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Patterns of harvesting foliage and bark from the multipurpose tree *Khaya senegalensis* in Benin: Variation across ecological regions and its impacts on population structure

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ABSTRACT

Non-timber forest products (NTFPs) represent important resources for millions of communities worldwide. Concerns over NTFP overexploitation has led to a growing number of studies on the ecological impacts of harvest. Few studies however, have addressed species harvested for multiple parts or investigated how spatial variation affects harvest patterns and their impacts. We documented rates and patterns of pruning and debarking and their impacts on density and population structure, for 12 populations of the multiuse tree, *Khaya senegalensis* (Meliaceae) in two ecological regions (Sudano-Guinean versus Sudanian) of Benin, West Africa. Half of the populations had low or no harvest and half were highly harvested. Patterns of pruning and debarking were size-specific, with harvesters tending to prefer larger trees. Foliage harvest pressures were very high across both regions, with >70% of trees harvested for 100% of their crowns. A significantly greater proportion of trees were harvested for foliage in the wetter Sudano-Guinean region than in Sudanian region. The reverse was true for the proportion of foliage and bark-harvested per tree. In the Sudano-Guinean region, high harvest populations had significantly lower densities of seedlings and saplings than low harvest populations. The size-class distribution coefficient of skewness was significantly correlated with rainfall, habitat, and soil type. Variation in harvesting patterns and their ecological impacts can be explained in large part by differences in water availability between the two regions. Effective conservation plans for *K. senegalensis* require close consideration of the environmental and land-use context in which populations occur.

1. Introduction

Non-timber forest products (NTFPs) play important roles in the livelihoods of hundreds of millions of rural and urban peoples across the globe (e.g., Ganesan, 1993; Bernal, 1998; Shackleton et al., 2002; Griffiths et al., 2003; Emanuel et al., 2005). For instance, many NTFP species with medicinal value are harvested for local healthcare needs as well as for sale in national and international industries (Stewart, 2003; Hamilton, 2004). However, the growing demand for NTFPs used for both subsistence uses and commercial trade (Hamilton, 2004; Botha et al., 2004a) has, in many cases, led to unsustainable management of forest resources (e.g., Cunningham and Mbenkum, 1993; Peres et al., 2003; Botha et al., 2004b).

The most direct ecological consequence of NTFP extraction is alteration of the rates of survival, growth and reproduction of harvested individuals. These changes can in turn affect the structure and dynamics of harvested populations (Peres et al., 2003; Ticktin, 2004). For example, repeated harvesting of *Waburgia salutaris* individuals in South Africa

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results in decreased basal diameter and height, and higher rates of fungal attack and mortality (Botha et al., 2004b). The impacts of NTFP harvest are also highly dependent on harvest patterns, and on size-specific harvest preferences (Nantel et al., 1996; Ticktin et al., 2002; Shackleton et al., 2005).

Although a growing number of studies have assessed the demographic impacts of NTFPs harvest (e.g., Pinard, 1993; Nantel et al., 1996; Bernal, 1998; Soehartono and Newton, 2001; Ticktin et al., 2002; Peres et al., 2003; Emanuel et al., 2005), very few have assessed spatial variation in harvest patterns or their impacts. This is important because NTFPs are often harvested in the context of other kinds of disturbances such as fire, logging, or grazing, and their responses to harvest may be affected by these factors (Sinha and Brault, 2005; Ticktin, 2005). Similarly, harvest and its impacts may also be affected by variation in environmental variables (Siebert, 2000; Ticktin and Nantel, 2004).

In addition, few studies have assessed patterns of harvest or their demographic impacts for species that are harvested for multiple plant parts. The multiple use of single species is however, widespread and common. For example, 51.35% of plant species harvested in western Burkina Faso are harvested for multiple parts and the situation is similar elsewhere (Taita, 2003; Kristensen and Balslev, 2003; Harris and Mohammed, 2003). The ecological impacts of harvesting multipurpose species may be greater than those of other species due to the combined effects of harvesting multiple parts. These species may therefore be at higher risk of overexploitation. Multipurpose NTFP species also often represent important resources for multiple user groups (Shackleton et al., 2002; Lykke et al., 2004), Gaining an understanding of patterns of harvest by different user groups and their impacts is essential for designing plans for sustainable management for these species.

We assessed patterns of NTFP harvest from the multipurpose tree, *Khaya senegalensis* (Desr.) A. Juss (Meliaceae), and its impacts on 12 populations spread across two contrasting ecological regions in Benin. *K. senegalensis* is heavily harvested for both its bark as well as its foliage by local people in Benin. During the dry season, the indigenous *Fulani* people heavily prune *K. senegalensis* trees to feed their livestock (Sinsin et al., 1989; Petit, 2003). The Fulani specialize in raising cattle, which are a vital source of income for them and an integral part of their culture. *K. senegalensis* stem bark is also a very important medicine used by traditional healers and local populations to cure several human diseases (Sokpon and Ouinsavi, 2002) as well as livestock diseases (Atawodi et al., 2002). It is an important medicine for malaria, one of the most dangerous and common diseases in Tropical Africa.*K. senegalensis* is also one of the best timber species in Benin, and was the first timber species exported from Africa early during the colonial era (Dalziel, 1937). Commercial companies as well as local populations illegally harvest the timber to depletion.

K. senegalensis is found in various vegetation types, including gallery forest, dry dense forest, woodland forest, savannah and in both the Sudano-Guinean and the Sudanian ecological regions of Benin (Sokpon and Ouinsavi, 2002). The Sudanian region is drier than Sudano-Guinean region, which has higher rates of annual rainfall, a longer rainy season, lower potential evapotranspiration and higher diversity of habitat (Natta, 2003).

We address the following questions:

(1) What are the rates and patterns of bark and foliage harvest for *K. senegalensis* and do these vary between the Sudanian and Sudano-Guinean ecological regions? We quantify rates and patterns of harvest at the level of individuals (% of each tree harvested) and populations (% of trees harvested), and according to size-classes.
(2) Does bark and fodder harvest affect *K. senegalensis* density and population structure (size-class distribution) and do the effects vary between the Sudanian and Sudano-Guinean ecological regions?
(3) Do other environmental factors and human activities also explain patterns of variation in harvest rates, population size-class distribution and density?
(4) What features of *K. senegalensis* harvest practices may best allow for sustained use and what additional management strategies may foster conservation?

Despite the great importance of NTFP to local people's livelihoods in Africa, this study is one of very few to quantify harvest patterns and their impacts for an African NTFP outside of South Africa.

2. Methods

2.1. Study areas and species

This study was conducted in the Republic of Benin (6–12°50′N and 1–3°40′E) in West Africa. Benin covers 112,622 km^2 and is located in the 'Dahomey gap' (Jenik, 1994), the dry corridor which consists mainly of savannah and splits the African rainforest block into two parts. The climate is generally dry, composed of a subequatorial Guineo–Congolean region (6°25′–7°30′N), the Sudano-Guinean region (7°30′–9°30′N) and the Sudanian region (9°30′–12°N). This study was carried out in the latter two regions, as this is where *K. senegalensis* is distributed. The Sudano-Guinean region is wetter with a longer rainy season and has a more diversified habitat for *K. senegalensis* than the Sudanian region (Table 1; Natta, 2003).

K. senegalensis is one of the most important tree species in the Meliaceae family in Africa. It grows up to 30 m high and 3 m girth, with a dense crown and short bole covered with dark grey scaly bark (Keay, 1989). The bark is bitter and yields gum when wounded. It is a shade intolerant semi deciduous tree (Sokpon and Ouinsavi, 2002).

2.2. Study design and data collection

To assess patterns of harvest and its ecological impacts across the Benin landscape, we studied 12 populations of *K. senegalensis* which varied according to their bark and foliage harvest intensity, ecological conditions and geographic location (Fig. 1, Table 2). Six populations were selected in the wetter Sudano-Guinean region and six in the drier Sudanian region. In the Sudanian region, the six populations were located in gallery forests, since this is where almost all *K. senegalensis* populations were found in this region. In the Sudano-Guinean region, we selected populations in various habitat types (gallery forest, dense dry forest, woodland) since there were not

Table 1 – Characteristics of the two ecological regions where *K. senegalensis* is distributed in Benin (adapted from Natta, 2003; Agbahungba et al., 2001)

	Sudano-Guinean region	Sudanian region
Location	(7°30′–9°30′N)	(9°30′–12°N)
Rainfall	1100–1300 mm	800–1100 mm
Temperature	25–29 °C	24–31 °C
Insolation	2305 h	2862 h
Relative Humidity	31–98%	18–99%
Climate type	Sub-humid or Sub-Sudanian	Sudanian dry
Active vegetation period	200 days	145 days
Vegetation	Woodlands, savannah, semi-deciduous forest, gallery forest	Savannah, gallery forest
Soil types	Ferruginous	Hydromorphic well drained, lithosol

enough populations in any one vegetation type. In each region, we selected populations by first surveying all the potential populations, and then randomly selecting three populations subject to high harvest rates of foliage and bark harvest (high harvest populations), and three populations subject to low rates of harvest or no harvest (low harvest populations). We defined high harvest populations as those having more than 50% trees pruned and more than 10% of trees debarked. Low harvest populations had less than 5% of trees pruned and less than 10% of trees debarked. We did not find populations with intermediate harvest intensities during our survey. We were also unable to locate any non-harvested populations in the Sudanian region and we found only one truly non-harvested population in the Sudano-Guinean region.

2.3. *Estimating harvest rates, patterns and impacts on population density and structure*

In each population, we established two 0.5-ha rectangular plots (50 m × 100 m in woodlands and dry dense forests, and 10 m × 500 m in gallery forests) to tag and sample all *K. senegalensis* trees with diameter at breast height (dbh) greater than 5 cm. The narrower shape of our plots in the gallery forests was due to the very small width of this forest type along the stream banks. Within each plot, five 0.1 ha square subplots (10 m × 10 m) were established to monitor seedlings and saplings (all individuals less than 5 cm diameter at base). For each *K. senegalensis*, we measured dbh, total height, trunk height, bark thickness, total number of branches, number of branches pruned, the number of years since last pruning, and percentage of trunk debarked. In most cases, debarking *K. senegalensis* consists of removing both the outer and inner bark. The percentage of debarking was defined as the percentage of outer or inner bark removed from the trunk (up to 2.5 m height). The scale used to estimate the percent trunk debarked and percent of branches pruned was adapted from Cunningham (2001).

We considered a branch to be any ramification that was less than 5 cm diameter at its base (where it originated). This is because when Fulani harvest *K. senegalensis*, they usually (since this is easiest for them) cut branches at point where the diameter is less than 5 cm. The number of branches was calculated as the total number of harvestable branches. We considered a branch pruned only when it had been cut three or less years ago. We did not distinguish between branches pruned once versus those pruned on multiple occasions because it is difficult to accurately trace the pruning history of branches back more than three years; we also learned from the Fulani that a tree (or branch) that has not been pruned for the past three years is likely to have recuperated to produce flowers and fruit, even when harvested multiple times.

For each population, we also recorded the following environmental characteristics: soil and habitat type, presence of water or rocks outcrops in the stream bed, signs of any past timber logging, fire frequency, official protection status, presence of any hemi-parasites (because some trees were attacked) on trees and distance of the population to neighboring farms.

2.4. *Data analyses*

We used partial log-linear analyses to test if the proportion of trees harvested (for bark or foliage or both) from each size-class depended on the ecological region in which they were found. To test if harvest intensity (for bark or foliage or both) at tree level differed significantly between the two ecological regions, Mann Whitney test was used. Harvest intensity was defined as the percent bark or foliage harvested from each tree.

To assess the impacts of harvest on *K. senegalensis* populations, we calculated *K. senegalensis* density and population structure (size-class distribution) at each of the 12 sites. We used dbh as a measure of tree size, though dbh was highly correlated with tree height (spearman's $rho = 0.891$, $p < 0.001$). To test the effects of ecological region (Sudano-Guinean versus Sudanian) and harvest intensity (high versus low harvest) on *K. senegalensis* adults and seedlings density, we used a two-way analysis of variance (Zar, 1999). This data was normally distributed with homogeneous variances.

To test if size-class distributions were independent of ecological region and harvest intensity we carried out log-linear analyses. To compare dbh class distributions between the 12 study populations, we used the coefficient of skewness of the distribution (Condit et al., 1998; Zar, 1999; Leakey et al., 2005). Spearman's rank correlation was used to identify the environmental parameters and other human activities which correlated with seedling and adult trees density, coefficient of skewness and pruning and debarking intensities. All variables evaluated were either continuous or ordinal. Habitat, soil type and topography were coded according to increasing gradients of water availability, water retention and slope, respectively.

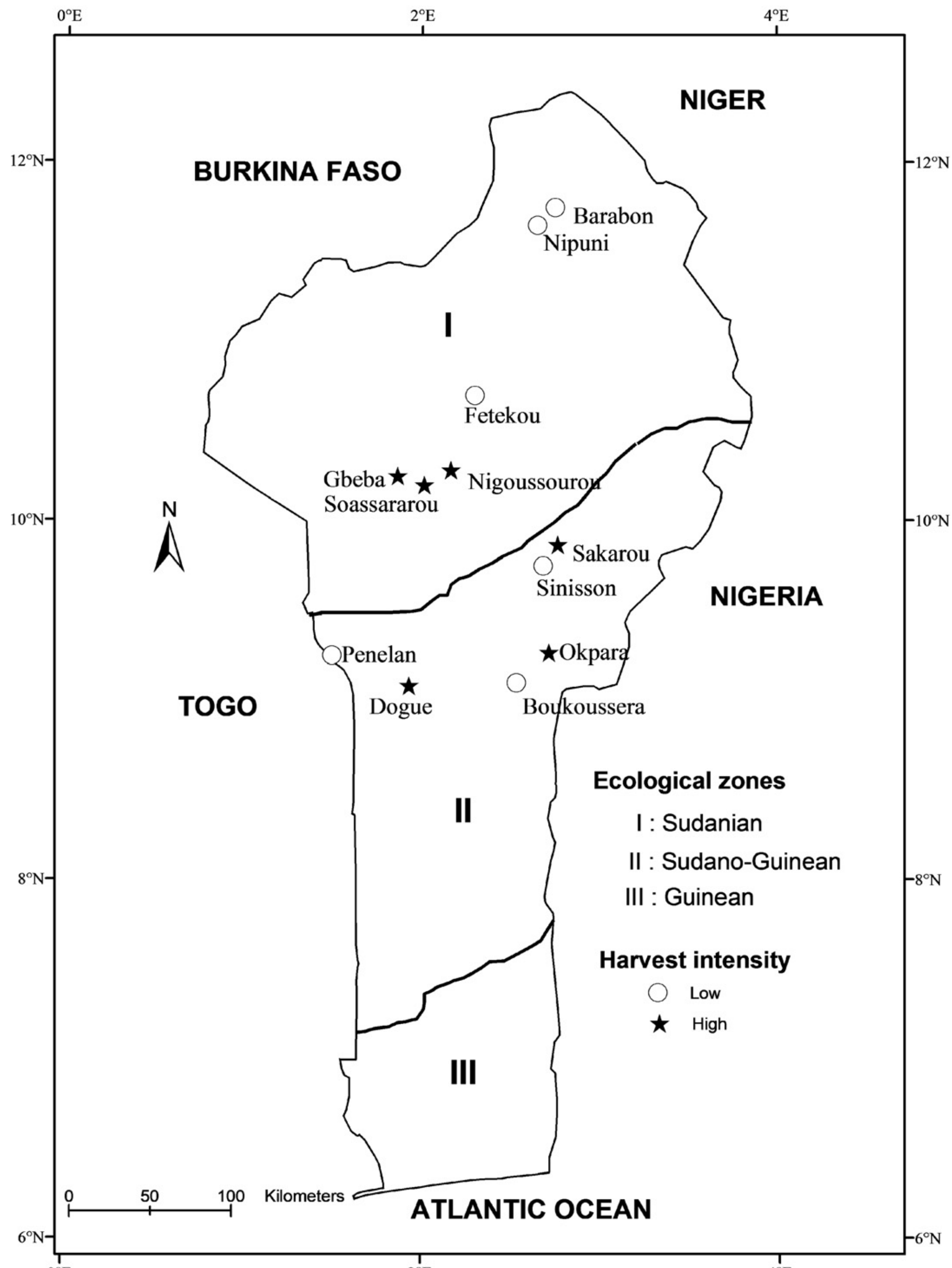

Fig. 1 – Distribution of 12 *Khaya senegalensis* study populations in two ecological regions of Benin.

3. Results

3.1. *Patterns of K. senegalensis foliage and bark harvest at the population level*

In the high harvest populations, 58.21 ± 6.80% of all trees were harvested for their foliage. The intensity of bark harvest was lower, with a mean of 17.69 ± 7.32% of trees debarked. Only 13.20 ± 5.45% of trees were subject to both debarking and pruning (Table 3). Across all high harvest populations, 62.70 ± 6.30% of trees were harvested in some way (pruned or debarked). For low harvest populations, this figure was 15.21 ± 6.21%.

The intensity of pruning and debarking at population level was significantly positively correlated with other measures of human disturbances (past logging, cattle grazing, sand collection, distance to farm) but not with any of the environmental variables measured. However, pruning intensity was signifi-

Table 2 – Characteristics and harvest intensity for 12 *K. senegalensis* populations selected in two ecological regions in Benin

Ecological region	Population (coordinates)	Habitat	Harvest intensity	Protection status	Other disturbances	
					Fire	Logging
Sudano-Guinean	Dogue (N9°05′–E1°56′)	Woodland	High	Unprotected	+	+
	Okpara (N9°16′–E2°43′)	Woodland	High	State Farm	+	+
	Sakarou (N9°52′–E2°46′)	Dry Forest	High	Community Forest	+	+
	Boukoussera (N9°06′–E2°32′)	Dry Forest	Low	Community Forest	–	+
	Sinisson (N9°45′–E2°41′)	Woodland	Low	Forest Reserve	+	+
	Penelan (N9°15′–E1°30′)	Gallery	Low	Forest Reserve	–	–
Sudanian	Barabon (N11°45′–E2°45′)	Gallery	Low	National Park	–	–
	Nipuni (N11°39′–E2°39′)	Gallery	Low	National Park	+	–
	Fetekou (N10°42′–E2°18′)	Gallery	Low	Forest Reserve	+	–
	Gbeba (N10°15′–E1°52′)	Gallery	High	Forest Reserve	+	+
	Nigoussourou (N10°17′–E2°10′)	Gallery	High	Unprotected	+	+
	Soassararou (N10°12′–E2°01′)	Gallery	High	Unprotected	–	+

Harvest intensity refers to harvest of both foliage and bark. High harvest populations have >50% of trees pruned and <10% of trees debarked; low harvest populations have <5% of trees pruned and <5% of trees debarked.

Table 3 – Percentage of *K. senegalensis* trees that were pruned debarked or debarked and pruned in two ecological regions in Benin

Harvest intensity/ ecological region	*N*	Percentage of trees pruned only (%)	Percentage of trees debarked only (%)	Percentage of trees pruned and debarked (%)
(a) High harvest populations				
Sudanian	3	59.38 ± 3.38	27.08 ± 13.07	20.28 ± 9.77
Sudano-Guinean	3	57.04 ± 14.80	8.30 ± 2.99	6.12 ± 1.77
Total	6	58.21 ± 6.80	17.69 ± 7.32	13.20 ± 5.45
(b) Low harvest populations				
Sudanian	3	6.67 ± 6.66	2.56 ± 2.56	0.00 ± 0.00
Sudano-Guinean	3	2.95 ± 1.48	16.85 ± 8.82	1.39 ± 1.38
Total	6	4.80 ± 3.16	9.71 ± 5.20	0.69 ± 0.69

Mean ± 1 standard error (SE). *N* is the number of population sampled.

cantly negatively correlated with official protection of populations (Table 4).

3.2. Size-specific patterns of *K. senegalensis* foliage and bark harvest

In high harvest populations in both the Sudano-Guinean and Sudanian regions, Fulani herders harvested mostly trees of medium to big sizes (dbh > 35 cm). In both regions, 100% of trees in the largest size-classes were harvested. However, in the wetter Sudano-Guinean region, a significantly higher proportion of trees were harvested within each dbh class than in the drier Sudanian region (Fig. 2a and b; log-linear $G^2 = 48.53$, $p = 0.002$). These differences were particularly salient in the smaller size-class (5–10 cm), where 7.04 ± 3.53% (0.67 ± 0.19 trees/ha) of the available trees were pruned in the drier Sudanian region, but in the Sudano-Guinean region this figure was 36.80 ± 19.14% (2.33 ± 0.19 trees/ha) (Fig. 2a and b).

In contrast to high harvest populations, in low harvest populations, Fulani herders targeted only trees of medium size (35–65 cm dbh; Fig. 2c and d). The one exception to this was one tree within 85 cm dbh class which was pruned in one population in the Sudanian region (Fetekou population).

The proportion of debarked trees increased with increasing size-classes in both ecological regions (Fig. 3a and b; $G^2 = 19.16$, $p = 0.7433$). Overall, local people harvested bark from 8.55 ± 4.04% of trees (2 ± 0.71 trees/ha) between 5 and 30 cm dbh and 45.02 ± 16.45% of trees (9.67 ± 5.84 trees/ha) between 35 and 95 cm dbh. Debarked trunks partially recovered through cambial regrowth, from the edge of the wounded bark inwards. In most cases, less than half of the wound recovered. Ringbarked trees (i.e. with bark removed in a strip that spanned the entire circumference of the trunk) did not recover but die. Only three trees were found ringbarked. These trees were in the Sudanian region and within populations located near villages (Nigoussourou and Soasararou).

3.3. Intensity of *K. senegalensis* pruning and bark harvesting at the level of individuals

Most of the *K. senegalensis* trees monitored were either non-harvested (0% crown removed) or pruned at 100% of their crown (Fig. 4a). On average, 84.67 ± 14.43% of harvested trees had 100% of their crown removed in the Sudanian region, while in Sudano-Guinean region this figure was 73.67 ± 13.05%. This difference was not significant. However, when considering only high harvest populations, a significantly greater proportion of

Table 4 – Spearman correlations between *K. senegalensis* population structure parameters, harvesting intensity and environmental variables

	Percent debarking	Percent pruning	Adult density	Seedling sapling density	Skewness coefficient
Percent debarking	+1.000	–	–	–	–
Percent pruning	+0.323	+1.000	–	–	–
Adult density	+0.250	−0.063	+1.000	–	–
Seedling, sapling density	+0.106	−0.232	+0.179	+1.000	–
Skewness coefficient	+0.035	− 0.014	−0.109	−0.098	+1.000
Habitat	+0.254	+0.201	−0.565*	−0.200	+0.709**
Soil type	−0.020	+0.095	−0.051	+0.118	+0.590*
Topography	+0.076	−0.419	+0.533	+0.265	−0.294
Presence of rock	−0.484	−0.220	−0.394	+0.306	+0.218
Stream depth	+0.066	−0.060	+0.397	−0.004	−0.642**
Fire frequency	+0.159	+0.495	−0.438	−0.521	+0.179
Past logging	+0.396	+0.698**	−0.237	−0.287	+0.548
Official protection status	−0.340	−0.875***	−0.024	+0.290	−0.145
Grass cover	−0.258	−0.138	−0.667**	−0.239	+0.273
Rainfall	+0.210	+0.066	−0.055	−0.150	+0.747***
Distance to farms	+0.592*	+0.411	−0.074	−0.272	+0.572*
Other human activity	+0.663**	+0.820**	+0.009	−0.121	+0.246
Presence of water	−0.308	−0.396	+0.219	−0.044	+0.218
Cattle grazing	+0.679**	+0.778**	−0.116	−0.043	+0.138
Hemi-parasite load	−0.440	−0.044	−0.219	−0.480	−0.480

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

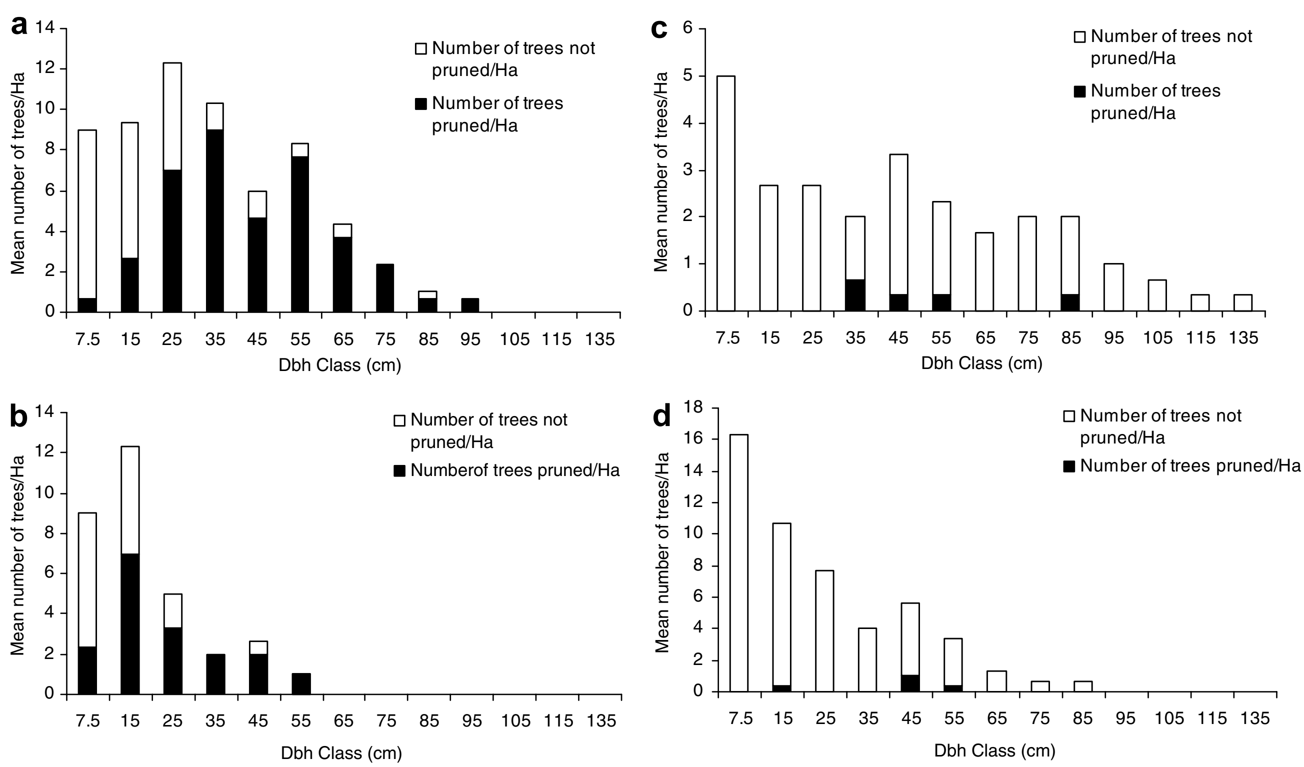

Fig. 2 – Mean density of *K. senegalensis* trees pruned per dbh class for high harvest (a,b) and low harvest populations (c,d) in two ecological regions in Benin: Sudanian (a,c) versus Sudano-Guinean (b,d).

trees in Sudanian region were more severely pruned (91.35 ± 1.83% of crown pruned) than those in Sudano-Guinean region (83.41 ± 3.92% of crown pruned; $U = 3000.5$, $p = 0.032$).

In some populations (e.g., Gbeba in Sudanian region) 100% of harvested trees had 100% of their crown pruned. Even in low harvest populations, harvested trees also had a high

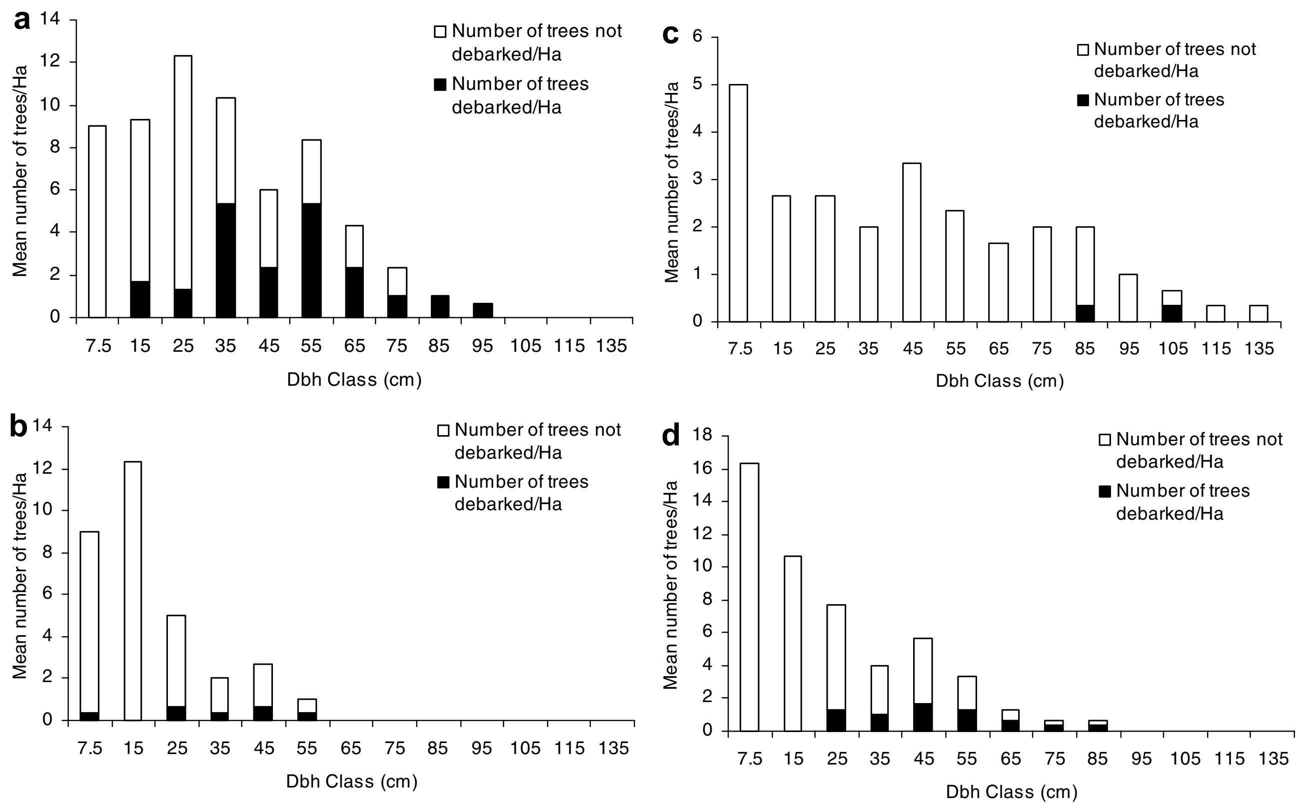

Fig. 3 – Mean density of *K. senegalensis* trees debarked per dbh class for high harvest (a,b) and low harvest populations (c,d) in two ecological regions in Benin: Sudanian (a,c) versus Sudano-Guinean (b,d).

percentage of their crown removed (66.67 ± 5.31%). However, trees in high harvest populations had a significantly higher proportion of crown removed than those in low harvest populations ($U = 2834.5$, $p = 0.000$). We also observed in the field - and the Fulani commented that - harvested branches resprout, but when the intensity and frequency of pruning is very high, trees may fail to develop new branches and old pruned branches may die.

In contrast to pruning, in most cases bark harvesters debarked less than 25% of the trunk (Fig. 4b). Most of the trees harvested for more than 50% of their trunk bark were found in populations near villages. As in the case of pruning, although there was large variation among populations within each region, trees in the drier Sudanian region faced higher debarking pressure (28.17 ± 4.13% of trunk debarked) than those in Sudano-Guinean region (16.0 ± 5.90% of trunk debarked; $U = 2429.5$, $p = 0.000$).

3.4. *Impact of foliage and bark harvest on K. senegalensis density*

The density of *K. senegalensis* stems varied greatly across the 12 populations. The average density of adult trees (dbh > 5 cm) was 43.16 ± 7.23 trees/ha and that of seedlings and saplings was 1255.83 ± 268.23 stems/ha. The density of adults in the six high harvest populations varied from 21 to 88 trees/ha, while seedling density varied from 180 to 2130 stems/ha. The same kind of variation was observed for low harvest populations: adult density varied from 25 to 64 trees/ha and seedlings and saplings density varied from 90 to 2600 stems/ha. However, in Sudano-Guinean region, there were significantly fewer seedlings and saplings in high harvest populations than in low harvest populations ($F = 26.471$, $p = 0.007$). This was not the case in the drier Sudanian region (Table 5). Adult density was significantly correlated with habitat type, with gallery forests having higher densities than woodlands (Table 4).

3.5. *Impact of foliage and bark harvest on K. senegalensis population structure*

In both ecological regions, high harvest populations lacked individuals in the largest size-classes (Fig. 5a and b). The largest *K. senegalensis* tree (dbh = 136.2 cm) was found in the drier region, in the "W" National Park.

Partial log-linear analyses for each ecological region revealed that in the drier Sudanian region, the distribution of individuals in each size-class was dependent on harvest intensity ($G^2 = 31.92$, $p = 0.0014$, Fig. 4a). However, this was not the case in the wetter Sudano-Guinean region ($G^2 = 13.25$, $p = 0.35$, Fig. 4b).

Population structure was also dependent on ecological region ($G^2 = 80.13$, $p < 0.0001$) (Fig. 5a and b). Regardless of the harvesting intensity, population structures in the Sudanian region were mostly close to the normality (skewness = 0.241–0.892) while populations in Sudano-Guinean region

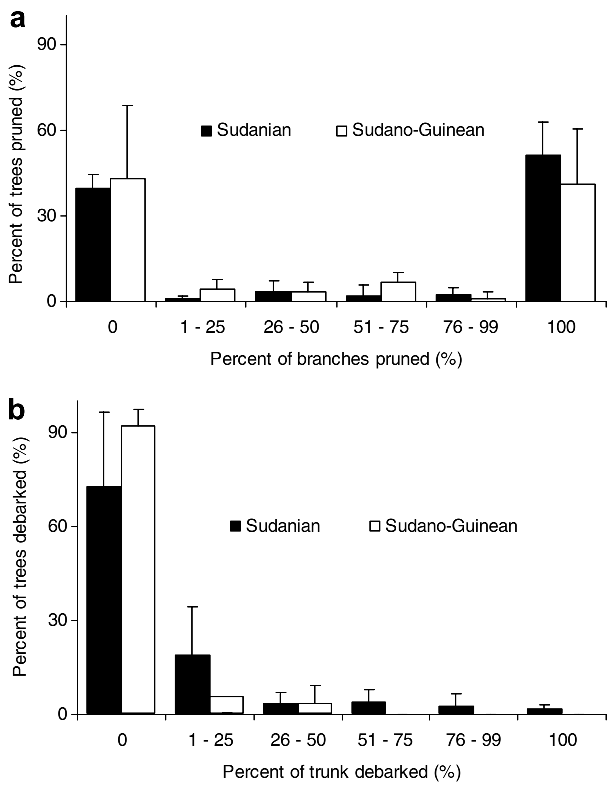

Fig. 4 – Frequency distribution of (a) foliage and (b) trunk bark harvesting intensities for *K. senegalensis* individuals in high harvest populations in two ecological regions in Benin. Means ± 1 SE.

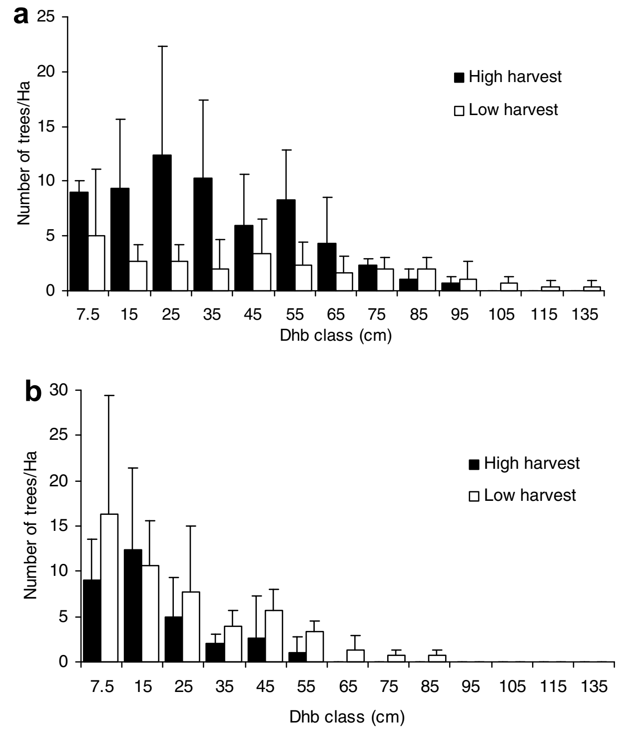

Fig. 5 – Size-class distribution (dbh) of *K. senegalensis* trees in high versus low harvest populations in two ecological regions in Benin: (a) Sudanian region and (b) Sudano-Guinean region. Means ± 1 SE.

showed an inversed J shape (skewness = 0.726–1.189) (Fig. 6). Overall however, there was great variation of population structure across populations (Fig. 6). This variation was significantly positively correlated with rainfall, habitat type, and soil type (Table 4).

Table 5 – Density of *K. senegalensis* adults (dbh > 5 cm) and seedlings and saplings (dbh ⩽ 5 cm) in high vs. low harvest populations and in two ecological regions in Benin

Life stage/ ecological region	N	Harvest intensity	
		High harvest	Low harvest
(a) Adults			
Sudanian	3	64.33 ± 19.34a	26.00 ± 0.57a
Sudano-Guinean	3	32.00 ± 12.01a	50.33 ± 13.16a
Total	6	48.16 ± 12.48	38.16 ± 8.02
(b) Seedlings and saplings			
Sudanian	3	1480.00 ± 640.02a	1483.33 ± 737.66a
Sudano-Guinean	3	353.33 ± 101.05a	1706.66 ± 242.85b
Total	6	916.66 ± 383.96	1595.00 ± 350.48

Values are mean numbers of stem per hectare ± 1 standard error (SE). Means in a row followed by the same letter are not significantly different (ANOVA, $p < 0.05$).

4. Discussion

Multipurpose NTFP species often represent important resources for local communities, including multiple user groups, and therefore can be at greater risk of overexploitation than single-use NTFP. An understanding of the rates and patterns of harvest as well as their ecological impacts in the differing contexts in which these species occur, can provide important insight for the sustainable management of these species.

4.1. *Rates and patterns of bark and foliage harvest*

Our results illustrate that *K. senegalensis* populations are subject to size-specific patterns of harvest for both foliage and bark, with harvesters tending to prefer larger trees. Most of the trees that were harvested were of medium or large size (dbh > 35 cm), and there was an increase of the proportion of trees harvested with increasing size of the tree. In South Africa, Shackleton et al. (2005) also found that for a number of multiuse tree species, the larger size-classes were harvested in the highest proportions. Similarly Geldenhuys (2004) reported that smaller trees found in southern African woodland were not bark-harvested. *Prunus africana* bark gatherers in Cameroon also selectively harvest bark from the largest trees available. However, in the case of *P. africana*, where overexploitation of large trees occurs, there is usually a shift to harvest smaller and smaller trees (Cunningham and Mbenkum, 1993).

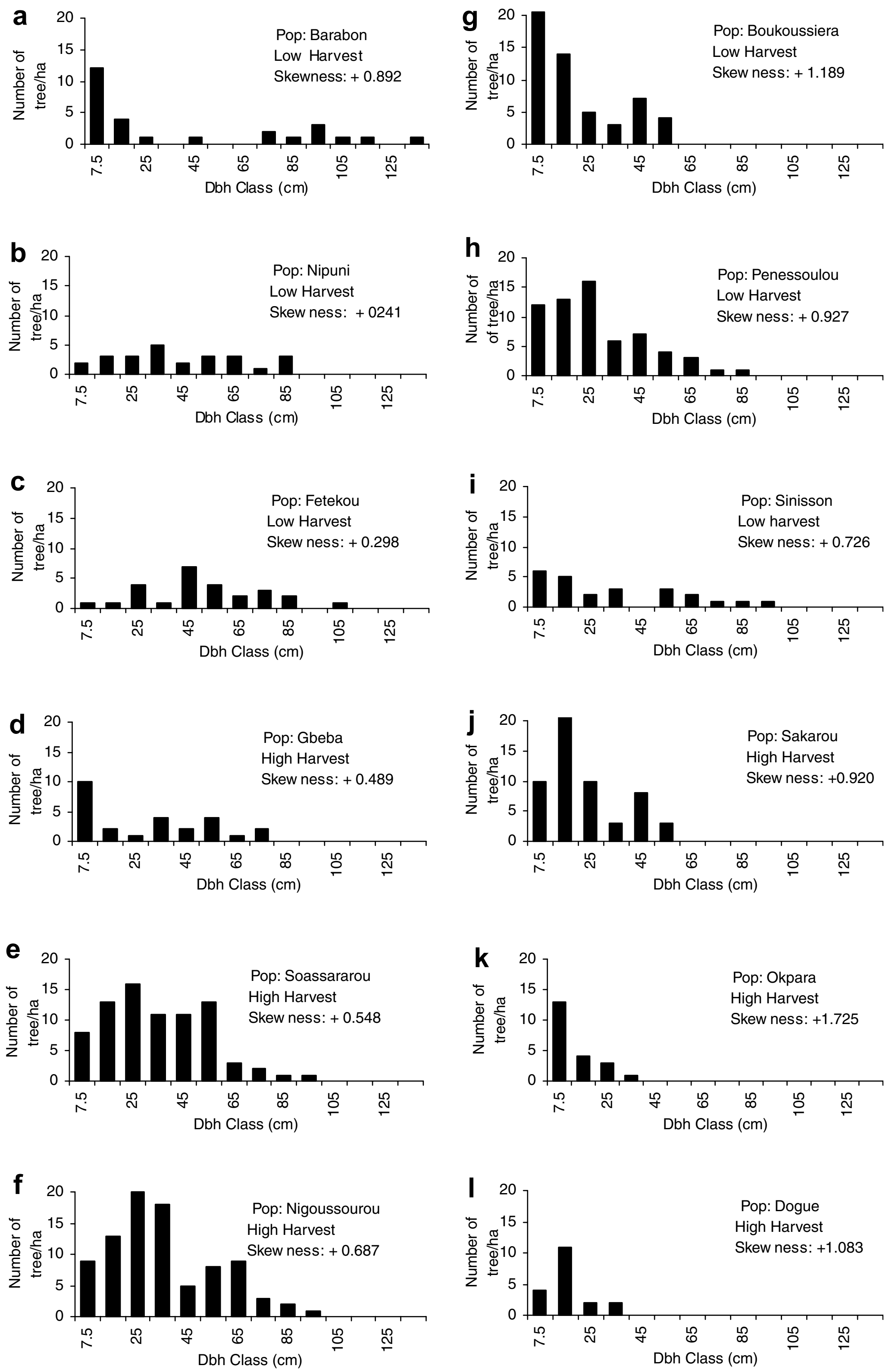

Fig. 6 – Size-class distribution (dbh) for each of 12 *K. senegalensis* populations subject to different harvest intensities (high versus low harvest) in two ecological regions in Benin: Sudanian: (a)–(f) and Sudano-Guinean: (g)–(l).

We found clear patterns with respect to the intensity of *K. senegalensis* foliage harvest at individual tree level. Most trees were either totally pruned or else not harvested at all. This is likely because pruning trees is a dangerous activity (Petit, 2003) which requires skill and experience. Big *K. senegalensis* trees with tall and straight trunks are difficult to climb, and according to the Fulani, only courageous and experienced harvesters exploit them. Therefore, Fulani harvesters maximize the amount of foliage harvested for each tree and thereby reduce the number of trees they need to climb.

For species that are of economic or cultural importance to indigenous or local communities, management practices to reduce the impacts of harvest are often developed (Joyal, 1996; Ticktin and Johns, 2002; Ghimire et al., 2005), even though not everyone in the community may follow these practices. In our study, we observed that *K. senegalensis* trees that were pruned at 75–99% of their crown cover still possessed a few top branches that had leaves. Leaving these top branches unpruned is a traditional Fulani practice locally referred to as "*sopoodu*". Fulani maintain that they leave the *sopoodu* to allow the tree to grow and reproduce. However, not all pruned trees we observed had a *sopoodu*, and not every *sopoodu* produced fruit. The probability that a *sopoodu* produces fruits may depend on its size and the number of branches left out. Unfortunately, the *sopoodu* management system is disappearing and the size of *sopoodu* varies from one tree to another and from one region to another. The Fulani we spoke with emphasized that the size of the *sopoodu* says a lot about the personality of the harvester, and also associated the small-sized *sopoodu* with young and inexperienced harvesters, and with immigrant Fulani harvesters who are not concerned about the regeneration of the species. Further investigation is warranted on the impact of leaving *sopoodu* on *K. senegalensis* fruit production and population structure.

4.2. Differences in harvesting patterns between ecological regions

The intensity of foliage harvest at population level (proportion of trees harvested per size-class in each population) was higher in the wetter Sudano-Guinean region than in Sudanian region. In contrast, foliage harvesting pressure at tree level (proportion of bark or foliage harvested per tree) was lower in the Sudano-Guinean region than in Sudanian region. These patterns may be explained by the movement of migratory Fulani harvesters, which is driven by differences in water availability in the two regions. *K. senegalensis* is the first fodder trees species that Fulani harvest at the beginning of the dry season, from January to May (Petit and Diallo, 2001, personal observation). At this time, once the herbaceous pastures have been burned, Fulani herders move southward from the Sudanian toward the Sudano-Guinean region, where there are better water resources available. As Fulani herders head south, their herds become increasingly hungry and they therefore harvest almost all the leaves of any *K. senegalensis* tree available along their migration corridor. This likely explains the high harvesting pressures on individual trees in Sudanian region.

Fulani herders then spend the peak of the dry season in the Sudano-Guinean region, harvesting *K. senegalensis* as well as other tree fodder tree species (e.g., *Afzelia africana* and *Pterocarpus erinaceus*). The high concentration of herds in the wetter Sudano-Guinean region due to this movement of Fulani from Sudanian region as well as to the high number of cattle that already exist in Sudano-Guinean region, likely explain the higher pruning pressure on small-sized *K. senegalensis* tree in that region.

In contrast to pruning patterns, there were no significant differences in the patterns of debarking at population level (percent trees debarked) between the two ecological regions. However, at tree level, there was significantly less debarking pressure (average percent trunk debarked per tree) in Sudano-Guinean region than in Sudanian region. This is likely because local people in southern (Sudano-Guinean as well as Guineo-Congolean) regions of Benin harvest bark from *K. senegalensis* trees found along roadsides and in state own or private plantations, which were established during colonial times (Sokpon and Ouinsavi, 2002, 2004). The Sudanian region has more wild populations of *K. senegalensis* and in many cases these populations are also close to farms. Local people in Sudano-Guinean region have therefore more opportunity to harvest bark from wild populations than from plantations.

4.3. NTFP harvesting impact on population density

In Sudano-Guinean region, heavy harvest appears to have led to significant decreases in seedlings and saplings density. However, this was not the case in Sudanian region. These differing responses to harvest could be due to ecological differences between the two regions combined with the above-mentioned differences in harvesting patterns. Fruit productivity in Sudano-Guinean region is significantly lower than in the drier Sudanian region and high harvest populations also produce significantly less fruits than low harvest populations in this region (Gaoue and Ticktin, in preparation). The latter may be due or at least confounded by the fact that a higher proportion of trees in Sudano-Guinean regions are harvested than in Sudanian region. Lowered fruit productivity of harvested populations could lead to reduced numbers of seedlings and saplings.

However, we also found enormous variation in densities of *K. senegalensis* even among populations with the same harvest intensity and in the same region. This large density variation is likely due to the impacts of other disturbances on these populations. For example, in the Sudanian region, Nipuni and Soassararou populations had the lowest seedlings/saplings densities. The Soassararou population is located in a harvested gallery forest with a rocky bed and sandy soils in some parts. To build concrete houses, farmers in the nearest villages collect sand from the bed of the stream. In some places, the soil was eroded by strong water flow and trees were uprooted. These additional human disturbances may explain the low seedling and sapling density observed in that population. Similarly, Nipuni population is located in a gallery forest in the "W" National Park, where 44% of *K. senegalensis* trees were infected by hemi-parasites of the Loranthaceae family (O.G. Gaoue, unpublished data). Hemi-parasites load has been illustrated to decrease rates of fruit production and increase adult mortality in other NTFP species (Sinha and Bawa, 2002) and may have an important effect on population structure. Hemi-parasites load, soil type and presence of rock outcrops, habitat type, and past human disturbances (e.g., fire, logging, sand collection in gallery forests) were significantly correlated with variation in seedling and adult density, and may be more important in determining the density in *K. senegalensis* populations than bark and foliage harvest intensity.

4.4. NTFP harvesting impact on population structure

Like density, the size-class distribution of a plant species may be affected by many factors (Condit et al., 1998) including light tolerance, life form (e.g., Pooter et al., 1996; Lykke, 1998; Tesfaye et al., 2002), habitat type (e.g., Wadt et al., 2005), climate, and management (e.g., Lykke, 1998; Tesfaye et al., 2002; Schwartz et al., 2002; Peres et al., 2003; Bhuyan et al., 2003). For *K. senegalensis,* variation in rainfall, habitat, soil type, and fire frequency were significantly correlated with the coefficient of skewness of the size-class distribution.

As in the case of density, difference in structure between populations in the Sudanian region (almost normally distributed structure) and in Sudano-Guinean region (negative exponential structure), and the finding that in Sudanian region alone, population structure was dependent on harvest intensity may be explained by differences in ecological factors and harvesting patterns between the regions. The higher harvest intensity (% of foliage and bark harvest per tree) in the Sudanian region combined with the region's lower rainfall and higher evapotranspiration rates (Natta, 2003) likely lead to slower growth and slower recuperation of trees after bark and foliage harvest.

The lower number of large trees found in the Sudano-Guinean region as compared to Sudanian region, and the differences in population structure, may also be related to the commercial logging that took place especially in the wetter and more productive Sudano-Guinean region. The first commercial logging of *K. senegalensis* timber occurred in the 1950s (Sokpon and Ouinsavi, 2004) and all the high harvest populations we studied in the Sudano-Guinean region (Sakarou, Okpara, Dogue) were logged in the past. In Sudanian region, the official protection status of the populations protect them from logging, and four out of the six populations that we surveyed in this region were located in protected areas. For example, even though the Gbeba population in Mekrou Reserve Forest (a protected area) was heavily pruned, it still had big trees (up to 80 cm dbh) because of limited logging.

The use of population structure as a tool to investigate the demographic health of harvested populations should however be taken with caution, as static information on size-class distribution is not necessarily a good predictor of future population trends (Condit et al., 1998).

4.5. Implications for sustainable management and conservation

The very heavy harvest pressure we documented for *K. senegalensis* in some populations, combined with their impacts on seedling and sapling densities and population structure suggests that continued harvesting in some populations presents conservation concerns over the long-term. The patterns of foliage harvest we observed, in terms of preferred size-classes and of the amount of foliage harvested from each tree, and the traditional concepts involved in pruning, provide insight on what kinds of conservation plans may be most appropriate. For instance, given the risk involved in climbing trees, and therefore the practice of harvesting most or all of the foliage, it is unrealistic to suggest that Fulani harvest only a small part of the tree. Instead, a management strategy in which a larger percentage of trees are totally spared may be more appropriate. However, the consequences on the genetic diversity should be assessed in order to opt for a tree-selection strategy that will maximize the genetic diversity. Similarly, for these harvested trees, the traditional concept of leaving significant-sized "*sopoodu*" can be emphasized and better passed down to the younger Fulani, many of whom do not fully follow the traditional management rules.

Although pruning levels are very high in the high harvest populations, Fulani harvesters preference of certain types of foliage may allow for the continued conservation (at least from pruning) of low harvest populations. This is because the Fulani prefer to harvest the young light green leaves, as opposed to the old dark green leaves that are found on trees that have been left unharvested over long periods (and avoided by cattle). Therefore those trees that have not been harvested for long periods have a high chance of escaping future harvesting. While very few trees have been left unharvested for long periods in high harvest populations, a very high percentage (an average of 95.6%) of these trees are found in low harvest populations. Of course, increased demand could lead to the exploitation of these populations in the future, and their status will therefore depend on their level of protection and availability of alternative harvest options.

Cunningham and Mbenkum (1993) and Stewart (2003) have noted that for *Prunus africana* in Cameroon, the establishment of plantations can be viewed not only as a way for *ex situ* conservation of threatened harvested plants, but also as a way of reducing the harvesting pressure on wild natural populations from which the bulk of medicinal products are harvested. In the case of *K. senegalensis,* the establishment of timber plantations of this species seems to have reduced debarking pressure in wild populations in the south of Benin. However, this is not the case for foliage harvest as in our countrywide survey of *K. senegalensis* populations in Benin, we rarely found *K. senegalensis* trees in plantations or along roadside that were pruned (except in Kouande in Sudanian region). Similar results were found in Burkina Faso where Fulani people avoided pruning *K. senegalensis* trees planted along roadsides or in plantations (Petit, 2003). The main reason for this is that Fulani fear complaints from private owners for harvesting their property. Encouraging Fulani to plant *K. senegalensis* around their own compounds may be a better option.

Our results demonstrate some of the ways in which harvesting patterns and responses to harvest for a given species may differ across ecological regions. They also illustrate the difficulty in assessing the impacts of NTFP harvest in the context of multiuse species that are exploited in habitats subject to multiple disturbances. Thus they clearly emphasize the importance of considering spatial variation in studies of NTFP harvesting and its impacts. Clearly, any conservation strategy for *K. senegalensis*, and other multiuse NTFP species like it needs to address the multiple harvesting as well as other human and environmental pressures to which populations are subject.

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