08
1st. quartile	0.10 /m	0.54m	60.1	0.68	0.29	0.81
2nd. quartile	0.17 /m	0.72m	76.6	1.33	0.35	0.97
3rd. quartile	0.30 /m	0.98m	99.0	2.11	0.45	1.06

Results

General observations (rainfall and size frequency distributions)

Most of the spatial variation in the mean annual rainfall gradient can be explained by the latitude of the rain station (r^2 = 0.63). Mean annual rainfall Pr (mm.a^{-1}) at any location can be estimated based on latitude L (Pr = 338.49 L + 7867.1), resulting in a gradient from 39 mm.a^{-1} to 164 mm.a^{-1} across the 14 rain gauges and within the three years investigated. The total average rainfall across the area was 60.3 mm.a^{-1}, 128.0 mm.a^{-1}, and 79.3mm.a^{-1} in 1995/96, 96/97, and 97/98 (from October through September), respectively.

A total of 2825 trees was measured (Table 1). On average, transects were 325 m in length (minimum: 50 m, maximum: 1200 m, extent of the study area along the rainfall gradient: ca. 15 km). Thus, average rainfall within transects is virtually constant. All results in the remainder of this section refer to separate analyses of all transects and to *A. reficiens* only. Tree density increased as rainfall increased (Fig. 1a). It appears that there is a maximum attainable density depending on the mean annual precipitation, which was not reached in most transects (Fig. 1a).

Mode and mean tree height were not correlated with mean annual precipitation (linear regression on log transformed mode and mean tree height: Mode: $r^2 = 0.046$, $P = 0.12$, $1–\beta = 0.34$; Mean: $r^2 = 0.028$, $P = 0.23$, $1–\beta = 0.22$). The observed modes ranged from 0.1 m to 2.6 m. The Gini coefficient increases very slightly with increasing precipitation ($y = 0.0023\,x + 0.13$; $r^2 = 0.09$; $F = 4.81$; $P = 0.033$; Fig. 1b), indicating that inequality in tree sizes is independent of rainfall.

In agreement with our hypothesis that local tree density is inversely related to tree size, we found mean tree height to be related to tree density in an L-shaped fashion (Fig. 2), independently of uni- and bimodality. At high tree densities (≥ 0.5 trees/m) only small mean tree heights (≤ 0.5 m), were observed (bush-encroachment) while the greatest mean tree heights (> 1.2 m) occur at low densities (< 0.2 trees/m; open savanna ; Fig. 2).

Modality of local size distributions

63% and 37% of the transect-tree size-frequency distributions were bimodal and unimodal, respectively. Both bi- and unimodality were equally spread across the entire rainfall gradient investigated; the distributions of latitudes of bimodal and unimodal transects had quartiles identical to the second decimal place: 1. –22.95; 2. –22.91; 3. –22.88; while minimum and maximum values were only slightly different (Unimodal: Min: –22.87; Max: –23.04; bimodal: Min:–22.86; Max: –23.01). The modes of unimodal distributions ranged between 0.2 m

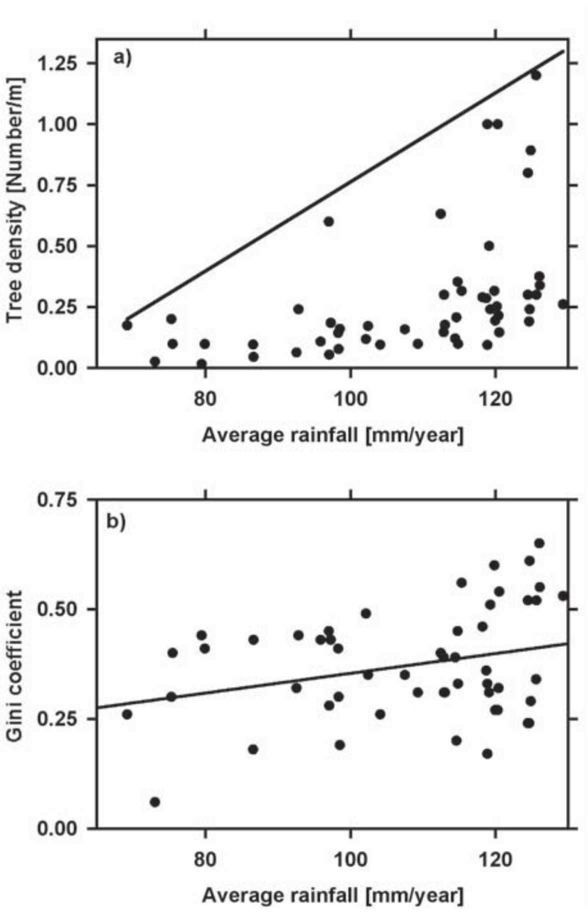

Fig. 1. Density of *Acacia reficiens* (**a**), and Gini coefficient (**b**) vs. mean annual rainfall of the transects. The upper boundary (black line) given in (**a**) follows the equation: $y = 0.018\ x - 1.08$.

and 1.20 m, but the modes of bimodal size frequency distributions are distributed across all tree sizes (Fig. 3). Also, modes of bimodal size distributions are asymmetric small individuals always smaller than 0.5 m (Fig. 3, closed symbols).

The size inequality of unimodal distributions was always relatively small (Gini ≤ 0.4, Fig. 3a) while the Gini coefficient of bimodal distributions may reach 0.65 (Fig. 3b). These differences were significant for distributions that are asymmetric due to small individuals ($T_{17,4} = 17.5$, $P = 0.02$; closed symbols in Fig. 3). In this case, the Gini coefficient tends to be larger for bimodal than unimodal distributions. The size inequality of bimodal distributions asymmetric due to large individuals decreases with increasing mode of the tree size distribution (Fig. 3b, open symbols).

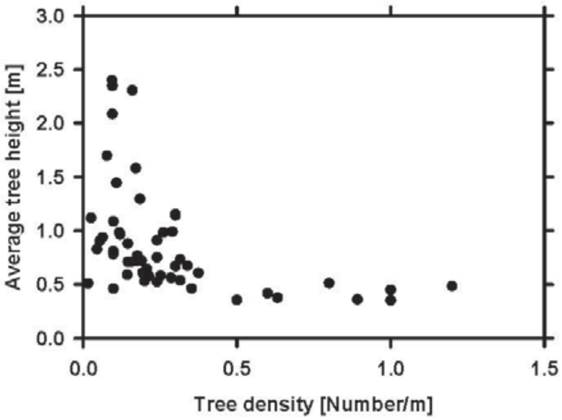

Fig. 2. Mean height vs. tree density of *Acacia reficiens* observed in the 53 transects.

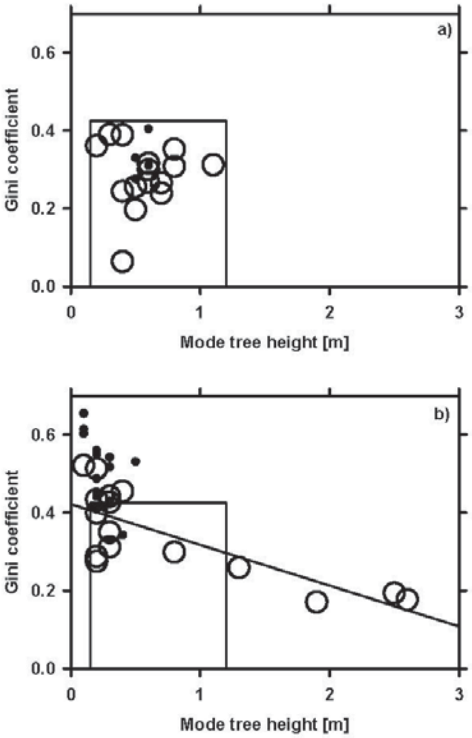

Fig. 3. Size inequality as measured by the Gini coefficient vs. mode shown separately for (**a**) unimodal and (**b**) bimodal tree size frequency distributions observed in the transects. Open symbols: Lorenz asymmetry < 1, i.e., asymmetry due to large trees, closed symbols: Lorenz asymmetry > 1, i.e., asymmetry due to small trees. The rectangular outline circumscribes data points of unimodal size distributions for easier comparison between unimodal and bimodal distributions. The trend line in (**b**) is based on distributions with Lorenz asymmetry <1 only ($y = 0.42 - 0.11\ x$; $r^2 = 0.60$; $F = 21.34$; $P < 0.001$).

Overall size frequency distribution

A regression showed that the size-frequency distributions declined exponentially ($y = 596.4.e^{-1.28}$; $N = 2335$; $r^2 = 0.88$; $P < 0.001$; Fig. 4, largest (cumulative) size class omitted). The fit improves considerably when considering trees > 0.2 m and ≤ 1.6 m only: $y = 1417.e^{-2.24}$; $N = 1547$; $r^2 = 0.99$; $P = 0.001$. Interestingly, tree sizes on the two transects laid out to measure tree density showed an almost perfectly negative exponential decline ($y = 46.351.e^{-0.549}$, $P < 0.001$). Maximum canopy diameter was 7.6 m (mean ± SE = 1.96 ± 0.208). Thus, on a landscape scale, tree size-frequency distributions decline about exponentially.

Comparing size-frequency distribution within and among transects

The medians of the tree densities and average tree heights observed in the single transects are similar to the average of these properties calculated across all transects (Table 1). However, both the coefficient of variation and the Gini coefficient calculated across all trees are greater than at least 75% of the coefficients calculated for single transects. This is because, at the landscape scale, the distribution is composed of cohorts of all ages while in single patches just one or two cohorts are present. Size inequality in patches with two very different cohorts can be as high or even higher than inequality of a monotonously-declining size-frequency distribution (Fig. 3b). However, many bimodal and all unimodal distributions have more equal sizes (Fig. 3).

As expected from the negative exponential overall size-frequency distribution, the Lorenz asymmetry is greater than 1, i.e., the distribution is asymmetric due to small trees. Most (at least 75%) single transects have a Lorenz asymmetry smaller than the asymmetry calculated for all trees together, while the skewness observed at the landscape level (1.63) is representative of the median skewness measured for the transects (Table 1). This can be understood when considering that most distributions with one mode at small and one at large tree sizes will be skewed to the right because, due to mortality, the frequency of the mode at large sizes is likely to be the smaller one. However, such a distribution can still be asymmetric due to large trees.

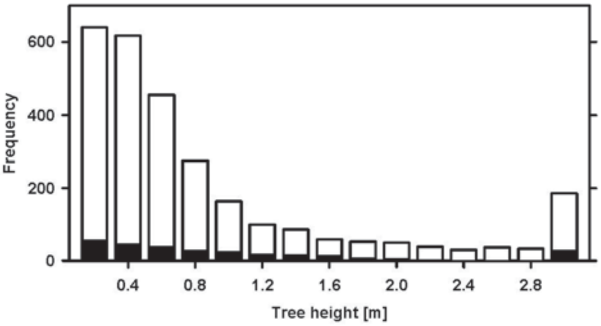

Fig. 4. Overall size frequency distribution of trees measured along 53 transects across the study area. Black bars: *Acacia senegal* and *Boscia foetida*; white bars: *A. reficiens*.

Tree size and nearest-neighbour distance

Distance to nearest neighbour increases significantly with canopy diameter ($r^2 = 0.87$, $F = 95.00$, $P < 0.001$, log-log scale; Ward in press). The regression line is not significantly different from the line indicating equality of nearest-neighbour distance and canopy diameter (Mann-Whitney Rank sum test: $T_{16,16} = 248.50$; $p = 0.57$). Mean nearest-neighbour distance divided by canopy size of individual trees is 1.12 for both small and large trees. However, the median of these ratios differs considerably: 0.68 for small and 1.03 for large trees. The range is much larger for small (7.2) than for large (2.0) trees.

Neighbour removal

Mean ± 1 SE of the initial canopy diameter was 23.50 ± 2.86 cm and 23.61 ± 2.90 cm for test and control trees, respectively. From 1997 to 1998, test trees grew significantly faster than control trees (increase in average canopy diameter = 25.31% ± 9.60 (test), 4.52% ± 8.26 (control), paired *t*-test: $t = 2.151$; $p = 0.032$). By 2000, one pair of trees had to be excluded from our analysis due to experimental problems. From 1998 to 2000, four test and four control trees shrank, most were even smaller than in 1997. Overall, from 1998 to 2000, test trees grew more slowly than control trees. However, this was not significant and the power of the test was very low (increase in average canopy diameter = 1.84% ± 9.86 (test), 18.54% ± 22.27 (control), paired *t*-test: $t = –0.765$, $P = 0.469$, $1 – \beta = 0.05$).

Density and size distribution of bushes in encroached patches

The number of bushes in the bush-encroached plots ranged in 1995 from about 50 to 250, while the mean canopy diameter in these plots ranged from about 50 cm to 90 cm. Within the five years between measurements, 14 - 50% of the trees died and the surviving trees grew little (the two extremes of average growth within the six plots were –3.4 cm and 8.1 cm growth). Average size inequality of the plots was 0.28 in 1995 and 0.30 in 2000. None of the changes in these properties (i.e., mortality, growth, and change in size inequality) were significantly correlated with the size and number of trees in 1995 or with each other except for mortality and number of trees in 1995 ($r = 0.818$, $P = 0.047$). Thus the number of bushes N in a plot was negatively related to the mean bush size CD in this plot ($N = 355.41 – 3.18\, CD$; $r^2 = 0.53$, $P = 0.007$).

Spatial extent of patches

A total of 68 patches was measured. On average, patches were 278 m in length (min: 50 m, max: 600 m) and exhibited one (64 patches) or two (4 patches) typical tree heights. A histogram of all tree heights shows a unimodal distribution with a maximum frequency at 3 m (18 patches) and minimum frequencies at 5 m (6 patches) and 0.5 m (5 patches). Comparing this to the more detailed height measurements, we conclude that small trees were mostly overlooked from the vehicle.

Acacia germination after grass clearing

There was no germination of woody plants in any of the grass removal plots over the three years.

Patchiness in soil nutrients

Soil organic carbon content under dead trees was significantly greater than under live trees or in the open areas between trees (Table 2a). Also, soil organic carbon content was significantly greater under large live trees than small live trees (Table 2b). In the bioassay, dry mass was significantly higher under live trees than in open areas (Table 2a). Soil nitrogen content under large trees was about twice as high as under small trees (Table 2b). However, there was no significant difference in soil phosphorus between large and small trees (Table 2b). Mean patchiness (Green's index) of organic carbon in non-encroached and encroached plots was close to zero (0.008 and 0.002 respectively), indicating a random distribution of organic carbon at these local scales (1 = maximum clumping) (Ludwig & Reynolds 1988).

Grass patchiness

Grass distribution on the ranches is very patchy, both between sites as well as within sites. In March 1998, mean ± SE grass height in unencroached plots on Quabis ranch was 6.16 ± 1.29 cm and on encroached plots it was 0.22 ± 0.07 cm. The mean ± SE of the coefficient of variation in grass height among plots was 1.129 ± 0.099 ($N = 12$ plots). The coefficient of variation in grass height at 50 randomly-selected points in a non-encroached valley (Zebra post, c.v. = 0.856) was significantly lower than in three encroached areas investigated on Quabis ranch (c.v. ranged from 1.092 to 1.215; $F = 96.584$, $P = 0.0001$, error df = 198). In the encroached areas, we found that the mean coefficient of variation in grass height in bush-cleared plots (1.381 ± 0.130 SE) in March 1998 was lower than in the adjacent control plots (1.859 ± 0.240) in all six pairs of plots ($F = 4.178$, $P = 0.046$).

Discussion

On a landscape scale, our savanna is at equilibrium. For the trees, this can be concluded from the overall negative exponential size frequency-tree distribution reflecting constant birth and death rates of individuals in stable (model) systems at equilibrium (Adler 1998). On a patch scale, the picture is different. Patches tend to be composed of even-sized trees (see also Skarpe 1991). It is often difficult to relate tree size and age because fire and heavy grazing often keep savanna trees within the 'topkill' zone or within the reach of browsers for many years (Midgley & Bond 2001). However, in our study site, fire is virtually absent and grazing is not especially heavy and therefore one can assume a correlation between tree size and age. Thus, there

Table 2. Soil nutrients under live trees, and dead trees, in the open areas between trees (**a**), and under small and large live trees (**b**). Explanations of measurements taken: C = soil organic carbon; N: total soil nitrogen; P: soil phosphorus: Bioassay: dry mass. The letters A, B, and AB, and the bottom rows summarize statistical results on differences among sites and Scheffe's *post hoc* test (Scheffe). A-A indicates that the *p*-value for measurements that are not significantly different, while A-B indicates that the *p*-values differ significantly between measurements. The corresponding *p*-values are given at the bottom row of the table. The live trees/dead trees/open and small live trees large live trees comparisons were conducted at different sites, explaining the low soil organic carbon content of the former measurements. Further details on the experiments are given in the text.

(a)	C (%)			Bioassay (g)		
	Mean	S.E.	Scheffe	Mean	S.E.	Scheffe
Live trees	0.421	0.130	A	0.189	0.012	A
Dead trees	1.128	0.140	B	0.157	0.015	AB
Open	0.262	0.026	A	0.129	0.013	B
	$F=13.376$		A-B: $p < 0.001$	$F = 5.020$		A-B: $p = 0.002$
	$p < 0.001$		A-A: $p = 0.240$	$p = 0.011$		A-A: $p = 0.109$
	$df = 42$			$df = 42$		B-B: $p = 0.174$

(b)	C (%)		N (ppm)		(P (mg/kg)	
	Mean	S.E.	Mean	S.E.	Mean	S.E.
Small live trees	1.602	0.051 A	543.9	48.344 A	20.4	1.267 A
Large live trees	2.434	0.164 B	965.6	150.949 B	18.2	1.236 A
	$t = 4.861$		$t = 2.661$		$t = 1.243$	
	$p = 0.0001$		$p = 0.022$		$p = 0.230$	
	$df = 28$		$df = 28$		$df = 28$	

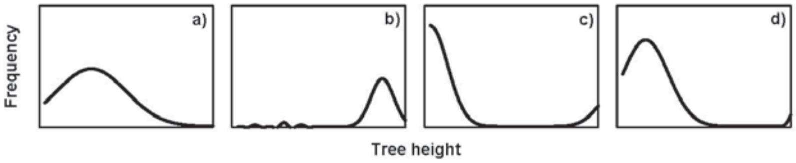

Fig. 5. Conceptual model of the development of tree size frequency distribution over time in patches. See Discussion for description.

are patches of trees, each composed of very few cohorts. Replacing time by location, we can observe the following cycle occurring in single patches: The unimodal distributions in Fig. 3a represent a cohort of relatively small trees. From the non-zero Gini coefficient we see that the distribution is spread around its mean, which can be explained by different growth rates of single plants. An idealized size-frequency distribution of that type is depicted in Fig. 5a. Of course, observed distributions are not as smooth and the details of the distribution will determine whether the Lorenz asymmetry is greater or smaller than 1. With time, the distribution shifts towards greater tree sizes. However, we did not observe any distributions showing both a peak at large tree size and an absence of small trees. What we observed were a few small trees interspersed among the large trees, leading to a bimodal distribution (Fig. 5b) with Lorenz asymmetry below 1 (Fig. 3b, open symbols at large modes). These small trees could belong to a neighbouring patch, or represent regeneration of the tree population in the form of unusual germination. The Gini coefficient of these distributions is rather low because most trees have more or less the same large size. By the time the large trees have become even larger and have almost died out, another bush encroachment event has taken place (Fig. 5c, Fig. 3b small modes). In this case, size inequality (Gini coefficient) can be quite high, because there are both many small trees and a relatively large number of large trees. The large number of small bushes leads to a Lorenz asymmetry coefficient above 1.0. Thus, distributions depicted in Fig. 5c are represented by the closed symbols at high values of the Gini coefficient in Fig. 3b. With time, the mode of the small trees moves towards larger tree sizes and the second mode becomes smaller and smaller (Fig. 5d, Fig. 3b smaller Gini coefficients at small modes irrespective of Lorenz asymmetry) eventually leading to a unimodal distribution (Fig. 5a).

Our results show that both bimodal and unimodal distributions occur across the rainfall gradient and that measures of central tendency are spread across the entire range of tree sizes independent of local rainfall intensity. Thus, the described cycle is the same across the entire rainfall gradient. This is not to say that precipitation would have no effect. Rather, we found that tree density increases with precipitation (Fig. 1a) (see also Smith & Goodman 1986 for this pattern in another *Acacia* species).

We also attribute to the rainfall regime the differences in response to neighbour removal between years. Due to the high rainfall in 1997/1998, test trees could take advantage of the reduced competition and grow faster than control trees. However, the lower rainfall in the next two seasons did not stimulate significant growth; in fact several trees shrank, probably due to trampling by herbivores. Therefore, in these two years, we could not find any differences in growth rate between the two groups.

Further evidence for inter-tree competition is provided by the relationship between nearest neighbour distance and tree size (see also Gutierrez & Fuentes 1979; Smith & Walker 1983; Smith & Goodman 1986; Ward in press), indicating that competition is a major determinant of spatial tree distribution at all life stages. If a decrease in tree density would be due to tree mortality independent of the location of neighbours, nearest-neighbour distances would span a large range of values. Even though our analysis was not based on combined canopy cover but on size of the focal tree, these two measures are practically equivalent in our study because the nearest neighbour is very likely to be of similar size to the focal tree (cf. Size frequency distributions).

Inter-tree competition is not sufficient to explain conversion of a densely-vegetated patch to open savanna. A further condition is that no new recruitment occurs, leading to a woodland with mixed age structure before the open savanna patch has developed. The most reasonable factor limiting *Acacia* germination is rainfall. If the frequency of rainfall seasons leading to *Acacia* germination is small compared to the longevity of these trees, there is a high probability of mature tree stands reverting back to open savanna before a germination event. Rainfall can also explain why bush encroachment occurs in patches. In arid and semi-arid savannas, seeds of woody plants need relatively high soil moisture content over a prolonged period to germinate and establish (Obeid & Seif El Din 1971; O'Connor 1995; Wilson & Witkowski 1998). Thus, several rain events in a single year are necessary. However, rainfall in savanna regions is often very patchily distributed, both in time and space (Sharon 1972; Ward et al. 2004). The spatial overlap of several rainfall events in a single year is a rare occurrence that, when it occurs, provides the opportunity for germination of woody plants within a small area in the order of several hectares. The rareness of such events increases the probability of mature tree stands reverting to open savanna before germination occurs.

Patchiness can also be observed at the scale of single trees (= within-patch dynamics). This study indicates that: (a) soil nutrient status under trees is greater than in open areas; (b) nutrients accumulate with time, and (c) soil nutrient status is retained after senescence, thereby ensuring increased soil fertility in the long term (cf. Facelli & Brock 2000). The increased soil nutrient status under trees is likely due to the far higher biomass of trees than grass (about 10-15 fold), leading to greater levels of organic carbon as the trees senesce. This patchiness persists long after tree death (at least 20 years in this study) as the dead plant material is incorporated into the soil. Ultimately, grasses re-colonize and nutrients drop again due to wind removal of dead grass material. However, in bush-encroached situations, the trees reduce wind-induced removal considerably. Also, because the trees are largely unpalatable to cattle, nutrients are not removed from the system and re-deposited elsewhere (e.g. around watering points), as is the case in unencroached ranching systems. Patchiness in African savannas has often been measured at the scale of single trees (Stuart-Hill et al. 1987; Belsky 1994). Unfortunately, such studies have not attempted to scale up their observations to the patch or landscape scale to determine whether the positive effects of trees also function at these larger scales and whether the dynamics at the larger scales work in the same cyclical manner. Thus, average grass height is suppressed in encroached plots and patchiness in grass growth within a given site increases with bush encroachment. Once bush encroachment disappears, this patchiness disappears and grass height tends to be uniform, i.e., in contrast to soil nutrients, grass patchiness is not retained. However, both forms of patchiness are likely to be cyclic because in patch-dynamic savannas each location is likely to have a history of having been a bush-encroached as well as an open savanna patch. Thus, increased patchiness in grass growth due to bush encroachment disappears on a rather fast time scale while soil nutrients take longer to return to the pattern observed in the grass within open-savanna patches.

Schlesinger et al. (1996) suggested that trees concentrate nutrients under their canopies via the depletion of nutrients in non-encroached areas – see also Stock et al. (1999). This would lead to a characteristic patchiness reflecting the size of the bushes within bush-encroached patches. However, given the random distribution of soil nutrients in both encroached and unencroached plots, there is no evidence that this patchiness occurs in our system. Once initiated, bush encroachment seems to lead to an improvement in soil quality and an increase in soil patchiness at a scale resembling patches of bush encroachment. This patchiness may add a positive feedback loop that sustains the patch dynamics of such savannas (Reynolds et al. 1999).

Conclusions

Patterns unique to any range of scales have unique causes and biological consequences. The key to understanding them lies in the elucidation of mechanisms underlying observed patterns (Levin 1992). Our field observations are in agreement with the concept of hierarchical patch dynamics (O'Neill et al. 1986; Wu & Loucks 1995).

We believe that our savanna is not merely patchy in space; rather it appears highly dynamic, with tree patches cycling between bush encroachment, mature tree stands, and open savanna. These cycles are driven by inter-tree competition and patchy rainfall. Soil nutrients track the tree patches; soil nutrient status increases with time in bush-encroached patches and decreases long after the last representatives of that cohort have died. The concept of hierarchical patch-dynamic systems appears appropriate for this savanna (see also the reviews of savanna ecology by Skarpe 1992 and Scholes & Archer 1997).

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