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Impacts of bark and foliage harvest on *Khaya senegalensis* (Meliaceae) reproductive performance in Benin

Orou G. Gaoue* and Tamara Ticktin

Botany Department, University of Hawaii at Manoa, 3190 Maile Way, Honolulu, HI 96822 USA

Summary

1. Increasing concern over the sustainability of harvesting non-timber forest products (NTFP) has led to a growing literature on the ecological impacts of NTFP extraction. A large proportion of NTFP are harvested for multiple plant parts, but few studies have assessed the impacts of harvesting multi-use species. In addition, few studies have assessed how harvest effects may vary across space. This information is necessary for designing effective conservation plans for the many NTFP species that are harvested from variable ecological contexts.

2. This study assessed the impacts of combined bark and foliage harvest on *Khaya senegalensis* (Meliaceae) reproductive performance in Benin. *K. senegalensis* bark is an important medicine for malaria, the leaves are pruned by indigenous Fulani herders as a critical source of fodder for their livestock, and the timber is highly prized. Data on reproductive characteristics were collected from 12 populations spread across two ecological regions (Sudanian and Sudano–Guinean). Half the populations had a history of high harvest intensity and half were subject to low/no harvest.

3. Trees produced more fruit and began fruiting at a significantly smaller size in the drier Sudanian region than in the wetter Sudano–Guinean region. However, pruning decreased fruit production significantly in the Sudanian region but not in the Sudano–Guinean region. Pruning had a significantly greater impact on fruit production in larger trees than in smaller trees. High harvest populations in the Sudano–Guinean region had significantly higher rates of seed production than low harvest populations, although the seeds were significantly lighter. There were no significant effects of debarking or combined debarking and pruning on reproductive performance.

4. *Synthesis and applications*. This study illustrates that heavy rates of foliage harvest can decrease rates and patterns of reproduction in *K. senegalensis*, and that the impacts may vary across environmental contexts. Lowered rates of reproduction may lead to decreases in *K. senegalensis* population size over the long term. Effective *ex situ* conservation strategies for *K. senegalensis* include increasing the availability of its fodder and bark by promoting *K. senegalensis* plantations programmes involving Fulani harvesters.

Key-words: ecological variation, fruit production, Fulani, multiple use species, non-timber forest products, West Africa

Introduction

The importance of non-timber forest products (NTFP) for local livelihoods and as a means to ensure forest conservation has been widely recognized (Iqbal 1993; Marshall & Newton 2003). NTFP extraction is considered to be less damaging to forest ecosystems than timber harvest and therefore more compatible with forest and species conservation. However, in recent years there has also been an increased awareness of the potential for NTFP to be over-harvested (e.g. Ticktin *et al.* 2002; Peres *et al.* 2003; Endress, Gorchov & Noble 2004; Nakazono, Bruna & Mesquita 2004; Emanuel, Shackleton & Baxter 2005).

One of the ways in which NTFP harvest can impact plant populations is by altering reproductive performance, including the number and size of fruits and seeds produced and the timing, frequency and probability of reproduction. This is especially true for NTFP harvest, that involves the removal of

*Correspondence author. E-mail: ogaoue@hawaii.edu

parts that are photosynthetically active or nutrient-rich or expensive to replace; or whose removal may damage the plant and leave it more vulnerable to subsequent infection, disease or attack. For example, leaf harvest of palms can significantly reduce the number of inflorescences and infruitescences produced per palm (Ratsirason, Silander & Richard 1996; Flores & Ashton 2000; Endress, Gorchov & Noble 2004), as well as the number of fruiting individuals in a population (Endress, Gorchov & Noble 2004). Similarly, in African savanna, successive pruning of *Adansonia digitata* L. branches leads to a decrease in mean fruit production (Dhillion & Gustad 2004). These effects may be caused by decreased photosynthetic capacity and/or reallocation of resources or stored reserves from reproduction to regrowth (Whitham *et al.* 1991; Fong 1992; Kigomo, Woodell & Savill 1994).

Although few studies have assessed the impacts of bark harvest on vital rates (Ticktin 2004), bark harvest can also be hypothesized to decrease reproductive performance. Bark is produced by a thin layer of cambium cells which surround the xylem and phloem tissues that transport water and nutrients to and from the roots and leaves. Bark also protects plants against fire, fungal and insect attack (Cunningham 2001). Removal of bark can therefore damage phloem or expose it to desiccation and fungal or parasite attack. This may disrupt the conduction of nutrients and hormones involved in flower bud production (Primack 1987; Mohr & Schopfer 1995), decreasing flower induction and therefore fruit and seed set. The need for resources to repair damage to bark could also result in lower resource allocation to reproduction.

The effects of foliage or bark harvest on reproductive performance may vary according to environmental gradients, with the negative impacts increasing with decreasing resource availability. For example, some NTFP species recuperate significantly faster from harvest in forest patches with higher light availability (Siebert 2000; Ticktin & Nantel 2004). Similarly, the impacts of harvest can also be expected to depend on the intensity and/or frequency of harvest. Thus multipurpose species, in which multiple plant parts are harvested from the same individuals, may, in some cases, be at higher risk of over-exploitation. Although multipurpose species make up a large proportion of NTFP world-wide (e.g. Harris & Mohammed 2003; Kristensen & Balslev 2003; Taita 2003), few studies have quantified the effects of harvest on them.

We assessed the impacts of foliage and bark harvest on reproductive performance of the multipurpose tree, *Khaya senegalensis* Desr (A.Juss), in two contrasting ecological regions in Benin, West Africa. *K. senegalensis* is harvested heavily for its leaves, which are pruned by the indigenous Fulani tribe to feed their livestock (Sinsin, Oloulotan & Oumorou 1989; Petit 2003). It is also harvested by local people for its bark (Gaoue & Ticktin 2007), which is used to treat various diseases including malaria, gastrointestinal diseases and anaemia (Arbonnier 2002; Kone *et al.* 2004). In addition to its value as an important source of foliage and bark, *K. senegalensis* is also highly prized for its timber. In Benin, *K. senegalensis* has a wide distribution, spanning both the Sudanian and the Sudano–Guinean ecological regions. The Sudanian region has lower rainfall, with a longer dry reason and higher rates of evapotranspiration than the Sudano–Guinean region. We hypothesized that high pruning and debarking pressure on *K. senegalensis* decreases reproductive output and that these effects are stronger in the Sudanian region than in the Sudano–Guinean region. Specifically, our objectives were to (1) assess the impacts of combined foliage and bark harvest of *K. senegalensis* on reproductive performance including seed mass, and number of fruits and seeds produced per tree, and (2) assess if and how the above impacts vary between ecological regions (Sudanian vs. Sudano–Guinean) of Benin.

Materials and methods

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 the 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 (Table 1).

K. senegalensis is one of the most important tree species in the Meliaceae family in Africa. It grows up to 30 m in height and 3 m in 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, semideciduous tree (Sokpon & Ouinsavi 2002).

STUDY DESIGN

We studied 12 populations of *K. senegalensis* that varied according to their bark and foliage harvesting intensity, ecological conditions and geographical location. Six populations were selected in the wetter

Table 1. Characteristics of the two ecological regions where *K. senegalensis* is distributed in Benin (data from Natta 2003; Assogbadjo *et al.* 2005)

	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
Length of plant growing season	200 days	145 days
Vegetation	Woodlands, savannah, dry dense forest, gallery forest	Savannah, gallery forest
Soil types	Ferruginous	Hydromorphic well-drained, lithosol

Table 2. Description of 12 *K. senegalensis* populations selected in two ecological regions in Benin. 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

Ecological region	Population	Coordinates	Habitat	Harvest intensity
Sudano–Guinean	Dogue	N9°05′–E1°56′	Woodland	High
	Okpara	N9°16′–E2°43′	Woodland	High
	Sakarou	N9°52′– E2°46′	Dry forest	High
	Boukoussera	N9°06′–E2°32′	Dry forest	Low
	Sinisson	N9°45′– E2°41′	Woodland	Low
	Penelan	N9°15′– E1°30′	Gallery	Low
Sudanian	Barabon	N11°45′–E2°45′	Gallery	Low
	Nipuni	N11°39′–E2°39′	Gallery	Low
	Fetekou	N10°42′–E2°18′	Gallery	Low
	Gbeba	N10°15′–E1°52′	Gallery	High
	Nigoussourou	N10°17′–E2°10′	Gallery	High
	Soassararou	N10°12′–E2°01′	Gallery	High

Sudano–Guinean region and six in the drier Sudanian region. In the Sudanian region, the six populations were located in gallery forests, as this is where almost all *K. senegalensis* populations are found in this region. In the Sudano–Guinean region, we selected populations in various habitat types (gallery forest, dense dry forest, woodland) as there were not enough populations in any one vegetation type. To select populations, we first surveyed all the potential populations, and then selected randomly three of the heavily harvested populations in terms of both foliage and bark (high harvest populations) and three less-harvested populations (low harvest populations) (Table 2). High harvest populations had 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% debarked. These harvesting categories were selected based on the range of harvested intensities observed in the field. We did not find any 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.

In each population, we established two 0·5-ha plots to tag and sample all *K. senegalensis* trees with diameter at breast height (d.b.h.) greater than 5 cm. For each individual in the plots, we measured d.b.h., total height, trunk height, bark thickness, percentage of trunk debarked, total number of branches, number of branches pruned and year since last pruning. 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 and/or inner bark removed from the trunk (up to 2·5 m height). The scale used to estimate the percentage of trunk debarked as well as the percentage of branches pruned was adapted from Cunningham (2001). We considered a branch pruned only when it had been cut 3 or less years ago.

ESTIMATION OF FRUIT AND SEED PRODUCTIVITY, AND SEED MASS

We estimated the number of fruits per tree on three to 18 fruiting trees per population for a total of 94 trees, and an average of 82·76 ± 13·98% fruiting trees sampled per population. When the number of fruits per tree was less than 100, all the fruits on the tree were counted. When the number of fruits was more than 100, we counted the number of fruits per branch on 25% of the fruit-bearing branches and extrapolated to the total number of fruit-bearing branches.

In each population, we selected all trees that had more than 10 fruits and then sampled 10 fruits from each to count the number of seeds per fruit. We also sampled and weighed two sets of 100 seeds from each tree. The average weight of 100 seeds was used as a measure of seed mass.

DATA ANALYSES

To assess whether combined bark and foliage harvest affects reproductive patterns, and whether this varies across ecological regions, we compared the following three variables between high and low harvest populations within each ecological region: minimum fruiting diameter (MFD), percentage of trees fruiting and percentage of mature trees (d.b.h. > MFD) fruiting. As the data for each of these variables were not normally distributed, the Kruskal–Wallis test was used for these analyses.

We used analysis of covariance (ANCOVA) to test the impacts of harvest (combined pruning and debarking intensity: high vs. low harvest) on the number of fruits per fruiting tree, number of seeds per fruit, and the mass of 100 seeds within each region. Tree d.b.h. was used as the covariate. To meet the normality assumption and homogeneity of variance for this analysis, we log-transformed the number of fruits per fruiting tree.

To test the effects of ecological region on reproductive output (number of fruits/tree, number of seeds/fruit and seed mass) we used a one-way ANCOVA in which pruning intensity, debarking intensity and d.b.h. were covariates. This also allowed us to separate the effects of region on reproductive outputs from the effects of pruning and/or debarking, and to test for any combined effects of bark and foliage harvest.

We also carried out a multiple linear regression to identify predictors of fruit production and to test if the predictability of theses variables differed between ecological regions. Specifically, we carried out linear regressions on the log-transformed values of the number of fruits per tree, with six independent variables: two harvest-related variables (percentgae branches pruning and percentage trunk debarked) and four morphological variables (d.b.h., tree total height, crown height, bark thickness). Pearson's correlation was performed between the independent variables to test multicollinearity. As there were significant strong correlations between d.b.h. and total height ($r = 0{\cdot}675$, $P < 0{\cdot}0001$), d.b.h. and crown height ($r = 0{\cdot}629$, $P < 0{\cdot}0001$), total height and crown height ($r = 0{\cdot}860$, $P < 0{\cdot}0001$) and a weak correlation between d.b.h. and bark thickness ($r = 0{\cdot}378$, $P = 0{\cdot}0002$), only one morphological variable (d.b.h.) was used in the regression model. We modelled fruit production using the full model, with ecological region modelled as an indicator variable (region = 1 if Sudanian, otherwise region = 0) (Kutner *et al.* 2005). The model tested was: $\log_{10}(\text{fruits/tree}) = \beta_0 + \beta_1(\text{pruning}) + \beta_2(\text{debarking}) + \beta_3(\text{d.b.h}) + \beta_4(\text{region}) + \beta_5(\text{region} \times \text{pruning}) + \varepsilon$. In the model, ε indicates the unexplained error associated with the model, β_0 is the intercept and $\beta_1, \beta_2, \beta_3, \beta_4, \beta_5$ indicate the partial regression slopes. We used the residuals normality plot, the residual vs. fitted plot and the residuals vs. leverage plots with Cook distance to diagnose the regressions models (Quinn & Keough 2005).

Both the ANCOVA and multiple linear regression analyses were conducted using the lm package in *R* version 2·4.1 program (http://www.R-project.org; The R Foundation for Statistical Computing, 18 December 2006).

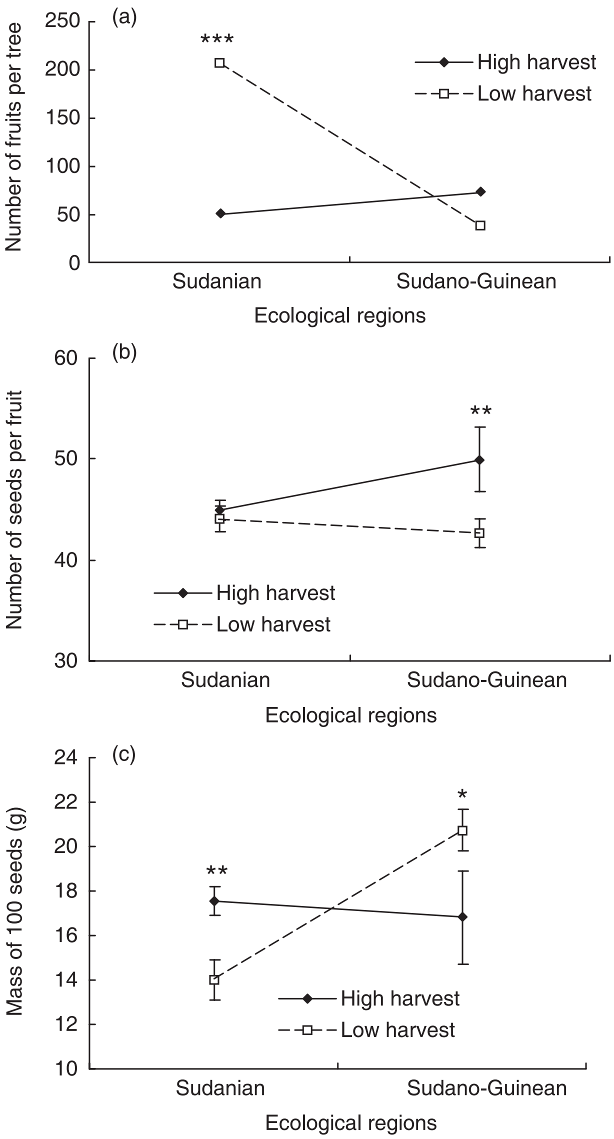

Fig. 1. Measures of reproductive output of *Khaya senegalensis* trees in high harvest vs. low harvest populations, and in two ecological regions in Benin: (a) number of fruits per tree, (b) number of seeds per fruit and (c) seed mass (g). S: Sudanian region, SG: Sudano–Guinean region. Values are mean ± 1 SE. Asterisks on the figure show significant differences between high vs. low harvest within each ecological region *$P = 0{\cdot}05$; **$P = 0{\cdot}01$; ***$P = 0{\cdot}001$.

Results

In the Sudanian region, the number of fruits per tree (ANCOVA, $P < 0{\cdot}001$) and the number of seeds per tree (ANCOVA, $P < 0{\cdot}001$) were significantly lower in high harvest populations than in low harvest populations (Fig. 1a). Trees in high harvest populations produced fruits at a significantly smaller size than those in low harvest populations (Kruskal–Wallis, $P = 0{\cdot}050$; Fig. 2a). There was no significant difference in number of seeds produced per fruit between high and low harvest populations (Fig. 1b). However, seed produced by trees in high harvest populations had higher mass than those in low harvest populations (ANCOVA, $P < 0{\cdot}001$; Fig. 1c).

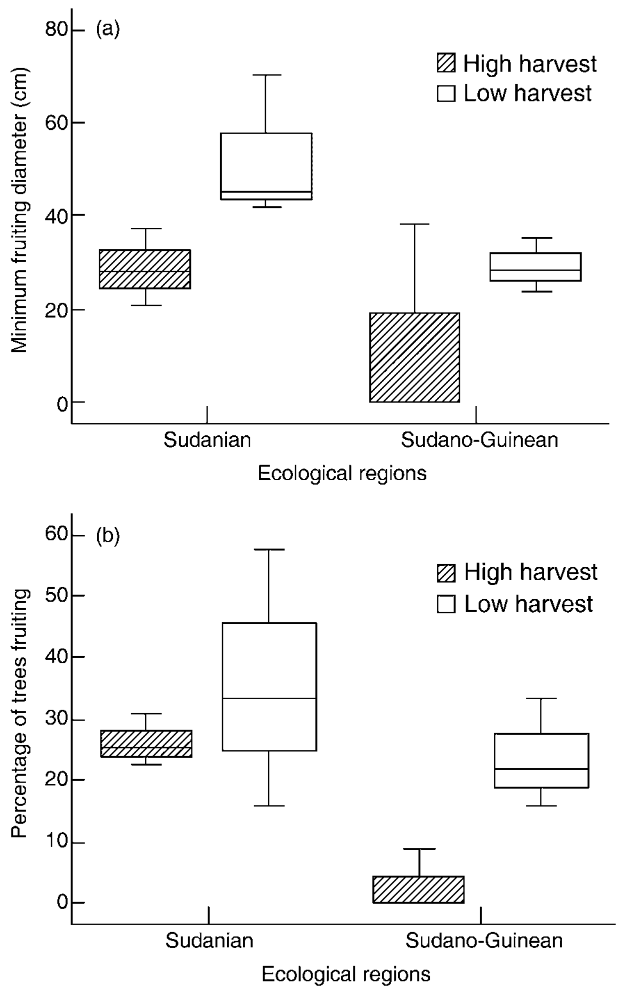

Fig. 2. Reproductive performance of *Khaya senegalensis* populations in high harvest vs. low harvest populations, and in two ecological regions in Benin: (a) minimum fruiting diameter (cm) and (b) percentage of trees fruiting (%). Boxplots show interquartile ranges and expected minimum and maximum values.

In contrast to the Sudanian region, there was no significant difference in fruit production per tree (ANCOVA, $P = 0{\cdot}334$; Fig. 1a) between high and low harvest populations in the wetter Sudano–Guinean region. There was also no significant difference in minimum fruiting diameter between populations subject to the two harvesting intensities (Fig. 2a). However, a significantly smaller proportion of trees produced fruits in high harvest than low harvest populations (Kruskal–Wallis, $P = 0{\cdot}046$; Fig. 2b). Trees in high harvest populations produced significantly more seeds per fruit than trees in low harvest populations (ANCOVA, $P = 0{\cdot}019$; Fig. 1b), but these seeds had lower mass than those produced in low harvest populations (ANCOVA, $P = 0{\cdot}031$; Fig. 1c).

Both the ANCOVA to test for differences in reproductive output between regions while controlling for differences in d.b.h., pruning intensity and debarking intensity and the multiple regression analysis illustrated that pruning had a significant impact on fruit production in the Sudanian region

Table 3. Analysis of covariance to test the effects of ecological region on *Khaya senegalensis* reproductive output with diameter at breast height (d.b.h.), tree pruning (percentage of tree crown pruned) and debarking (percentage of trunk bark removed) intensities as covariates; d.f.: degree of freedom; Asterisks represent the significance level for each term of the model: *P = 0·05; **P = 0·01; ***P = 0·001

		Log_{10}(fruit)		Seeds/fruit		Seed mass	
Source of variation	d.f.	*F*-value	*P*	*F*-value	*P*	*F*-value	*P*
Region	1	14·6992	0·0002501***	0·0128	0·91019	14·5252	0·0002704***
d.b.h.	1	27·4231	0·0000012***	0.1874	0·66628	2·4051	0·1248907
Pruning	1	14·5489	0·0002675***	0·3173	0·57481	2·0464	0·1564610
Debarking	1	0·0486	0·8260016	0·9425	0·33456	0·9957	0·3213618
Region × d.b.h.	1	10·5452	0·0017032**	0·0122	0·91223	1·0807	0·3016786
Region × pruning	1	6·0858	0·0157634*	2·9647	0·08896	12·3873	0·0007164***
Dbh × pruning	1	5·7125	0·0191961*	0·5479	0·46133	0·0044	0·9472546
Region × debarking	1	0·3782	0·5403064	0·0004	0·98351	0·0499	0·8238086
Dbh × debarking	1	0·1613	0·6890526	1·2091	0·27481	2·2205	0·1401209
Pruning × debarking	1	0·6305	0·4295368	0·7238	0·39744	0·0726	0·7882350
Region × d.b.h. × pruning	1	0·1102	0·7407509	2·2160	0·14052	2·3146	0·1321039
Region × d.b.h. × debarking	1	0·2550	0·6149798	0·1640	0·68657	0·6664	0·4167398
d.b.h. × pruning × debarking	1	1·0348	0·3121046	0·1007	0·75182		
Residuals	80						

Table 4. Linear regression model for *Khaya senegalensis* fruit production between two ecological regions. The independent variables are pruning intensity, debarking intensity, tree d.b.h., ecological region (used as indicator variable: region = 1 if Sudanian, otherwise, region = 0). The model tested was: $\log_{10}$(fruits/tree) = $\beta_0 + \beta_1$(pruning) + β_2(debarking) + β_3(d.b.h.) + β_4(region) + β_5(region × pruning) + ε; adj. R^2: adjusted R^2

Model	Adj. R^2	*P*
Sudanian: $\log_{10}$(fruits/tree) = 4·749 + 0·218 (d.b.h.) – 0·0178 (pruning) Sudano–Guinean: $\log_{10}$(fruits/tree) = 2·399 + 0·218 (d.b.h.).	0·367	< 0·0001

but not in the Sudano–Guinean region (region × pruning, P = 0·0157; Fig. 1a, Tables 3 and 4). The increase in fruit production per tree with increasing d.b.h. was greater in the Sudanian region than in the Sudano–Guinean region (region × d.b.h., P = 0·0017), since trees in the Sudano–Guinean region began producing fruit at a significantly smaller size than trees in the Sudanian region (Fig. 2a). In addition, pruning caused a greater decrease in fruit production in larger trees than it did in smaller trees (pruning × d.b.h., P = 0·0191). The interaction between pruning intensity and debarking intensity was not significant (P = 0·4295).

Seed mass was significantly lower in the Sudanian region than in the Sudano–Guinean region (P = 0·000284). However, the pruning × region interaction was significant (P = 0·0012), as pruning increased seed mass in the Sudanian region but decreased it in the Sudano–Guinean region (Fig. 1b). There were no significant differences between regions in the number of seeds per fruit or any significant interactions between pruning or debarking intensity and region for this variable.

Discussion

K. senegalensis foliage and bark are harvested heavily by indigenous and local peoples across the Sudanian and Sudano–Guinean regions of Benin. Our results illustrate that harvest of foliage can have significant impacts on *K. senegalensis* reproductive performance, but that responses to harvest vary significantly between the two ecological regions.

In the drier Sudanian region, high harvest populations had significantly lower rates of fruit and seed production than low harvest populations, and trees began reproducing at a smaller size. These effects are consistent with other studies that have illustrated that defoliation in woody plants can cause reductions in the number of fruits produced per inflorescence and the number of seeds produced per fruit (Obeso 1993; Ratsirason, Silander & Richard 1996; Flores & Ashton 2000; Endress, Gorchov & Noble 2004). These effects may be caused by decreased photosynthetic capacity, and/or reallocation of resources or stored reserves from reproduction to regrowth (Whitham *et al*. 1991; Fong 1992; Kigomo, Woodell & Savill 1994).

In contrast, there were no significant effects of harvest on fruit production observed in the Sudano–Guinean region. Even when differences between regions in d.b.h., pruning and debarking intensity were controlled for (covariates) in the ANCOVA, pruning still had a significantly greater effect on fruit production in the Sudanian region than in the Sudano–Guinean region. This suggests that the differential effect of pruning between the regions is explained at least in part by ecological differences. The longer dry season and higher rates of evapotranspiration in the Sudanian region make it a much more stressful environment for plants than the Sudano–Guinean region during the dry season. The added stress of high rates of foliage removal, which takes place specifically during the dry season, may therefore be expected to have a greater impact on trees in the Sudanian region than in the Sudano–Guinean region. The more stressful conditions of the Sudanian region may also explain why trees in this region begin to fruit at a significantly larger size than those in the Sudano–Guinean region. Other research has demonstrated that a plant's ability to compensate loss can depend on the resources available to it for recuperation (Obeso 1993), and that allocation of plant resources to reproduction may decrease under stressful conditions (Bazzaz *et al*. 1987; Primack 1987; He, Wolfe-Bellin & Bazzaz 2005).

However, the observed differences in response to harvest between the two regions may also be compounded by existing differences in harvesting rates and patterns between the two regions. High harvest populations in the Sudanian region have significantly higher levels of foliage harvested per tree (91·35 ± 1·83% of crown pruned) than in the Sudano–Guinean region (83·41 ± 3·92% of crown pruned) (Gaoue & Ticktin 2007). However, these differences in pruning intensity result from the migratory patterns of the Fulani, which are driven in turn by the ecological differences between the regions. During the dry season Fulani harvesters, in pursuit of both water and fodder for their herds, move southward from the drier Sudanian toward the Sudano–Guinean region, where there are better water resources available. As Fulani head south their herds become increasingly hungry, and they therefore harvest almost all the foliage of any *K. senegalensis* tree available along their migration corridor. This probably explains the high pruning pressures on trees in Sudanian region (Gaoue & Ticktin 2007).

In contrast, because most of the Fulani herds spend the peak and remaining part of the dry season in the Sudano–Guinan region, a greater proportion of trees are pruned in that region than in the Sudanian region (Gaoue & Ticktin 2007). This may help to explain the significantly lower proportion of fruiting trees in high harvest populations in the Sudano–Guinean region. It is also possible that differences in *K. senegalensis* habitat within the Sudano–Guinean region could confound some of the effects of harvest in this region.

Our results indicate that bark harvest does not contribute significantly to the observed effects of pruning on reproduction, and that there are no additive effects of combined pruning and debarking. This is probably because bark harvest intensity was fairly low across all populations (17·69 ± 7·32% of trees were debarked), and only 13·20 ± 5·45% of trees were subject to both debarking and pruning (Gaoue & Ticktin 2007).

Plants may increase the probability of successful germination and establishment by investing resources in producing a large number of seeds or by increasing the size of seeds produced, as larger seeds tend to have a better chance of germinating and producing larger viable seedlings with a better probability of establishment than smaller seeds (Kidson & Westoby 2000; Baraloto, Forget & Goldberg 2005; Moles & Westoby 2006). For *K. senegalensis* this trade-off between seed size and seed number appears to vary between the two ecological regions. In low harvest populations, trees in the Sudanian region produced more seeds than those in the Sudano–Guinean region, but these seeds had lower mass. In addition, the decreased rates of seed production in high harvest populations in the Sudanian region were accompanied by an increase in seed mass, while the reverse was true for the trees in high harvested populations in the Sudano–Guinean region. Further investigation will be necessary to assess whether seed mass does indeed affect germination and establishment of *K. senegalensis* in both regions.

IMPLICATIONS FOR CONSERVATION

This study illustrates that heavy rates of foliage harvest can decrease rates and patterns of reproduction in *K. senegalensis*, and that the impacts may vary significantly across differing environmental and/or harvesting contexts. Lowered rates of reproduction may lead to decreases in *K. senegalensis* population size over the long term. However, this is difficult to test in *K. senegalensis* and other NTFP species like it that are subject to multiple sources of disturbance. For instance, other research has illustrated that, in some areas, high harvest populations of *K senegalensis* have lower densities of seedlings and saplings (Gaoue & Ticktin 2007), but these results are difficult to interpret as *K. senegalensis* populations are subject to many other confounding disturbances that also affect seedling germination and survival, including grazing and dredging.

None the less, reports from local Fulani harvesters indicate that populations are decreasing, due most probably to the logging pressure to which this species is also subject. Logging would contribute to a decrease in fruit production at the population level, as it decreases the number of reproductive individuals. In addition, the increasing populations of Fulani harvesters migrating into Benin from other neighbouring countries, and the increasing drought in the region, are leading to increasing harvesting pressure of *K. senegalensis*. This can be expected to increase the negative effects of harvest. There is therefore a need to develop better *ex situ* conservation strategies for *K. senegalensis* in order to provide other sources of fodder to Fulani cattle. Our results indicate that priority should be placed clearly in the Sudanian region, where the impacts of pruning on *K. senegalensis*, regardless of harvest intensity, are more severe. This may be achieved most effectively through the promotion of *K. senegalensis* plantation programmes involving Fulani harvesters. *K. senegalensis* plantations (although for timber) have been established successfully in other parts of the country.

To date, most studies of the effects of NTFP harvest have reported results from less than three populations (Ticktin 2004). Our work underscores the great importance of assessing the impacts of NTFP harvest in a range of locations and environmental conditions in order to design effective conservation and management plans.

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