Contributed Paper

Effects of Harvest of Nontimber Forest Products and Ecological Differences between Sites on the Demography of African Mahogany

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Abstract: *The demographic impacts of harvesting nontimber forest products (NTFP) have been increasingly studied because of reports of potentially unsustainable harvest. Nevertheless, our understanding of how plant demographic response to harvest is altered by variation in ecological conditions, which is critical for developing realistic sustainable-use plans, is limited. We built matrix population models to test whether and how variation in ecological conditions affects population responses to harvest. In particular, we examined the effect of bark and foliage harvest on the demography of populations of African mahogany (*Khaya senegalensis*) in two contrasting ecological regions of Benin, West Africa. K. senegalensis bark and foliage harvest significantly reduced its stochastic population growth rates, but ecological differences between regions had a greater effect on population growth rates than did harvest. The effect of harvest on population growth rates ($\Delta\lambda$) was slightly stronger in the moist than in the drier region. Life-table response experiments revealed that the mechanism by which harvesting reduced λ differed between ecological regions. Lowered stasis (persistence) of larger life stages lead to a reduction in λ in the drier region, whereas lowered growth of all life stages lowered λ in moist region. Potential strategies to increase population growth rates should include decreasing the proportion of individuals harvested, promoting harvester-owned plantations of African mahogany, and increasing survival and growth by promoting no-fire zones in gallery forests. Our results show how population responses to harvest of NTFP may be altered by ecological differences across sites and emphasize the importance of monitoring populations over the climatic range in which they occur to develop more realistic recommendations for conservation.*

Keywords: Africa, ecological variability, fulani, *Khaya senegalensis*, life-table response experiment, matrix models, nontimber forest products, NTFP, stochastic growth rate

Efectos de la Cosecha de Productos Forestales No Maderables y Diferencias Ecológicas entre Sitios sobre la Demografía de Caoba Africana

Resumen: *Los impactos demográficos de la cosecha de productos forestales no maderables (PFNM) han sido estudiados con mayor intensidad debido a reportes de cosechas potencialmente no sustentables. Sin embargo, nuestro entendimiento de cómo se altera la respuesta demográfica de las plantas debido a la variación en las condiciones ecológicas, lo cual es crítico para el desarrollo de planes de uso sustentable realistas, es limitado. Construimos modelos poblacionales matriciales para probar sí y como la variación en las condiciones ecológicas afecta las respuestas de la población a la cosecha. En particular, examinamos el efecto de la cosecha de corteza y follaje sobre la demografía de poblaciones de caoba africana (*Khaya senegalensis*) en dos regiones ecológicamente contrastantes de Benin, África Occidental. La cosecha de corteza y follaje de K. senegalensis significativamente redujo sus tasas de crecimiento poblacional estocástico, pero las diferencias ecológicas entre regiones tuvieron un mayor efecto sobre las tasas de crecimiento poblacional que*

la cosecha. El efecto de la cosecha sobre las tasas de crecimiento poblacional (λ) fue ligeramente mayor en la región húmeda que en la seca. Los experimentos de respuesta de tablas de vida revelaron que el mecanismo mediante el la cosecha redujo a λ difirió entre regiones ecológicas. Un menor balance (persistencia) de etapas de vida avanzadas llevó a una reducción en λ en la región más seca, mientras que un menor crecimiento de todas las etapas de vida disminuyeron λ en la región húmeda. Las estrategias potenciales para incrementar las tasas de crecimiento poblacional incluyen la disminución de la proporción de individuos cosechados, la promoción de plantaciones de caoba propiedad de quien las cosecha y el incremento de la supervivencia y el crecimiento mediante la promoción de zonas sin fuego en los bosques de galería. Nuestros resultados muestran cómo se pueden alterar las respuestas de la población a la cosecha de PFNM por las diferencias ecológicas entre sitios y enfatizan la importancia del monitoreo de poblaciones a lo largo del rango climático en que ocurren para desarrollar recomendaciones de conservación más realistas.

Palabras Clave: África, experimento de respuesta de tabla de vida, Fulani, *Khaya senegalensis*, modelos matriciales, PFNM, productos forestales no maderables, tasa de crecimiento estocástico, variabilidad ecológica

Introduction

How harvesting affects the population dynamics of nontimber forest product (NTFP) species has been an important question in conservation biology over the past two decades (e.g., Pinard 1993; Ticktin et al. 2002; Zuidema et al. 2007). Nontimber forest products are biological materials (e.g., leaves, barks, fruits) other than timber that are extracted from forests for human use (de Beer & Mcdermott 1989). These products are sources of medicine, food, and construction material for millions of people worldwide (Bawa et al. 2004), and an understanding of their demography is critical for developing sustainable harvest guidelines. In tropical regions NTFP harvest is often proposed as a sustainable alternative to more destructive land uses that can simultaneously improve the livelihoods of local people. Some authors have been critical of this view, however (Belcher & Schreckenberg 2007).

The growing number of studies on the ecological impacts of NTFP harvest have yielded variable findings. Some studies show that NTFP harvest negatively affects reproduction and population growth rate (e.g., Peres et al. 2003; Rijkers et al. 2006), whereas others show that harvest may not affect population dynamics at all (e.g., Emanuel et al. 2005; Guedje et al. 2007). This difference in harvest response occurs because the tolerance of any plant species to harvest depends on many factors, including the harvested plant's life history, part harvested, environmental conditions, and management practices (Ticktin 2004). Of these factors, the least explored is the impact of environmental conditions on NTFP demographic responses to harvest. Although many NTFP species are harvested over large and environmentally variable regions and plant demographic patterns can be highly influenced by environmental variation (Horvitz & Schemske 1995; Menges 2000), most NTFP studies used three or fewer populations (Ticktin 2004). Ignoring variation in environmental conditions and how it affects NTFP dynamics and responses to harvest can lead to conclusions about sustainability that may be suboptimal or even erroneous.

Results of a small number of studies demonstrate that demographic patterns of harvested NTFP vary with habitat type and forest age (e.g., Escalante et al. 2004; Ticktin & Nantel 2004). Nevertheless, if and how the impacts of harvest interact with variation in environmental conditions remains largely unaddressed (but see Ghimire et al. 2008).

Matrix projection modeling (Caswell 2001) is widely used to investigate population dynamics from long-term data collected on permanent plots and is now increasingly used in studying the demographic effects of NTFP harvest (e.g., Ticktin et al. 2002; Endress et al. 2004; Ghimire et al. 2008). Deterministic matrix population models suppose time-invariant dynamics within the studied systems. Many populations, however, experience spatiotemporal variation in environmental conditions. Stochastic matrix population modeling is an alternative that takes environmental stochasticity into account, and it is one way to incorporate differences in environmental conditions and in rates of NTFP harvest in modeling the impact of NTFP harvest. Nevertheless, our understanding of the mechanisms underlying the reduction (or not) in population growth rates as a response to NTFP harvest is still limited. Life-table response experiment (LTRE) is a retrospective technique used to identify life-history transitions that are most responsible for observed variation in population growth rates (Caswell 2001). In the context of harvest, LTRE may be used to identify the mechanisms by which harvesting NTFP may alter population growth rates.

African mahogany (*Khaya senegalensis* [Desr.] A. Juss [Meliaceae]) is a multipurpose tree found in two contrasting ecological regions of Benin, West Africa: a drier Sudanian region and a moist Sudano–Guinean region. African mahogany foliage is heavily harvested by the indigenous Fulani people to feed their livestock and is one of the few sources of fodder in the dry season (Gaoue & Ticktin 2007). For the Fulani, raising cattle is a vital source of income and an integral part of their culture. African mahogany bark is harvested by local farmers (Gaoue & Ticktin 2007) and is used as an important

Table 1. Population growth rates (λ and 95% bias corrected CI) for 12 *Khaya senegalensis* populations studied in two ecological regions of Benin for 2004–2005 and 2005–2006.

Ecological region	Population (coordinates)	Vegetation type	Harvest intensity[a]	2004-2005 λ (95% CI)	2005-2006 λ (95% CI)
Sudano–Guinean[b]	Dogue (09°05 N, 1°56E)	woodland	high	1.000 (0.999-1.1000)	1.000 (0.999-1.001)
	Okpara (09°16 N, 2°43E)	woodland	high	0.9600 (0.960-1.000)	1.000 (0.960-1.000)
	Sakarou (09°52 N, 2°46E)	dry forest	high	1.000 (1.000-1.003)	0.999 (0.999-1.000)
	Boukoussera (09°06 N, 2°32E)	dry forest	low	1.042 (0.991-1.118)	0.999 (0.999-1.000)
	Sinisson (09°45 N, 2°41E)	woodland	low	1.003 (1.000-1.007)	1.035 (0.968-1.153)
	Penelan (09°15 N, 1°30E)	gallery	low	0.837 (0.688-0.916)	0.999 (0.999-1.000)
Sudanian[c]	Barabon (11°45 N, 2°45E)	gallery	low	0.999 (0.999-1.001)	1.003 (0.999-1.007)
	Nipuni (11°39 N, 2°39E)	gallery	low	1.000 (1.000-1.001)	1.000 (0.999-1.000)
	Fetekou (10°42 N, 2°18E)	gallery	low	0.999 (0.999-1.000)	0.999 (0.999-1.000)
	Gbeba (10°15 N, 1°52E)	gallery	high	0.999 (0.999-1.000)	1.006 (1.000-1.015)
	Nigoussourou (10°17 N, 2°10E)	gallery	high	0.999 (0.999-1.000)	1.002 (1.000-1.004)
	Soassararou (10°12 N, 2°01E)	gallery	high	0.957 (0.885-1.000)	0.968 (0.904-1.000)

[a]*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.*
[b]*Annual rainfall, 1100-1300 mm; average temperature, 24-31 °C; active vegetative growth period, 200 days.*
[c]*Annual rainfall 900-1100 mm; average temperature, 25-29 °C; active vegetative growth period, 145 days.*

medicine to treat various diseases including malaria, gastrointestinal diseases, and anemia (Arbonnier 2000). In addition, it is highly prized for its timber (CTFT 1988). Removal of foliage and bark is expected to decrease individual growth and productivity. We investigated the demographic response of African mahogany to combined bark and foliage harvest in Benin (West Africa) and tested whether and how the response is altered by ecological differences between dry and moist regions. Specifically, we followed the dynamics of harvested and unharvested *K. senegalensis* populations in the two ecological regions and used deterministic and stochastic matrix population models and factorial LTRE to address the following research questions: Does bark and foliage harvest reduce population growth rates? Do differences in environmental conditions affect population growth rates? Is the effect of harvest on population growth rates stronger in the drier region than in the moist region? Is the overall effect of harvest on population growth rates greater than the effect of ecological differences? What mechanisms underlie the reduction (or not) of population growth rates by bark and foliage harvest? And, are these mechanisms different between ecological regions? We considered the implications of our results for sustainable harvest and conservation of African mahogany and other NTFP that span wide climatic or ecological ranges.

Methods

Study System

Benin (6°-12°50 N and 1°-3°40E) (West Africa) is in the Dahomey Gap, a dry corridor of savanna that splits the African rainforest block into two parts. The climate is dry, with subequatorial Guineo-Congolean (6°25-7°30 N), Sudano–Guinean (7°30-9°30 N), and Sudanian regions (9°30-12°N). We carried out our study in the Sudano–Guinean and Sudanian regions, where African mahogany is found. The Sudano–Guinean region is wetter and has a longer rainy season and a more diversified habitat than the Sudanian region (Table 1). African mahogany is a shade-intolerant semideciduous tree that grows up to 30 m high and is found mostly on alluvial soils along gallery forest, although it can occur on reddish clayey lateritic soils (CTFT 1988).

To assess the demographic impacts of harvesting bark and foliage across the Benin landscape, we studied 12 populations of African mahogany that had different bark and foliage harvest intensity, ecological conditions, and geographic location (Table 1). We studied six populations in each ecological region. In the Sudanian region, populations were in gallery forests because this is where almost all African mahogany populations were found. In the Sudano–Guinean region, we studied populations in

various vegetation types (gallery forest, dense dry forest, woodland) because there were not enough populations in any vegetation type (Table 1). African mahogany population density varied from 27 stems/ha to 208 stems/ha in 2004 and from 29 stems/ha to 237 stems/ha in 2005 (O.G.G., unpublished data).

We surveyed 29 populations of African mahogany across the study areas and estimated their size and harvesting intensity. From this set of populations, in each ecological region, we randomly selected three populations subject to high rates of foliage and bark harvest (high-harvest populations) and three populations subject to low rates of harvest or no harvest (low-harvest populations). High-harvest populations had more than 50% of trees pruned (branches harvested by people) (mean [SD] =58.21% [6.80]) and more than 10% of trees debarked (mean = 17.69% [7.32]). Low-harvest populations had <5% of trees pruned (mean = 4.80% [3.16]) and <10% of trees debarked (mean = 9.71% [5.20]) (Gaoue & Ticktin 2007). No populations had intermediate harvest intensities. We also did not locate any unharvested populations in the Sudanian region and found only one unharvested population in the Sudano–Guinean region. One population (Penelan) that was not harvested until 2004 was heavily logged in 2005. We therefore analyzed the data with and without this population. Pruning and debarking take place mostly on mature trees (diameter at breast height [dbh] >30 cm; Gaoue & Ticktin 2007).

Demography Censuses

In 2004 in each population, we established two 0.5-ha rectangular plots (50 × 100 m in woodlands and dry, dense forests and 10 × 500 m in gallery forests, where forest width is rarely >10 m) to tag all *K. senegalensis* trees with dbh >5 cm. Within each plot, five 0.1-ha square subplots (10 × 10 m) were established (one subplot in each corner of the 0.5-ha plot and one in the center of the plot) to monitor seedlings and saplings (basal diameter <5 cm).

Demographic data were collected annually from all *K. senegalensis* individuals within the plots and subplots for 3 years (2004–2006). At each census, we measured individual diameter at breast height, total height, pruning, and debarking intensities as the percentage of crown removed and trunk debarked, respectively (see Gaoue & Ticktin 2007, 2008). We considered a branch pruned only when it had been cut three or fewer years previously. We did not distinguish between branches pruned once versus those pruned on multiple occasions because it was difficult to accurately trace the pruning history of branches back more than 3 years. We learned from the Fulani that a tree (or branch) that has not been pruned for 3 years is likely to recover and will reproduce. For each population, we recorded soil and vegetation type, presence of water or rock outcrops in the stream bed,

signs of past logging and fire, protection status, and presence of loranthaceae hemiparasites on branches (only one population had a few trees attacked).

Transition-Matrix Parameterization and Projection

On the basis of biological characteristics and preliminary analyses (Gaoue & Ticktin 2007, 2008), the trunk size of larger trees, and stem size of seedlings and saplings (diameter at base [db]), we categorized African mahogany into five life stages: seedlings (db < 2 cm), saplings (2 cm ≤ db < 5 cm), juveniles (5 cm ≤ dbh < 20 cm), small reproductive individuals (AD1) (20 cm ≤ dbh < 40 cm), and large reproductive individuals (AD2) (dbh ≥ 40 cm). We used the 20-cm dbh cut off to identify reproductive from nonreproductive trees because it represents the minimum fruiting diameter for African mahogany in the study region (Gaoue & Ticktin 2008). For reproductive trees, we defined the two life stages with a cut off of 40 cm, which represents the diameter breast height at which most trees fruit (O.G.G., unpublished data). Individuals <5 cm db were divided into two stages: seedlings (< 2 cm db) and saplings (2–5 cm db) on the basis of our field observations of differences in survival (individuals < 2 cm rarely survive after fire). African mahogany seeds are not viable after 1 year in the soil (O.G.G., unpublished data), so we did not include a seed-bank category in the model.

We built 42, 5 × 5 Lefkovich stage-based transition matrices (Caswell 2001) directly from annual census field data. In the few instances in which there were very few individuals in a given life stage, we used the appropriate regional and harvesting-level mean values for this transition. To calculate fertility rates (mean number of seedlings produced per tree in each life stage) for each matrix, we counted the number of fruits produced by each individual at each annual census (Gaoue & Ticktin 2008) and the number of seedlings produced within each plot. We multiplied the plot-level seedlings to fruit ratio by the number of fruit produced by each individual in a given population to obtain the fertility of each tree. For populations and years when no fruiting occurred, we used a low value of 0.0001 for fertility to make the matrices irreducible. We built 24 single-population matrices (two annual matrices for each of the 12 populations: 2004–2005 and 2005–2006). For each of the two transition years, we built a summary matrix for each harvest level (pooled data for high vs. low harvest), for each ecological region (pooled data for Sudanian vs. Sudano–Guinean), and for each of the four combinations of the two levels of harvest and two ecological regions. We also built an overall summary population matrix for each of the two yearly transitions. To calculate demographic parameters for each population or summary matrix, we used the basic matrix population model (Caswell 2001), which projects the size and structure of populations over time:

$$\mathbf{n}(t+1) = \mathbf{A}\,\mathbf{n}(t), \qquad (1)$$

where **A** is a 5×5 stage-based matrix and $\mathbf{n}(t)$ is a vector of the number of individuals in each of the five life stages in year t, $\mathbf{n}(t+1)$ is the population vector in the following year $t+1$. The dominant eigenvalue (λ) of the time-invariant matrix **A** is equivalent to the deterministic population growth rate (Caswell 2001). We determined the stable-stage distribution, sensitivity, and elasticity matrices for each of the 42 matrices. We calculated λ for each population and summary matrix and determined the 95% bias-corrected percent confidence intervals of each λ with 2000 bootstrap runs.

Stochastic Modeling of Population Growth Rates

To account for year-to-year and environmental variability when analyzing the sustainability of NTFP harvest in the two ecological regions, we calculated the stochastic population growth rates (λ_s) by averaging successive growth rates over a long simulation with 50,000 iterations (Stubben & Milligan 2007). For each combination of ecological region and harvesting level described previously, we simulated stochastic population growth rates with random alternations of the two yearly transition matrices (2004–2005 and 2005–2006) from each population (total of six matrices for each region–harvest combination). We also used Tuljapurkar's (1990) second-order approximation to calculate $\log \lambda_s$, and found the values were close to those we obtained from the simulation; thus, we report only the simulations.

Effect of Harvest and Ecological Variation on Population Growth Rates

We tested the effects of foliage and bark harvest and ecological differences on projected population growth rates by comparing the bootstrapped confidence intervals of both the deterministic and stochastic λ values between the two different harvest intensities and ecological regions. When the confidence intervals did not overlap, we considered there to be a significant difference between the λ_s values.

We used a fixed factorial-design LTRE (Caswell 2001) to decompose the observed effects of harvesting bark and foliage, of ecological regions, and of their interactions on population growth rates. An LTRE is analogous to the analysis of variance, so we refer to ecological region and harvest as "treatments," as is the custom for LTRE (Caswell 2001: 258). In our LTRE, we modeled λ as a linear function of the effect of ecological differences, harvesting intensity, and their interactions (Caswell 2001):

$$\lambda^{(ij)} = \lambda^{(..)} + \alpha^{(i)} + \beta^{(j)} + (\alpha\beta)^{(ij)}, \qquad (2)$$

where a given $\lambda^{(ij)}$ for ecological region i and harvesting level j is a function of the sum of the dominant eigenvalue $\lambda^{(..)}$ of the mean of all matrices $\mathbf{A}^{(..)}$, the main effect of the ith level of ecological region, $\alpha^{(i)}$, the main effect of the

jth level of the harvest, $\beta^{(j)}$, and the harvest × ecological region interaction effect $(\alpha\beta)^{(ij)}$.

We decomposed the total effect of harvest, ecological region, and their interaction on the variation of λ into contributions from different vital rates (stasis, shrinkage, growth, and fertility) and life stages (seedling, sapling, juvenile, and small and large reproductive adults). The contributions to the main effects were calculated by multiplying the difference in each matrix element (a_{ij}) between the overall average population matrix $\mathbf{A}^{(..)}$ and the average matrix for each respective treatment (harvesting intensity or ecological region) $\mathbf{A}^{(i.)}$ or $\mathbf{A}^{(.j)}$ by the sensitivity of that element in the midway matrix between $\mathbf{A}^{(..)}$ and $\mathbf{A}^{(i.)}$ or $\mathbf{A}^{(.j)}$ (Caswell 2001):

$$\alpha^{(i)} = \sum_{i,j} \left(a_{ij}^{(i.)} - a_{ij}^{(..)} \right) \left. \frac{\partial\lambda}{\partial a_{ij}} \right|_{\frac{1}{2}(\mathbf{A}^{(i.)} - \mathbf{A}^{(..)})} \qquad (3)$$

$$\beta^{(j)} = \sum_{i,j} \left(a_{ij}^{(.j)} - a_{ij}^{(..)} \right) \left. \frac{\partial\lambda}{\partial a_{ij}} \right|_{\frac{1}{2}(\mathbf{A}^{(.j)} - \mathbf{A}^{(..)})} \qquad (4)$$

The contribution to the interaction effect was calculated as follows:

$$(\alpha\beta)^{(ij)} = \sum_{i,j} \left(a_{ij}^{(ij)} - a_{ij}^{(..)} \right) \left. \frac{\partial\lambda}{\partial a_{ij}} \right|_{\frac{1}{2}(\mathbf{A}^{(ij)} - \mathbf{A}^{(..)})} - \alpha^{(i)} - \beta^{(j)}. \qquad (5)$$

All demographic analyses were done in R (version 2.6.1, R Development Core Team 2007) with the package "popbio" (Stubben & Milligan 2007).

Results

The population growth rate of *K. senegalensis* populations pooled over ecological regions and harvesting intensities was significantly <1 in 2004–2005 ($\lambda = 0.9587$; 95% CI = 0.9376–0.9757), but it increased to 1.0008 (95% CI = 0.9840–1.0181) in 2005–2006. The range of λ values over all populations decreased in the second transition year ($\lambda = 0.8369$–1.0419 in 2004–2005; $\lambda = 0.9677$–1.0350 in 2005–2006). The population with the highest growth rate (Boukoussera: $\lambda = 1.0419$, CI = 0.9906–1.1179) was a low-harvest population conserved by Fulani people in the Sudano–Guinean region (Table 1). The population (Penelan) with the lowest λ (= 0.8369; CI = 0.6882–0.9166) was a low foliage- and bark-harvested population, which was heavily logged in 2005. The six largest and most reproductive trees were removed and their timber extracted. We removed this population from further analyses.

The stochastic growth rate for *K. senegalensis* populations in Benin was significantly <1 ($\lambda_s = 0.9887$; 95% CI = 0.9865–0.9909), which suggests an overall projected decline in population size. When we included the population that was logged (Penelan) in our analyses, the
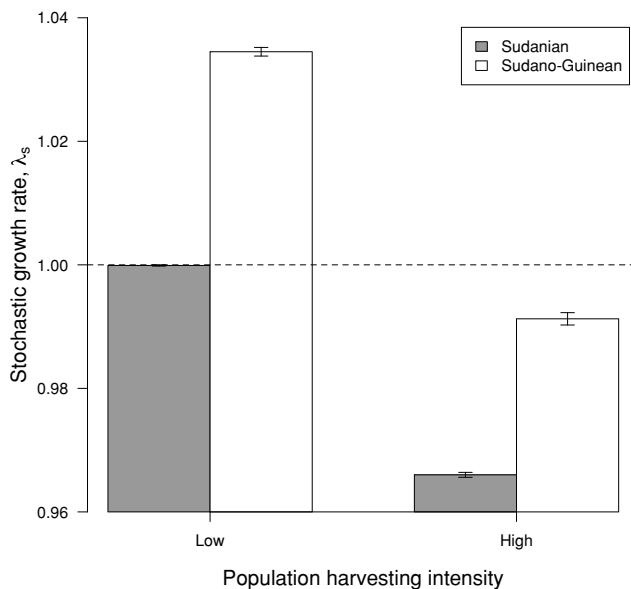
Figure 1. Interactive effects of ecological differences and bark and foliage harvest on the stochastic growth rates of African mahogany populations (error bars are 95% CI).

overall stochastic population growth rate ($\lambda_s = 0.9783$; CI = 0.9762–0.9804) was further reduced by 0.0103. Irrespective of harvest intensity, populations in the Sudanian region were projected to decline ($\lambda_s = 0.9823$; CI = 0.9819–0.9826), but populations were projected to increase in the Sudano–Guinean region ($\lambda_s = 1.0139$; CI = 1.0127–1.0153).

In each ecological region, high-harvest populations (Sudano–Guinean: $\lambda_s = 0.9913$; 95% CI = 0.9903–0.9923; Sudanian: $\lambda_s = 0.9659$; CI = 0.9655–0.9664) had significantly lower λ_s than low-harvest populations (Sudano–Guinean: $\lambda_s = 1.0345$; CI = 1.0338–1.0352; Sudanian: $\lambda_s = 0.9999$; CI = 0.9998–1.0000). In both regions, λ_s for high-harvest populations was significantly <1 (Fig. 1). The effect of bark and foliage harvest was small ($\Delta\lambda_s = 0.0148$; Fig. 1), however, and ecological differences between the two regions had twice as strong an effect on population dynamics ($\Delta\lambda_s = 0.0316$) as did harvest. The effect of harvest on population dynamics was slightly stronger in the Sudano–Guinean region ($\Delta\lambda_s = 0.0432$) than in the drier Sudanian region ($\Delta\lambda_s = 0.0339$; Fig. 1). Ecological differences also had a slightly stronger effect in low-harvest populations ($\Delta\lambda_s = 0.0346$) than in high-harvest populations ($\Delta\lambda_s = 0.0253$).

Prospective and retrospective analyses showed that survival of juvenile and adult plants had the highest contributions to future and past variations in deterministic population growth rate. Individual stasis (persistence in the same life-history stage) of African mahogany contributed 96% to the total elasticity, and growth contributed only 2.9%. Stage-specific elasticities for stasis var-
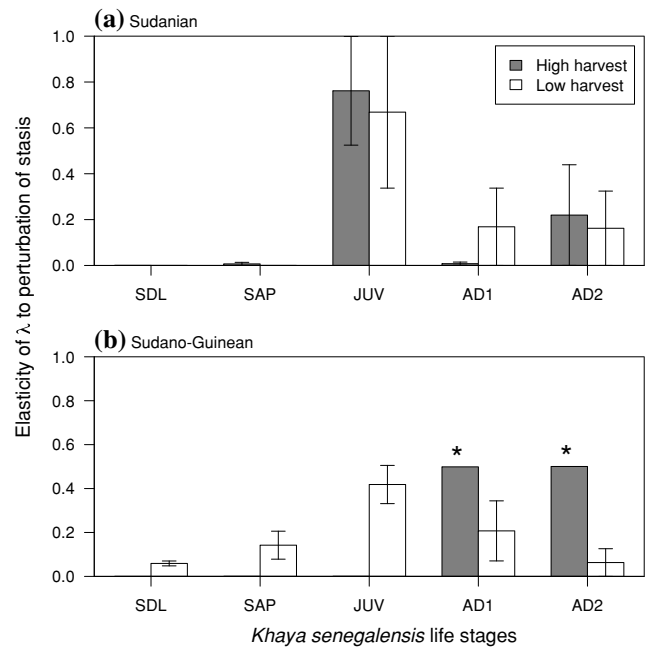

*Figure 2. Elasticity of African mahogany (*Khaya senegalensis*) population growth rate (λ) to perturbation of stasis (96% of total elasticity) in low- and high-harvest populations for the (a) Sudanian and (b) Sudano–Guinean ecological regions (SDL, seedling; SPL, sapling; JUV, juvenile; AD1, small reproductive individual; AD2, large reproductive individual; error bars, 1SE between the two transition years, 2004–2005, 2005–2006). An asterisk (*) means error bars were not included for small and large reproductive individuals for high-harvest populations in the Sudano–Guinean region because for these stages we used pooled values; thus, there was no variation.*

ied between high- and low-harvest populations in both ecological regions (Fig. 2). In the Sudanian region, population growth rate was most sensitive to the stasis of juveniles and adults. In 2004–2005 in the low-harvest populations only, stasis of small adults also had high elasticity (Fig. 2). In the Sudano–Guinean region, the importance of the stasis of different life stages to population growth rates differed markedly between the two harvesting levels. In low-harvest populations, stasis of sapling, juveniles, and small adults had the highest elasticities, whereas in the high-harvest populations, stasis of small and large adults had the highest elasticity values (Fig. 2).

The LTREs illustrated that the differences in observed λ across populations subject to different harvest intensities and in different ecological regions were mainly driven by differences in individual stasis (53.4%) and growth (38.2%) of individuals. Shrinkage (1.9%) did not have a strong effect on Δλ, and fertility contributed only 6.4%

Table 2. Life-table response experiment (LTRE) contributions of ecological region, harvest intensity, and their interaction to differences in population growth rates of African mahogany.[a]

	Total LTRE effect		Mean LTRE effect per vital rate			
LTRE effect[b]	2004–2005	2005–2006	stasis[c]	shrinkage[d]	growth[e]	fertility[f]
Ecological region						
Sudanian	−0.0083	−0.0123	0.0096	−0.0022	−0.0166	−0.0012
Sudano-Guinean	0.0611	0.0092	−0.0018	0.0077	0.0220	0.0072
NTFP harvest						
High harvest	−0.0263	−0.0026	−0.0002	−0.0010	−0.0068	−0.0065
Low harvest	0.0273	−0.0139	0.0068	0.0014	−0.0057	0.0050
Region × harvest						
Sudanian, high harvest	0.0119	0.0022	−0.0045	0.0013	0.0084	0.0019
Sudanian, low harvest	0.0076	0.0219	0.0179	−0.0011	0.0003	−0.0022
Sudano-Guinean, high harvest	0.0028	−0.0075	0.0402	−0.0020	−0.0346	−0.0059
Sudano-Guinean, low harvest	−0.0338	−0.0201	−0.0169	−0.0022	−0.0132	−0.0044

[a]Negative values of LTRE contribution for a given vital rate mean it contributed to a reduction in λ.
[b]Means (SE) of the total contribution of ecological region, NTFP harvest, and region × harvest to variation in λ across years and populations are, respectively, $|\alpha^i| = 0.0227 (0.0128)$, $|\beta^j| = 0.0175 (0.0058)$, and $|\alpha\beta^{ij}| = 0.0135 (0.0039)$ (NTFP, nontimber forest products). See text for definitions of variables.
[c]Persistence of individuals in the same size class between 2 consecutive years.
[d]Regression of individuals from a larger size class to a smaller size class.
[e]Recruitment of individuals to a larger size class from a smaller size class.
[f]Contribution of reproductive individuals to the total number of seedlings produced.

(Table 2, Fig. 3). Specifically, although there was some variation over time, the observed variation in λ values across the different harvest and ecological contexts was mostly explained by differences in stasis and growth of juvenile and small reproductive trees and the fertility of large reproductive trees. The higher λ value observed for populations in the Sudano-Guinean region than in the Sudanian region was explained mostly by the higher growth
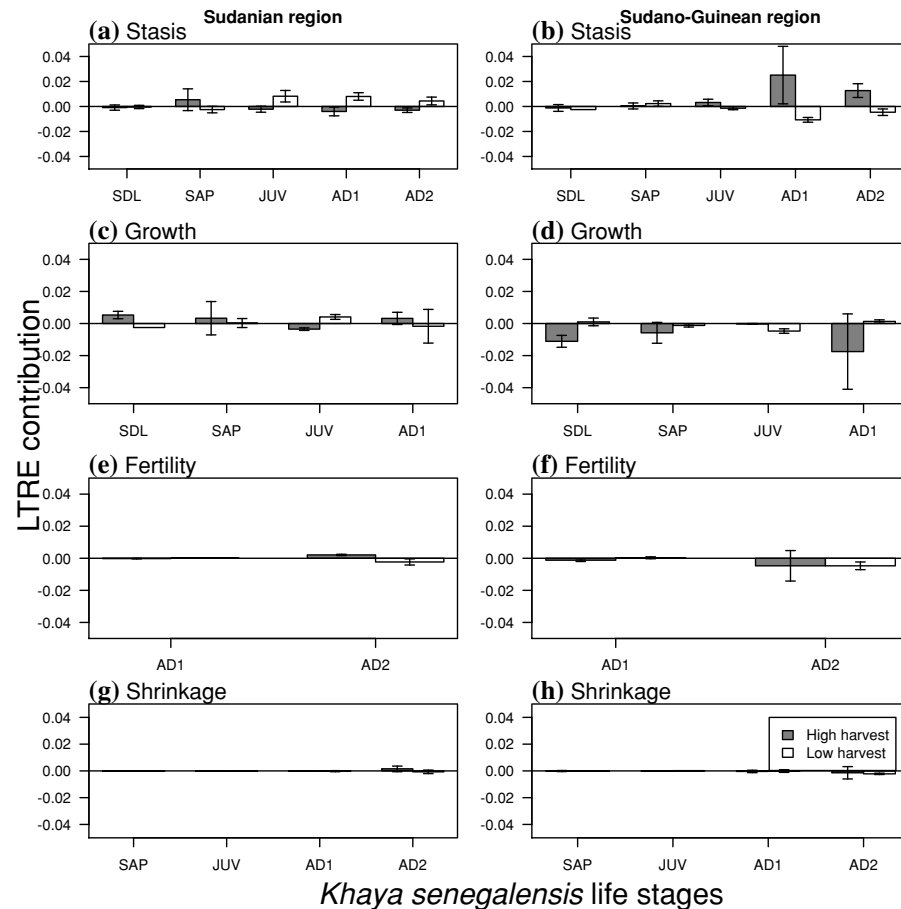

Figure 3. Life-table response experiment (LTRE) contributions of each life stage and vital rate (stasis, shrinkage, growth, fertility) to the variation of African mahogany (Khaya senegalensis) population growth rates between high- and low-harvest populations in the Sudanian (a, b, c, d) and Sudano–Guinean (e, f, g, h) regions (SDL, seedling; SPL, sapling; JUV, juvenile; AD1, small reproductive; AD2, large reproductive; error bars are 1 SE between the 2 transition years, 2004–2005, 2005–2006).

rates (Table 2) of juveniles, saplings, and seedlings in that region.

In the Sudano–Guinean region, the biggest contributors to the observed differences in λ between high- and low-harvest populations were lowered growth and higher stasis of all size classes in the high-harvest populations. This contrasts with the Sudanian region, where the biggest contributor to the observed differences in λ between high- and low-harvest populations was less stasis in juvenile, small, and large reproductive trees in the high-harvest populations (Fig. 3). Less stasis in small reproductive trees seems to be partly a result of higher growth of individuals in that life stage in high-harvest populations, but this was not the case for juveniles.

The two-way LTRE (ecological region × harvesting level) showed that ecological variation (mean [SD] $|\alpha^i|$ = 0.0227 [0.0128]) had a stronger effect on the differences in λ values across populations than did bark and foliage harvest (mean $|\beta^j|$ = 0.0175 [0.0058]) or the interaction of ecological region x harvesting (mean $|\alpha\beta^{ij}|$ = 0.0135 [0.0038]) (Table 2).

Discussion

Although NTFP are heavily harvested from woody species worldwide, and especially in highly populated regions of Africa and Asia, the demographic study of NTFP harvesting impacts has been dominated by cases studies of Latin American NTFP, especially palms (see Ticktin 2004). Most of these studies have analyzed the effect of NTFP harvest in single ecological contexts and used deterministic approaches. Nevertheless, given that many NTFP are harvested over large and ecologically variable regions and that environmental stochasticity is likely to increase with observed and forecasted changes in climate, there is a need to incorporate ecological variation into the study of NTFP species dynamics and responses to harvest. We did this and our results provide insight into the drivers of the reduction of population growth rates by NTFP harvest and how these mechanisms may depend on the environment.

Impact of NTFP Harvest in Different Ecological Contexts

Stochastic growth rates were ≥1 for African mahogany in low-harvest populations, but were significantly <1 in high-harvest populations in both regions, which indicates high harvest of bark and foliage is likely leading to long-term population decline. Regardless of harvest intensity, stochastic population growth rates were lower in the drier Sudanian region than in the Sudano–Guinean region, and this was largely due to lower rates of growth of juveniles, saplings, and seedlings in the Sudanian region. The λ_s of low-harvest populations in the Sudanian region was not significantly different from one (λ_s = 0.9999;

95% CI = 0.9998–1.0000), which indicates they were just stable but not growing. This is likely because Sudanian region populations are subject to a harsher and drier climate, with rainfall dropping to 900 mm in the region, compared with the maximum of 1200 mm in the Sudano–Guinean region. In addition, the Sudanian region is more affected by desertification and soils are the poorest in the region. Due to limited water and nutrient resources in the dry region, African mahogany distribution in this region is more limited to gallery forest, where water is available longer than in woodland and dry dense forest (Gaoue & Ticktin 2007). Studies on the demography of herbaceous species illustrate that sites with a shortage of resources (water or nutrients) or large disturbances tend to have lower growth rates (e.g., Sletvold & Rydgren 2007; Ghimire et al. 2008).

The impacts of foliage and bark harvest on population growth rates differed slightly between the two ecological regions. The marginal effect of harvest on λ_s was weaker in the drier region. Regardless of harvesting intensity, the effect of ecological variation on $\Delta\lambda_s$ was twice that of harvesting. Our results suggest that in stressful or high-disturbance contexts (e.g., in the drier Sudanian region or in high-harvest populations), the marginal effect of additional disturbance or stress may be more reduced than one might expect. The reasons for this are unclear. One hypothesis that may explain a reduced marginal effect of an additional disturbance when the other disturbance is at a higher level may be related to a saturation effect. For example, harvest may have less of an effect in the drier region if some of the individuals that may die due to harvest would in any case have high mortality due to the dry climatic conditions. The implications of our results are limited by the relatively short duration of the study.

Contributors to Differences in Population Growth Rates across Populations

Few researchers have used retrospective techniques (LTRE) to investigate the mechanisms responsible for observed variation in population growth rates among NTFP harvest treatments (but see Ticktin & Nantel 2004; Zuidema et al. 2007; Ghimire et al. 2008). Nevertheless, our results for *K. senegalensis* are consistent with the results of other studies that show observed Δλ in woody plant populations (trees, shrubs, and subshrubs) in tropical and temperate regions are largely driven by differences in stasis and growth of adults (e.g., Hoffmann 1999; Miriti et al. 2001; Davelos & Jarosz 2004), irrespective of disturbance type. The higher contribution of adult survival to Δλ in long-lived plants can be explained by the longer time they need to reach reproductive size and their large reproductive output.

The mechanisms by which bark and foliage harvest reduced population growth rates in high-harvest populations differed between the two ecological regions.

Harvest reduced growth of individuals of all size classes in the Sudano–Guinean region, but did not affect their survival. In the drier Sudanian region, harvest reduced population growth rates by reducing the survival of juveniles and reproductive trees. In the Sudano–Guinean region, the lower growth in heavily harvested populations was likely due to reduced foliage cover and therefore lower photosynthetic capacity. In the Sudanian region, trees are under more stressful conditions and have less chance of recovery after harvest. This likely explains the increased mortality in that region. A possible explanation for the lower growth of seedlings in high-harvest populations in the Sudano–Guinean region is the effect of wildfire. High-harvest populations in that region have significantly lower densities of seedlings than low-harvest populations (Gaoue & Ticktin 2007). This can lead to greater grass cover, which constitutes a higher fuel load for wild fires. Fire in the Sudano–Guinean region mostly reduces seedling growth by partially burning their main stems.

Implications for Sustainable Harvest

The low stochastic growth rates for *K. senegalensis* populations in Benin, especially for harvested populations, suggest that the species may be facing a long-term persistence problem and that the current rates of pruning (>75% of trees pruned at 100% of foliage) and debarking (<20% trees with <25% of their trunk debarked; Gaoue & Ticktin 2007) are likely not sustainable. Other demographic studies of foliage-harvesting effects show sustainable harvest rates varying between 20% and 25% for palms (Ratsirarson et al. 1996; O'Brien & Kinnaird 1996; Zuidema 2000) and 75% for herbaceous species (Ticktin et al. 2002).

The differential population growth rates and impacts of harvest on λ_s between Sudanian and Sudano–Guinean regions suggests that different management practices may be needed in the two regions. The lower λ_s for populations in the Sudanian region suggests that sustainable harvest rates should be lower in the Sudanian region. Because climbing trees is a dangerous activity, Fulani harvesters maximize the amount of foliage harvested per tree, and in most cases harvest over 80% of the crown (Gaoue & Ticktin 2007). Therefore, it would be unrealistic to promote a lowered intensity of harvest. It would be more culturally appropriate to promote a reduction in the percentage of trees harvested in each population and potentially in the frequency of harvest, although that is not something we assessed here.

Nevertheless, in reality promoting sustainable harvest limits will be difficult given the high dependence of the Fulani on this species. A concurrent strategy needed to promote lower rates of harvest would be to increase population sizes through the promotion of Fulani-owned *K. senegalensis* plantations. In discussions with Fulani

herders on ways to increase population growth, they suggested that they receive assistance in planting their own *K. senegalensis* around their compounds and farms (O.G.G. & T. T., unpublished data). Given the low population growth rates in the Sudanian region, it should be a priority for plantation projects. Although this solution may appear simplistic, its relevance stems from the fact that the idea is endogenous and that in contrast to many plantations established in the region during the colonial era these plantations would be Fulani-owned. In the Sudano–Guinean region, where illegal logging rates are one of the highest in the country (O.G.G., personal observation), promotion of government-owned plantations of faster-growing timber species will help reduce the pressure on wild *K. senegalensis* in the medium term.

Our results showed that in high-harvest populations, the elasticity of population growth rates to perturbation of juvenile and adult survival was highest and the LTRE illustrated that harvest affects African mahogany population growth by reducing the survival of individuals in the Sudanian region and by reducing their growth in the Sudano–Guinean region. Therefore, a third conservation strategy would be to promote specific management practices to increase survival and growth. Because drought, wild bush fire, and illegal logging are three other significant disturbances that affect *K. senegalensis* survival and growth, addressing these threats could increase population growth rates. One way to decrease the additional effect of fire and increase population growth rates would be to promote and test the effects of "no fire" in gallery forests because, contrary to savanna, they do not require fire to be maintained. This could be particularly important in the Sudanian region, where most populations are found in gallery forests.

Our results illustrate how the biological responses of plants to NTFP harvest may vary across ecological conditions and point to the importance of monitoring populations over the climatic range of the harvested species and over longer time periods to generate a more realistic understanding of their dynamics and therefore more realistic management plans.

Acknowledgments

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