Non-timber forest product harvest in variable environments: modeling the effect of harvesting as a stochastic sequence

Orou G. Gaoue,[1,2,4] Carol C. Horvitz,[1] and Tamara Ticktin[3]

[1]*Department of Biology, Institute of Theoretical and Mathematical Ecology, University of Miami, Coral Gables, Florida 33146 USA*
[2]*Universite de Parakou, BP 123, Parakou, Benin*
[3]*Department of Botany, University of Hawaii at Manoa, Honolulu, Hawaii 96822 USA*

Abstract. With increasing reports of overexploitation of wild plants for timber and non-timber forest products, there has been an increase in the number of studies investigating the effect of harvest on the dynamics of harvested populations. However, most studies have failed to account for temporal and spatial variability in the ecological conditions in which these species occur, as well as variability in the patterns of harvest intensity. In reality, local harvesters harvest at variable rather than fixed intensity over time. Here we used Markov chains to investigate how different patterns of harvesting intensity (summarized as return time to high harvest) affected the stochastic population growth rate (λ_s) and its elasticity to perturbation of means and variances of vital rates. We studied the effect of bark and foliage harvest from African mahogany *Khaya senegalensis* in two contrasting ecological regions in Benin. *Khaya* populations declined regardless of time between harvests of high intensity. Moreover, λ_s increased with decreasing harvesting pressure in the dry region but, surprisingly, declined in the moist region toward $\lambda_s = 0.956$. The stochastic elasticity was dominated by the stasis of juveniles and adults. The declining growth rate with decreasing harvest pressure in the moist region was mainly driven by the declining mean survival rates of juveniles and adults. Our results suggest that modeling the temporal variability of harvest intensity as a Markov chain better mimics local practices and provides insights that are missed when temporal variability in harvest intensity is modeled as independent over time and drawn from a fixed distribution.

Key words: African mahogany; Benin, West Africa; contrasting ecological conditions; effect of NTFP harvest; environment-specific elasticity; harvest return time; Khaya senegalensis; *Markov chain; matrix models; stochastic elasticity; tropical trees.*

INTRODUCTION

Non-timber forest products (NTFP) are biological materials other than timber, which are extracted from forests for human use (de Beer and Mcdermott 1989). These resources include seeds, flowers, fruits, leaves, roots, bark, and latex, and have been harvested as sources of food, medicine, and construction materials by indigenous people for thousands of years. The harvest of non-timber forest products across tropical forests, savannah, and woodlands is very common, given its economic and sociocultural importance (Bawa et al. 2004, Ticktin 2004). Many species chronically harvested for their NTFP are facing declines over time (Peres et al. 2003, Silvertown 2004). The importance of investigating the effect of NTFP harvest goes beyond the sustainability of harvesting itself, and has implications for the fate of more complex ecological interactions between harvested plants and animal species that depend on the former as sources of food or shelter while serving as

dispersal agents or improving seed germination (e.g., Silvertown 2004).

Harvesting is most often modeled as a source of mortality within the framework of density-dependent population growth (e.g., Beddington and May 1977, Boyce et al. 1999, Jonzen et al. 2002, Poysa et al. 2004). A key point is that, in classical theory of both grazing (e.g., Noy-Meir 1975, Caughley and Lawton 1981) and harvest (King 1997: Chapter 4), net production of biotic resources has density-dependent dynamics; net production is higher at lower density (individuals or biomass) and zero at maximum sustainable density (carrying capacity). In this context, harvest, by reducing density to be lower than carrying capacity, leads to enhancement of short-term net production rate. Maximum sustainable yield in such systems occurs at a lower density than carrying capacity. Applications have emphasized figuring out which density best optimizes the yield. This kind of theory is appropriate for fisheries or timber, where harvest leads to removal of individuals or biomass from populations that were at or near their carrying capacity prior to harvest, and maximum sustained yield is achieved at a population level that is well *below* the carrying capacity. However, it may not necessarily be

applicable to harvest of non-timber forest products (e.g., bark, foliage, fruits) where harvest does not generally kill harvested individuals directly but may affect their survival probability, growth, or fertility, and populations may not be at a density-driven equilibrium. The focus for NTFP has been on evaluating how harvest impacts asymptotic population dynamics modeled by projection matrices. Such an approach has also been used in evaluating the effects of herbivores on plants (Ehrlen 2003, Maron and Crone 2006, Farrington et al. 2009). In this framework, harvest is expected to have a negative or neutral effect on population growth rate depending upon its effects on matrix parameters and the sensitivity of population growth to changes in the parameters.

Over the past two decades, more than 50 published studies have modeled the impact of harvesting various types of NTFPs on plant population growth rate, including harvest of fruit and seed (Bernal 1998, Peres et al. 2003, Emanuel et al. 2005), palm foliage and heart (Pinard 1993, Boot and Gullison 1995, Olmsted and Alvarez-Buylla 1995, Endress et al. 2004, Zuidema et al. 2007), roots (Nantel et al. 1996, van der Voorta and McGraw 2006), herbs, ramet, and foliage (Nault and Gagnon 1993, Ticktin et al. 2002, Ghimire et al. 2008), and tree foliage and bark (Guedje et al. 2003, 2007, Gaoue and Ticktin 2010). Most studies have assumed that harvest intensity is constant across years. The few that have included variability in harvest intensity over time (e.g., Nantel et al. 1996, Ticktin et al. 2002, Ghimire et al. 2008, Gaoue and Ticktin 2010), assumed that each year's intensity of harvest was independent from prior years (independently and identically distributed [i.i.d.] processes; Caswell 2001) and neglected any environmental or temporal autocorrelation. However, abundant evidence indicates that harvest intensity of NTFP varies over space and time and that ecological characteristics like moisture and temperature also vary across the regions where harvest takes place (Gaoue and Ticktin 2007, Ghimire et al. 2008). Moreover, harvesters often adjust current harvesting intensity at a site based on their expectation of successful yield and of resource recovery time in the context of local patterns of previous harvesting. Other factors may interact to determine which site to harvest in a given year, including variation in tree density across the landscape and land-use tenure. That is, local people often decide how much and when and where to harvest based on their knowledge of the response of harvested individuals to previous harvest (Berkes et al. 2000, Turner et al. 2000, Ghimire et al. 2005). However, in some contexts where access to resources is highly competitive or where traditional harvesting practices are lacking or unknown, decisions about whether and how much to harvest may be independent of previous results. Then, harvest intensity and frequency may be higher than local people themselves would consider sustainable (e.g., Joyal 1996, Gaoue and Ticktin 2009).

At the population level, the temporal sequence of intensities of harvest can matter even when the overall harvesting frequency remains the same. For example, one would expect populations or individuals harvested for five consecutive years at high intensity (H), followed by three consecutive years at low-intensity (L) harvest, and then two years at medium-intensity (M) harvest (HHHHHLLLMM) to exhibit weaker recovery and fitness than one that had been harvested following the sequence HLHLHMLHMH, even though they both had been harvested five times at high intensity, three times at low intensity, and twice at medium intensity. The return time for each harvesting intensity is therefore crucial in understanding how populations respond to harvest, with longer return time to high harvest levels expected to confer higher resiliency.

The response of population to a given harvest sequence may also vary depending on the ecological context, specifically according to differences in soil moisture, fertility, and rainfall. For example, the resilience of populations to frequent high harvest may be weaker when populations are stressed by drought. Therefore, to gain a realistic understanding of the ecological impacts of NTFP harvest and to better manage NTFP populations, it is critical to understand how and why populations respond to variation in the pattern of harvest intensity over time and in different ecological contexts.

Khaya senegalensis (Meliaceae) is a tropical tree, well known as a source of mahogany timber, but also heavily harvested by indigenous people in Africa for its foliage as dry-season fodder for cattle and its bark as source of medicine (Gaoue and Ticktin 2007, 2010). In this study, we explicitly modeled foliage and bark harvesting sequences over time as a Markov process to investigate the effects of the variation in harvesting intensities at the population level on the dynamics of *Khaya* populations in two contrasting ecological regions in Benin, West Africa. The finite-state Markov chain model (Caswell 2001, Tuljapurkar et al. 2003) we used here relaxes the assumption that harvest intensities are independent over time and drawn from a fixed distribution. This approach has been used in many contexts, including studies of the effects of fire (e.g., Silva et al. 1991, Caswell and Kaye 2001) and of plant–insect interactions in hurricane-prone environments (Horvitz et al. 2005). In our study, the Markov chain model supposes that the sequence of harvesting intensity, in addition to the frequency of harvest, matters.

For long-lived species such as *Khaya*, previous studies suggest that the long-term per capita growth rate is sensitive to changes in the probability that adults remain reproductive over time (Silvertown et al. 1993, Pfister 1998, Morris and Doak 2002, Franco and Silvertown 2004, Morris et al. 2008). In this study, we asked if the relative importance of stasis to asymptotic growth rate would be altered when ecological conditions and the sequence of harvest intensity change. Recent theoretical

advances in stochastic demography (Tuljapurkar et al. 2003, Horvitz et al. 2005, 2010, Tuljapurkar and Haridas 2006, Ezard et al. 2008, Aberg et al. 2009, Ezard and Coulson 2010) provide important tools to investigate the response of populations to the stochastic variation of vital rates and the most important demographic processes driving changes in population growth rate when the environment varies. We conducted stochastic elasticity analysis to understand the population response to perturbation of mean and/or variance in vital rates (Tuljapurkar et al. 2003).

In this paper, we addressed the following questions: (1) How does harvest intensity of *Khaya* foliage and bark affect demographic rates? (2) When harvest intensity varies over years, how does the frequency and sequence of harvest intensity (summarized as the return time to high harvest) affect (a) the mean and variability of matrix elements, (b) the stochastic growth rate of the population, and (c) the sensitivity of the stochastic growth rate to perturbations of means and variabilities of matrix elements and harvest-level-specific matrix elements? For each question, we compared the results across moist and dry regions, with the expectation that dry regions are more stressful for *Khaya* than moist regions.

METHODS

Study system

Khaya senegalensis (Desr.) A. Juss is a valuable tree in the mahogany (Meliaceae) family. *Khaya* grows in the wild through a wide range of habitats (gallery forests, dry forest, savanna woodland) in tropical Africa, from 8° N to 14° N and across the continent, from the Senegal in the west to the Uganda in the East (Normand and Sallenave 1958, CTFT 1988). It is a semi-deciduous, shade-intolerant, and slow-growing tree that may reach up to 30 m in height and 3 m in girth (CTFT 1988, Keay 1989). *Khaya* is monoecious, wind-dispersed, with flat winged seeds, and small white hermaphroditic flowers that are insect-pollinated (CTFT 1988).

Khaya leaves, fruits, and bark contain a wide range of biological compounds with anti-feedant, repellent, anti-inflammatory, and antimicrobial potentials (Govindachari and Kumari 1998, Lompo et al. 1998, Nakatani et al. 2000) that may confer high commercial interest in the insecticide and health industries to the species (Muellner et al. 2003). *Khaya* is heavily harvested across West Africa for its timber, bark, and foliage. The bark is used for medicine by traditional healers and local populations to cure several human and livestock diseases (Atawodi et al. 2002). The foliage is harvested by Fulani people during the dry season as a critical source of fodder for cattle (Petit 2003, Gaoue and Ticktin 2007, 2008). The Fulani specialize in raising cattle, which are a vital source of income for them and an integral part of their culture. *Khaya* is also one of the best timber species, and the first timber species exported from Africa during the colonial era (Normand and Sallenave 1958).

Commercial companies and local populations illegally harvest the timber to depletion.

We studied the dynamics of *Khaya* populations in two contrasting ecological regions where it occurs in Benin, West Africa. The Sudanian region is dry with lower rainfall, fewer rainy months, higher mean temperature than the moist Sudano-Guinean region. Details about the ecological differences between the dry and moist regions are provided elsewhere (Gaoue and Ticktin 2007, 2008, 2010).

Khaya senegalensis *population dynamics*

We collected data on growth, survival, and fruit production over four years (2004–2007) in 12 1-ha permanent plots equally distributed in the dry and moist ecological regions of Benin. In the dry region, *Khaya* only occurs in one type of habitat: gallery forest. In contrast, in the moist region it occurs not only in gallery forest, but also in dense dry forest and woodland. Our study plots were chosen to sample this regional difference: only one habitat in the dry and diverse habitats in the moist region. We estimated the percentage of trees harvested (pruned and/or debarked) in each population. In previous work, Gaoue and Ticktin (2010) categorized *Khaya* populations in two groups of different harvest intensities (low and high). In this study, we recognized three levels of harvest intensity (low, medium, and high). Each population was classified as belonging to one of the three levels depending on the proportion of trees harvested for foliage and bark. Low-harvest populations had <25% of trees harvested; medium-harvest populations had 25–50% of trees harvested, and high-harvest populations had >50% of trees harvested. In the moist region, there were three low-, two medium-, and one high-harvest population; while in the dry region, there were three low-, one medium-, and two high-harvest populations. We classified individual trees in each population into five life stages using the basal diameter (for seedlings and saplings) and diameter at breast height (dbh; for juvenile and adults) as the metric of size: seedlings (diameter at base <2 cm), saplings (2–5 cm), juveniles (5–20 cm), small reproductive adults (20–40 cm), and large reproductive adults (dbh ≥ 40 cm). For each population and year, a population projection matrix model was developed from empirical data (Caswell 2001):

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

where **A** is a 5×5 stage-based projection matrix, $\mathbf{n}(t)$ is a 5×1 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 $t + 1$. We averaged the elements of the projection matrices across populations and years by harvest level to obtain three matrices **L**, **M**, and **H** in each region. For these matrices, we obtained the survival rate of each stage by summing rows 2–5 and the conditional growth rate of each stage, defined as the probability of advancing to the next stage given survival,

by taking the ratio of the sub-diagonal element over the corresponding survival rate. The diagonal elements are *stasis* probabilities, and the sub-diagonal elements are *unconditional* probabilities of advancing to the next stage. The dominant eigenvalue λ of each matrix is a summary measure of the average demographic quality of the environment for *Khaya* under different harvest intensities in each region, since it represents a projection of what the average per capita rate of increase in a population would be if it were constantly harvested at that level over a long time.

Modeling harvesting sequence as a Markov process

We modeled the temporal sequence of harvest intensity as a stochastic Markov process using $K \times K$ Markov transition matrices **C** that define probability rules to generate a temporal sequence of harvest intensities that a given population will experience over the long run (Tuljapurkar et al. 2003, Horvitz et al. 2005). Each matrix element $c_{\alpha\beta}$ represents the probability that a population that is currently harvested at intensity β will be harvested at intensity α the next year. We used Markov chains with three states corresponding to the three harvest intensities (low, medium, and high); therefore, $K = 3$. To generate plausible sequences of harvest intensities for a given population, we created 36 different three-state Markov chains, each chain simulating a specific management option. In this way, we altered both the frequency and sequence of high-, medium-, and low-harvest years for a given population over the long term. For example, we considered situations in which high-harvest years were most likely to be followed by low-harvest years, and contrasted these with the opposite pattern, high-harvest years most likely to be followed by another high-harvest year. To examine whether *Khaya* responds differently between ecological regions, we applied each of the Markov chain models to populations in the moist and dry regions.

Associated with each Markov chain model are several properties, including (1) the stationary distribution or ergodic frequency of levels of harvest intensity, (2) the value of the serial autocorrelation, and (3) the return time, i.e., the average number of years it takes to return to a high-harvest year after one has occurred. To estimate the return time to high harvest for each model, we considered high harvest intensity as the absorbing state and calculated the first passage time for populations starting at a high harvest level to be absorbed, using the sum of the column β = high level of harvest intensity, of the fundamental matrix **N** (Caswell 2001:112). Time between harvests should allow individual trees to recover, and thus, at a population level, the higher the return time, the lower the harvest pressure. The return times for the 36 Markov chains ranged from 1.11 to 99.11 years. To understand the effect of temporal patterns of harvest on the average fitness of the population over the long run, we examined correlations between the stochastic growth rate and return time in

each region. We used the following stochastic matrix population model:

$$n(t + 1) = X_t n(t)$$

where $n(t)$ and $n(t+1)$ are the population vectors at time t and $t+1$. $\mathbf{X}_t$ is the random population projection matrix (L, M, or H) selected at a given time t, as prescribed by a stochastic sequence of harvest levels generated by one of the Markov chain models. We calculated the stochastic growth rate λ_s for each of the 36 harvest level sequences, from numerical simulation of 100 000 time steps (Tuljapurkar et al. 2003, Horvitz et al. 2005):

$$\log(\lambda_s) = \lim_{t \to \infty}(1/t)\log[P(t)/P(0)]$$

where $P(t)$ is the population size, i.e., the sum of the elements of $n(t)$ at a given time t. Also, using these sequences, we examined how the mean and variability of three key matrix elements with the highest elasticity values (the stasis entries for juveniles, for small reproductives, and for large reproductives) changed with increasing return time in each region. Then we examined sensitivity of λ_s to perturbation of the means, variabilities, and harvest-level-specific values of matrix elements.

Perturbation analysis

For each stochastic sequence, we calculated the elasticity of λ_s to perturbation of the mean ($\mathbf{E}^\mu$) and of the variance ($\mathbf{E}^\sigma$) for each matrix element and the harvest-level-specific elasticities ($\mathbf{E}^\beta$) for each matrix element (see Tuljapurkar et al. 2003, Horvitz et al. 2005, Ezard et al. 2008). The harvest-level-specific elasticities ($\mathbf{E}^\beta$) quantify the sensitivity of the stochastic growth rate to perturbing a rate only when the population is at a given level of harvest (β = low, medium, or high). To obtain a summary of the relative importance of stasis, growth, and fertility to the influence on λ_s, we summed the relevant entries of the elasticity matrices. For stasis, we summed all the diagonal elements, for unconditional growth, we summed all the sub-diagonal and lower triangle elements, and for fertility, we summed the relevant top row elements.

RESULTS

Demographic rates for low, medium, and high levels of harvest intensity

Projected per capita population growth rate.—For *Khaya*, the lowest level of harvest intensity, if maintained constantly through time, would result in the highest per capita population growth rate in both the moist and the dry regions (Fig. 1a). At this level of harvest intensity, the dry region, on average, is a higher quality environment for *Khaya* than the moist region. The medium and high levels of harvest intensity, if maintained constantly through time, would result in per capita population growth rates that are not distinct from one another. Despite these broad patterns in projected
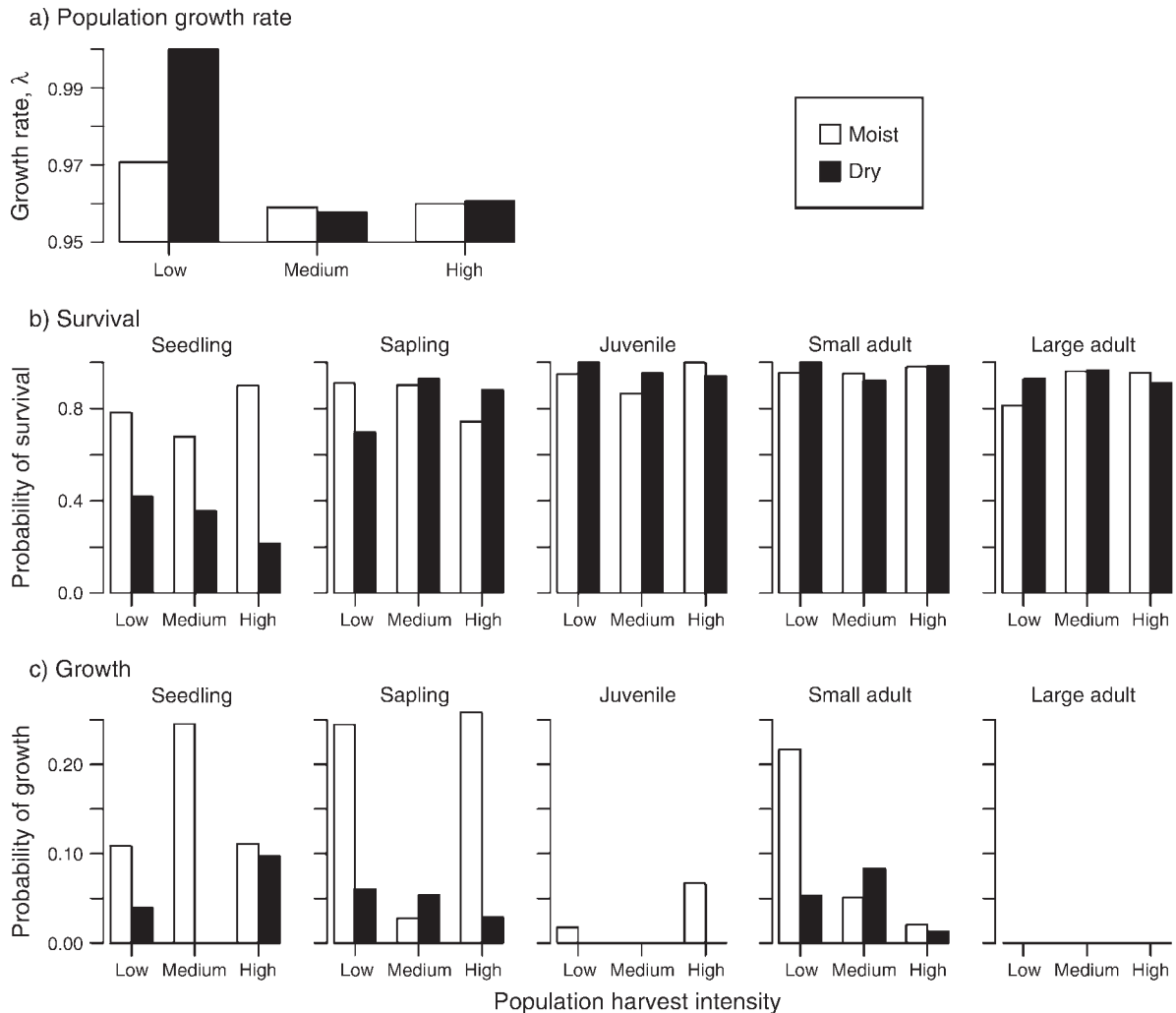
FIG. 1. (a) Population dynamics of African mahogany *Khaya senegalensis* in Benin for each harvest intensity (low, medium, and high), (b) stage-specific survival, and (c) conditional growth rate for each harvest intensity in moist and dry regions.

population growth rates, underlying stage-specific vital rates varied by region and harvest intensity in different ways.

Survival.—Seedlings survive considerably better in the moist than in the dry region (Fig. 1b). In the dry region, seedling survival decreased as harvest intensity increased, while in the moist region, it unexpectedly increased. Regional survival differences for the other stages were much smaller than for seedlings. Sapling survival in the dry region increased from low- to medium-harvest intensity, while in the moist region it decreased. Juvenile survival in the dry region was barely affected by harvest level, while in the moist region it was highest at high harvest intensity. Survival of small adults was very high, with minimal effects of either region or harvest intensity. Survival of large adults in the dry region was barely affected by harvest level, but in the moist region it increased with harvest intensity. One

summary note of interest is that in the moist region, survival of three stages (seedlings, juveniles, and large adults) was highest at the highest intensity of harvest.

Conditional growth.—Advancing one or more stages was possible for four stages at each of three harvest levels. For eight of these 12 stage–harvest-level combinations, conditional growth was better in the moist than in the dry region, usually considerably so (Fig. 1c). No more than 25% of survivors transitioned to a higher stage in any stage–harvest combination; most survivors remained in the same stage. Seedling growth in the dry region was lowest at intermediate harvest intensity, while in the moist region, it was highest at intermediate harvest intensity. Sapling growth in the dry region decreased with harvest intensity, while in the moist region, it was lowest at intermediate harvest intensity. Juveniles in the dry region did not grow into a larger stage, while in the moist region, they grew best at high
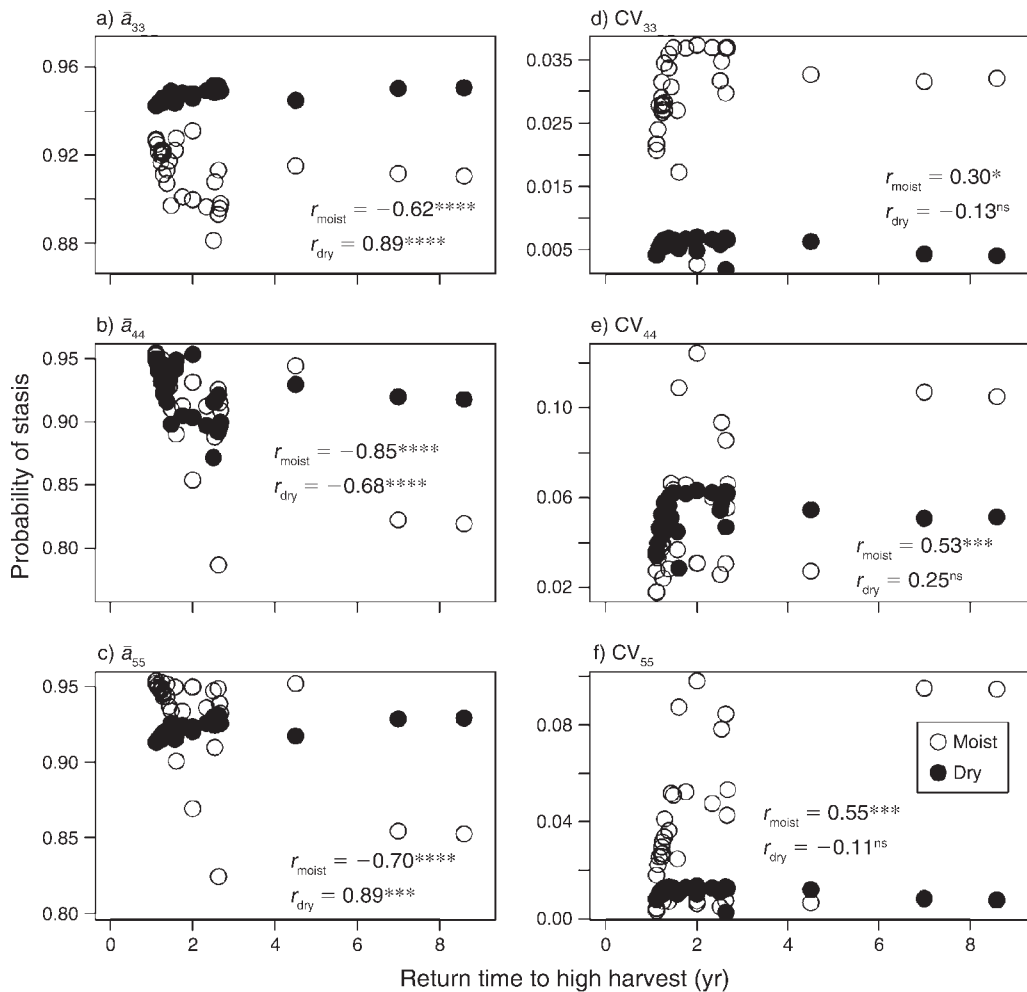
FIG. 2. Mean stasis of (a) juveniles, $\bar{a}_{33}$, (b) small adults, $\bar{a}_{44}$, and (c) large adults, $\bar{a}_{55}$, and (d–f) corresponding coefficients of variation for each harvesting sequence in moist vs. dry regions. Statistical significance of Spearman correlation coefficients is indicated by asterisks.

* $P < 0.05$; *** $P < 0.001$; **** $P < 0.0001$.

harvest intensity. Small adults in the dry region grew best at intermediate harvest intensity, while in the moist region they grew considerably better at low harvest intensity than at medium or high harvest intensity.

Demographic rates of populations experiencing variable levels of harvest

To understand means and variabilities of vital rates when populations experience variable levels of harvest, for each Markov chain, we obtained a long sequence of harvest intensities and calculated the corresponding mean and coefficient of variation for each matrix element a_{ij}. We focused on matrix elements a_{33}, a_{44}, and a_{55}, which had the highest elasticity values, and present the stasis probabilities of juveniles, small adults, and large adults, and the probabilities of remaining in the same stage from one year to another. Mean stasis probabilities of juvenile $\bar{a}_{33}$, small $\bar{a}_{44}$, and large adults $\bar{a}_{55}$ significantly decreased with increasing return time in

the moist region, while in the dry region the stasis of juveniles and small adults increased, but the stasis of small adults decreased (Fig. 2a–c). Overall, stasis probabilities were lowest in the moist region. There was less variability in stasis in the dry region than in the moist region (Fig. 2d–f). Variability in stasis slightly increased with decreasing harvesting pressure in the moist region.

Khaya populations were in decline ($\lambda_s < 1$) for all Markov chain models in both the dry and the moist regions. However, for a given Markov chain model, the decline in population size was faster in the dry region than in the moist region ($\lambda_{sdry} < \lambda_{smoist}$; Fig. 3). The stochastic population growth rate, λ_s, increased in the dry region, but surprisingly declined toward $\lambda_s = 0.956$ in the moist region when harvest pressure decreased (Fig. 3). When harvest pressure was high (low return time), the difference in λ_s between dry and moist regions
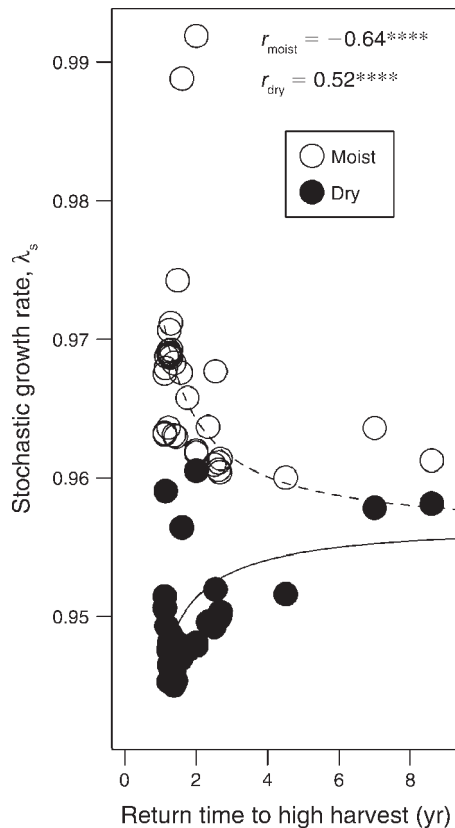
Fig. 3. Stochastic growth rates λ_s increased (in the dry region) or decreased (in the moist region) with increasing mean return time to high harvest. The regression lines were obtained from significant nonlinear Micheal is-Menten models. Statistical significance of Spearman correlation coefficients is indicated by asterisks.

**** $P < 0.0001$.

was the highest, and that difference was the lowest when harvesting pressure was low.

Elasticity of λ_s to perturbation of mean or variance: $\mathbf{E}^\mu$ and $\mathbf{E}^\sigma$

The stochastic growth rate λ_s was most sensitive to perturbation of the mean value of stasis elements (Fig. 4). The pattern of the elasticity of λ_s to perturbation of mean vital rates was remarkably different between the dry and moist regions. In the dry region, where ecological conditions were harsher, λ_s was only sensitive to perturbation in mean stasis value, except for few cases (Fig. 4b). In the moist region, the elasticity of λ_s to mean stasis remained high (>90%), regardless of harvesting pressure and was also sensitive to perturbation of mean unconditional growth and, in few cases, of fertility, mainly when harvesting pressure was high (Fig. 4a).

In the moist region, the elasticity to perturbation of stasis was dominated by stasis of adults (e_{44} and e_{55}, Fig. 5a). With decreasing harvesting pressure, the elasticity to mean stasis of small adults, e_{44}, decreased ($r = -0.87$, P

< 0.0001), but there was no trend in the variation of e_{33} or e_{55}. In the dry region, the elasticity to perturbation of mean stasis was dominated by stasis of juveniles (e_{33}; Fig. 5b); e_{33} was the lowest when harvesting pressure was high, and increased moderately with decreasing harvesting pressure. The same trend was observed for e_{55}, but the contrary was observed for e_{44} ($r = -0.55$; $P < 0.001$). Consistently in both regions, the elasticity of λ_s to perturbation of mean stasis of juveniles e_{33} and large adults e_{55} tended to increase with decreasing harvesting pressure, while it decreased for small adults.

The effect of perturbing the variability of vital rates on λ_s was small (in absolute value: 0.004–0.01) in both ecological regions and across all return times. This effect was stronger in the moist than in the dry region (Fig. 6). Although λ_s was less sensitive to perturbation of mean fertility (than to mean stasis or growth) in both ecological regions (Fig. 4), it was more sensitive to variability in mean fertility rates in the moist region (Fig. 6a). Variability in fertility and growth will have a negative effect on λ_s in the moist region, while variability in stasis will increase growth rate. There was no consistent trend in the elasticity to variability in vital rates across return time.

Harvest-level-specific elasticity, $\mathbf{E}^\beta$

The response of λ_s to perturbation of a particular vital rate differed markedly depending upon the context at the time of perturbation as defined by the level of harvest intensity when the perturbation is made. Moreover, there was a clear and strong correlation between the $\mathbf{E}^\beta$ and the return time to high harvest (Fig. 7). For low- or medium-harvest populations, the elasticity of λ_s to stasis and growth increased with increasing return time ($r_{low} = 0.64$, $r_{medium} = 0.66$, $P < 0.001$; Fig. 7). For high harvest populations, the relative importance of stasis and growth to λ_s was the highest (0.90) when harvesting pressure was the highest and it declined quickly with increasing return time to high harvest ($r_{high} = -0.99$, $P < 0.0001$; Fig. 7a). For return time greater than two years, the elasticity to stasis in high-harvest populations was no longer the highest; at that point, stasis in medium-harvest population had the greatest influence on λ_s.

DISCUSSION

In defining ecological thresholds or sustainable harvesting limits for plant resources, most emphasis has been placed on identifying the proportion of resources that can be extracted without jeopardizing the biological system. Previous models have assumed either that there would be no harvest between harvest episodes or that populations would be harvested at a fixed rate over time, or at a variable but time-independent rate, and few studies have investigated how frequently a population should be harvested (e.g., Olmsted and Alvarez-Buylla 1995, Endress et al. 2004). In reality, local people often change how much they
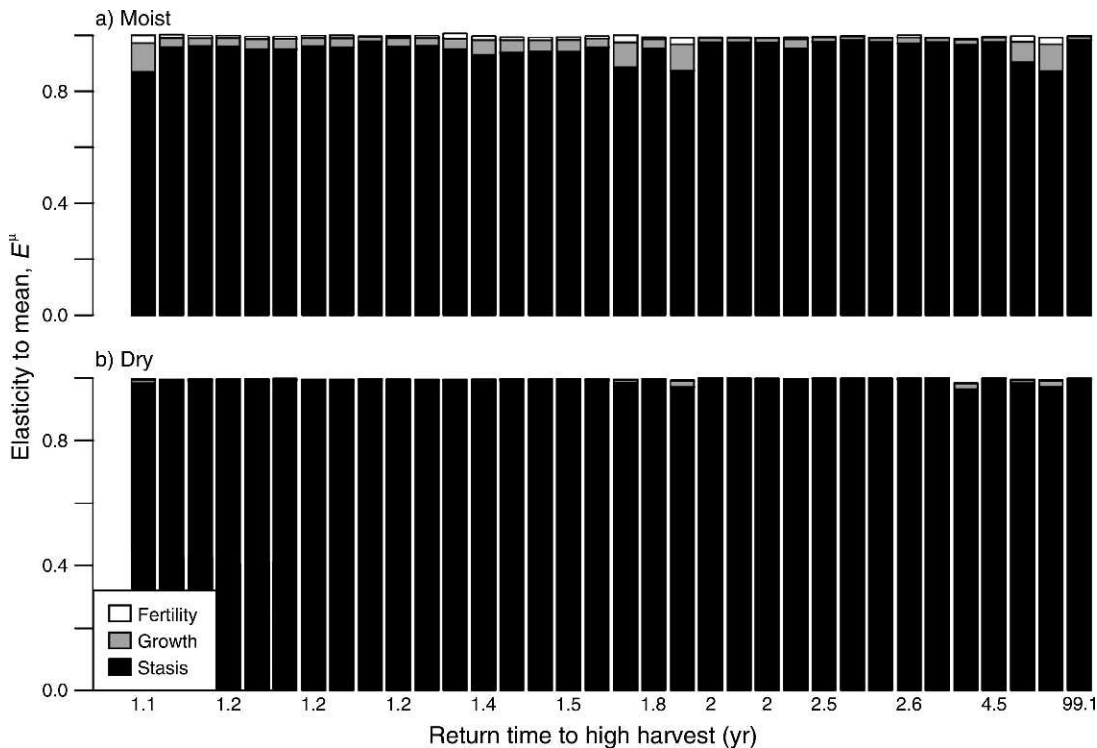
Fig. 4. Elasticity, E^μ, of the stochastic growth rate to perturbation of mean stasis, growth, and fertility in the (a) moist and (b) dry regions. The elasticity is dominated by stasis in both regions.
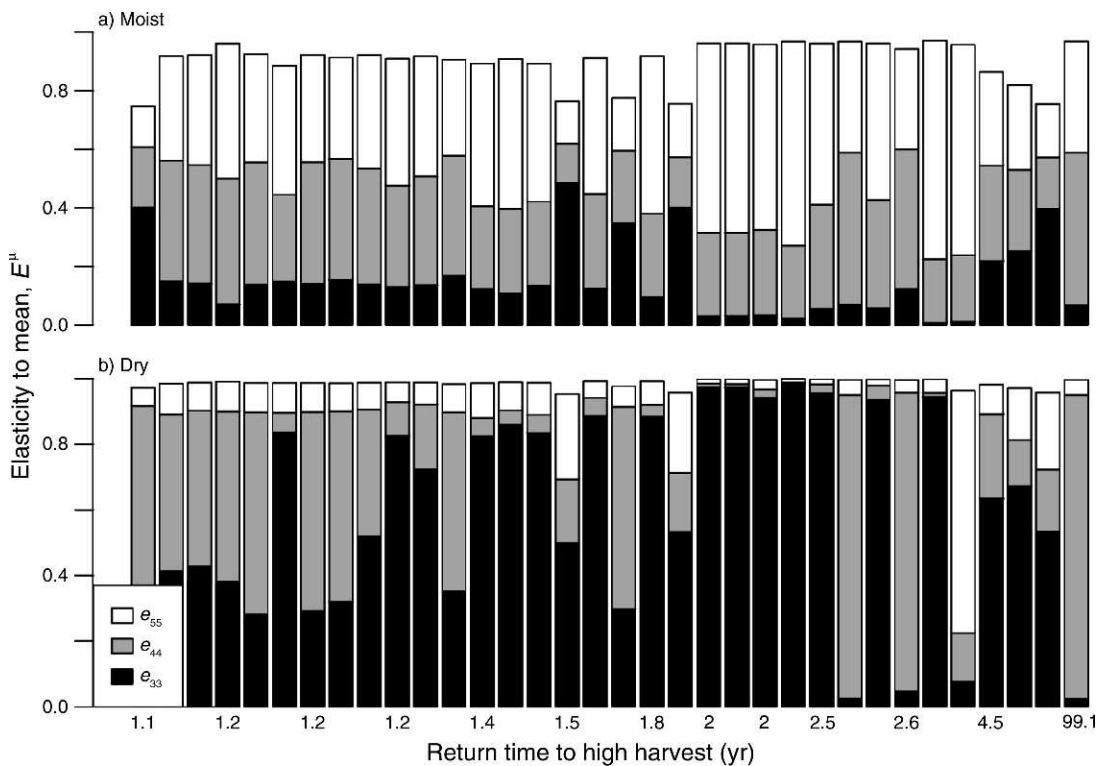

Fig. 5. Variation of the elasticity of λ_s to mean stasis of juveniles (e_{33}), small adults (e_{44}), and large adults (e_{55}), with increasing return time in the (a) moist and (b) dry regions.
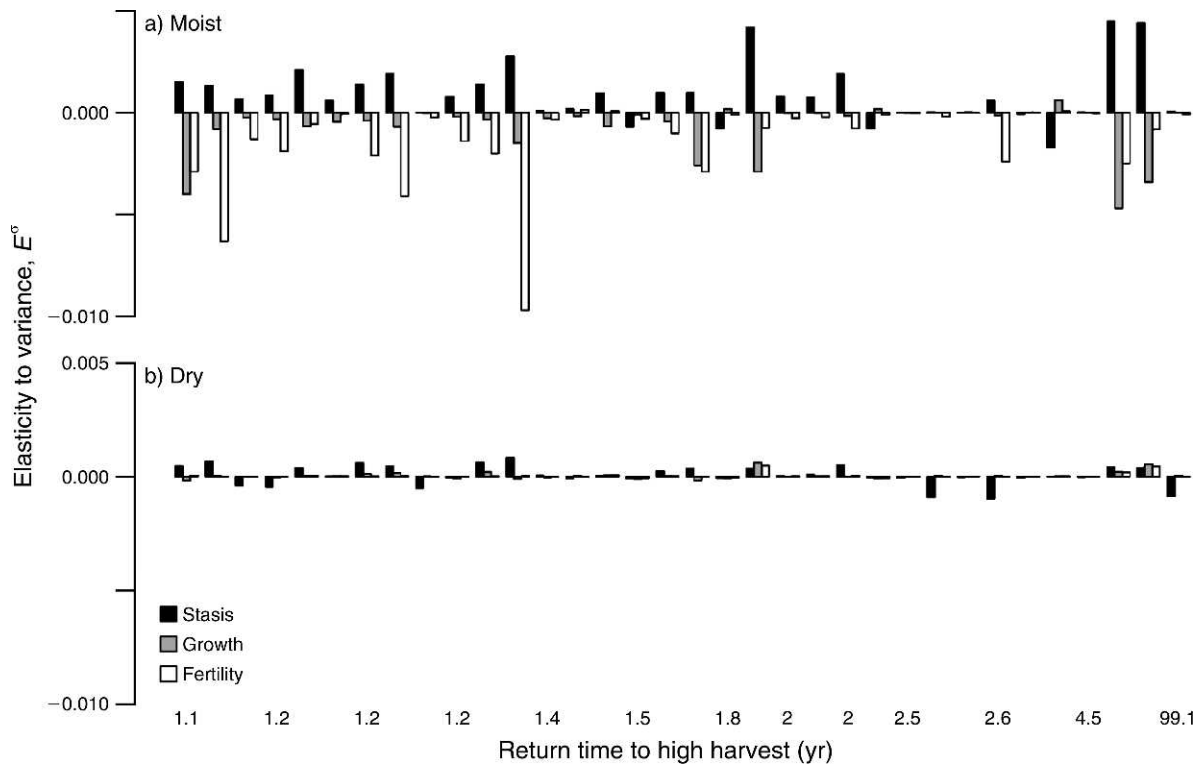
FIG. 6. Elasticity, E^σ, of the stochastic growth rate to perturbation of the variability of stasis, growth and fertility in (a) moist and (b) dry regions.

harvest each year based on economic, social, and ecological considerations, including local evaluations of the state of the resource. Therefore, decisions on how much to harvest in a given year often depend on what was harvested the previous year. Our approach of modeling *Khaya* NTFP harvesting levels as a stochastic Markov process sequence demonstrates that the temporal sequence of harvest intensity matters. Our results illustrate that the stochastic growth rate and its elasticity to changes in the mean and variance of the vital rates correlated with the return time to high harvest. This approach provides an understanding of the demographic processes that determine population dynamics of harvested species when harvest intensity varies stochastically over time, and how the relative importance of various demographic processes may change when harvesting pressure varies.

The response of *Khaya* to increasing harvesting pressure depended on the ecological context in which the populations were found. While reducing harvesting pressure (increasing the return time to high harvest) increased population growth in the dry region, it reduced it in the moist region. The results from the dry region are expected and similar to other studies on the effects of plant harvest (Nantel et al. 1996, Svenning and Macia 2002, Ticktin et al. 2002) or herbivore browsing (Knight et al. 2009) on population dynamics. In contrast, the increase in population growth rate with

increasing harvesting pressure in the moist region is similar to the response of populations to disturbance such as fire (Silva et al. 1991, Menges et al. 2006) or hurricanes (Horvitz et al. 2005) where increasing disturbance tends to improve habitat quality, for instance, increasing light penetration by increasing canopy openness, or removing litter and therefore increasing the availability of safe sites, or removing pest or herbivore insects that were limiting growth or survival. In our study, NTFP harvest was not expected to have similar beneficial effects. However, our results can be explained by analyzing the coupled variation of mean vital rates and their elasticities across harvesting sequences. In the moist region, the mean stasis rates of juveniles, $\bar{a}_{33}$, small, $\bar{a}_{44}$, and large, $\bar{a}_{55}$, adults decreased with increasing return time to high harvest. In contrast, the elasticity to mean stasis of juveniles, e_{33}, and large, e_{55}, adults did not vary significantly with return time to high harvest. Only e_{44} was negatively correlated with return time. Therefore, the stochastic dynamics of populations in the moist region was mainly driven by the decreasing survival of juvenile and large adults when harvesting pressure decreased. While it is not clear what specific mechanisms drive these decreasing survival rates at lower harvesting pressure, one hypothesis is that it is a result of increased light penetration and a subsequent increase in photosynthesis in pruned individuals (Anten and Ackerly 2001, Martinez-Ramos et al. 2009). From a
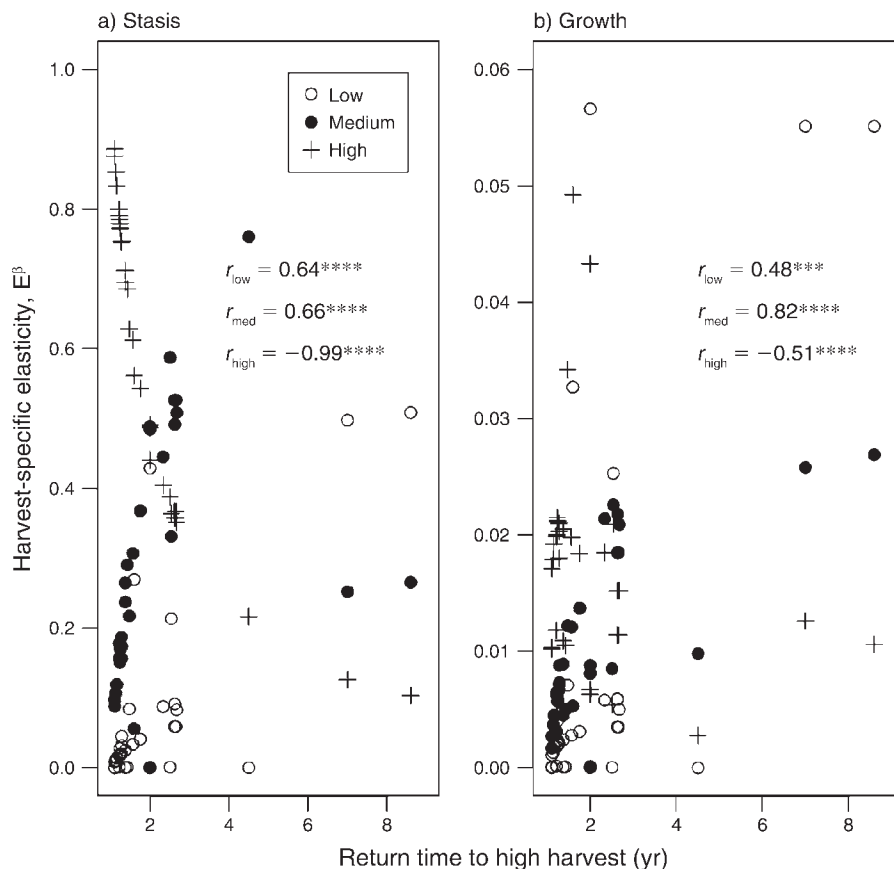
FIG. 7. Environment-specific elasticity, E^{β}, for (a) stasis and (b) growth for each harvest intensity: low, medium, and high. *** $P < 0.001$; **** $P < 0.0001$.

short-term perspective, this increase in the quantity and improvement in the quality (fewer tannins) of new foliage has nutritional benefits for the cattle. However, when harvesting is too frequent, the benefit gained from foliage harvest may be outweighed by the cost of constant compensatory growth.

In contrast to our previous study where we simulated an i.i.d. (independent and identically distributed) environment and found that low-harvest populations were projected to increase in the moist region ($\lambda_s > 1$; see Gaoue and Ticktin 2010), in this analysis *Khaya* populations were projected to decline regardless of harvesting pressure or ecological context. From a management perspective, this difference in the results between an i.i.d. and Markovian environment suggests that populations would increase only if they are consistently harvested at a low level over time, but if the sequence of harvest includes medium- or high-intensity years, populations are likely to decrease. In our study region, *Khaya* harvest often takes place at high intensity with low return time (Gaoue and Ticktin 2007, 2009) and it is unrealistic to expect a *low-harvest* i.i.d. scenario.

Our results show that, in the dry region where populations are already experiencing stressful ecological conditions, *Khaya* populations are more buffered against variance in vital rates. Our results also show that increasing harvest pressure (return time to high harvest) tends to increase the relative importance of stasis and more so when ecological conditions are stressful. In a context where populations already face drought related stress, population growth tends to be driven mainly by the ability of individuals to resist perturbation and persist. The importance of stasis for long-lived species has been reported by other studies (e.g., Silvertwon et al. 1993, Morris and Doak 2002) and may be explained by a long-term selection for high survival in these species and a buffer against environmental variability (Morris et al. 2008). Although the context dependent variation in the importance of demographic processes for population fitness is rarely reported (e.g., Menges and Quintana-Ascencio 2004, Sletvold and Rydgren 2007, Knight et al. 2009), the few studies that have reported this are consistent with our results on *Khaya* and illustrate that the elasticity of the deterministic growth rate to stasis increased with increasing disturbance. This pattern supports the theory that plants in stressful environments tend to invest in greater stasis than growth or reproduction (Grime 1977) and suggests that for populations heavily and chroni-

cally harvested for their NTFPs, there is an increase selection pressure for individuals that are resilient to harvest and therefore with higher survival rates. This also has implications for future harvest and the economy of NTFP harvest for local populations. If frequent high-intensity harvest will shift the life history strategies of harvested species toward reduced growth (reduced leaf production) and reproduction (reduced fruit production), as a trade-off for higher survival, then, for species that are harvested for their foliage, fruits, and seeds, frequent harvest may lead to decreasing productivity. In terms of management, the greater increase in elasticity of stasis in the dry region suggests that the key management approach there should be toward ensuring greater survival of the adult plants.

We further show that the importance of demographic processes to population growth also depends on the harvest states in which the population is found prior to perturbation. For example, for high harvest populations, with greater return time to high harvest (low harvesting pressure), population growth is sensitive to growth or reproduction in addition to stasis. But if the population is in a low- or medium-harvest state, the elasticity of the stochastic growth rates may show completely different trends. This has significant management implications as it suggests that the choice of the demographic processes to manipulate for population management should be carefully considered and adapted depending on the state in which the population is. However, with frequent harvest, the population growth rate may never reach an asymptote and the long-term behavior of harvested populations may be less of immediate use for managers than their transient behavior after harvest (Caswell 2001, Koons et al. 2005, Ezard et al. 2008). Future demographic analyses of non-timber forest product harvest impact should focus both on the asymptotic and transient behavior of harvested populations to be able to suggest a coupled short- and long-term management strategies for end-users.

The way we use Markov chains in this study may be suitable for most indigenous resource management strategies where harvesting decisions are made based on responses of the resource (e.g., postharvest density or yield) to recent harvest activities and the historical patterns of yield at a site. However, in some indigenous communities (see Berkes and Kislalioglu Berkes 2009, Peloquin and Berkes 2009) and for park managers who have the possibility of documenting harvesting history, it is possible to use a different approach to account for the effect of long-term history of harvest on population dynamics. A delay difference/differential equation models or autoregressive moving average (ARMA) matrix model (see Mode 1988, Tuljapurkar and Istock 1993, Caswell 2001) could be used to model future population dynamics as a function of present, but also past harvest effect.

What insights do we gain from the approach we used in this study? First, modeling variation in the patterns of

harvest intensities over time using Markov chains is much more realistic than the i.i.d. (independent and identically distributed) approach; the latter assumes that at each time step the next environmental state is independent of the current environmental state. The i.i.d. approach has often been used to model stochastic dynamics of NTFP harvested populations, and we show that the two approaches provide different results. Therefore, not doing this can lead to management decisions that are potentially erroneous. Second, the results vary across contexts and management decisions must be localized to explicitly consider the context dependent resilience of resources to perturbation. The fact that the population growth rate decreases in the moist region as harvest pressure decreases, but that the opposite was found in the dry region, has important management implications and suggest a different approach in managing (quota of harvest, public awareness, et cetera) populations in the two regions. One of the difficulties in using Markov chains in modeling the effect of harvest is the lack of sufficient longitudinal data to accurately define the state-by-state transition probabilities in the Markov chain. In our study, we simulated a wide range of Markov chains that mimicked various management options and this approach could be used like a sensitivity analysis to investigate the effect of variation in management options on future long-term population behavior. Another approach would be to calculate the sensitivity of population growth rate to perturbation of the Markov chain elements. The mathematical framework for this type of sensitivity analysis exists and has been recently introduced to ecologists by Steinsaltz et al. (*in press*).

LITERATURE CITED

Aberg, P., C. J. Svensson, H. Caswell, and H. Pavia. 2009. Environment-specific elasticity and sensitivity analysis of the stochastic growth rate. Ecological Modelling 220:605–610.

Anten, N. P. R., and D. D. Ackerly. 2001. Canopy-level photosynthetic compensation after defoliation in a tropical understorey palm. Functional Ecology 15:252–262.

Atawodi, S. E., D. A. Ameh, S. Ibrahim, J. N. Andrew, H. C. Nzelibe, E. O. Onyike, K. M. Anigo, E. A. Abu, D. B. James, G. C. Njoku, and A. B. Sallau. 2002. Indigenous knowledge system for treatment of trypanosomiasis in Kaduna state of Nigeria. Journal of Ethnopharmacology 79:279–282.

Bawa, K. S., W. J. Kress, N. M. Nadkarni, S. Lele, P. H. Raven, D. H. Janzen, A. E. Lugo, P. S. Ashton, and T. E. Lovejoy. 2004. Tropical ecosystems into the 21st century. Science 306:227–228.

Beddington, J. R., and R. M. May. 1977. Harvesting natural populations in a randomly fluctuating environment. Science 197:463–465.

Berkes, F., J. Colding, and C. Folke. 2000. Rediscovery of traditional ecological knowledge as adaptive management. Ecological Applications 10:1251–1262.

Berkes, F., and M. Kislalioglu Berkes. 2009. Ecological complexity, fuzzy logic, and holism in indigenous knowledge. Futures 41:6–12.

Bernal, R. 1998. Demography of the vegetable ivory palm *Phytelephas seemannii* in Colombia, and the impact of seed harvesting. Journal of Applied Ecology 35:64–74.

Boot, R. G., and R. E. Gullison. 1995. Approaches to developing sustainable extraction systems for tropical forest products. Ecological Applications 5:896–903.

Boyce, M. S., A. R. E. Sinclair, and G. C. White. 1999. Seasonal compensation of predation and harvesting. Oikos 87:419–426.

Caswell, H. 2001. Matrix models: construction, analysis and interpretation. Sinauer Associates, Sunderland, Massachusetts, USA.

Caswell, H., and T. Kaye. 2001. Stochastic demography and conservation of an endangered perennial plant (*Lomatium bradshawii*) in a dynamic fire regime. Advances in Ecological Research 32:1–51.

Caughley, G., and J. H. Lawton. 1981. Plant-herbivore systems. Pages 132–166 *in* R. M. May, editor. Theoretical ecology: principles and applications. Sinauer and Associates, Sunderland, Massachusetts, USA.

CTFT [Centre Technique Forestier Tropical]. 1988. *Khaya senegalensis* (Desr.) A. Juss. Bois et Forets des Tropiques 218:43–56.

de Beer, J. H., and M. McDermott. 1989. The economic value of non-timber forest products in South East Asia. The Netherlands Committee for IUCN, Amsterdam, The Netherlands.

Ehrlen, J. 2003. Fitness components versus total demographic effect: evaluating herbivore impacts on a perennial herb. American Naturalist 162:796–810.

Emanuel, P. L., C. M. Shackleton, and J. S. Baxter. 2005. Modeling the sustainable harvest of *Sclerocarya birrea* subsp. *caffra* fruits in the South African lowveld. Forest Ecology and Management 214:91–103.

Endress, B. A., D. L. Gorchov, and R. B. Noble. 2004. Non-timber forest product extraction: effects of harvest and browsing on an understory palm. Ecological Applications 14:1139–1153.

Ezard, H. G. T., and T. Coulson. 2010. How sensitive are elasticities of long-run stochastic growth to how environmental variability is modeled? Ecological Modelling 221:191–200.

Ezard, H. G. T., J. M. Gaillard, J. M. Crawley, and T. Coulson. 2008. Habitat dependence and correlations between elasticities of long-term growth rates. American Naturalist 172:424–430.

Farrington, S. J., R. Muzika, D. Drees, and T. M. Knight. 2009. Interactive effects of harvest and deer herbivory on the population dynamics of American ginseng. Conservation Biology 23:719–728.

Franco, M., and J. Silvertown. 2004. A comparative demography of plants based upon elasticities of vital rates. Ecology 85:531–538.

Gaoue, O. G., and T. Ticktin. 2007. Patterns of harvesting foliage and bark from the multipurpose tree *Khaya senegalensis* in Benin: variation across ecological regions and its impacts on population structure. Biological Conservation 137:424–436.

Gaoue, O. G., and T. Ticktin. 2008. Impacts of bark and foliage harvest on *Khaya senegalensis* (Meliaceae) reproductive performance in Benin. Journal of Applied Ecology 45:34–40.

Gaoue, O. G., and T. Ticktin. 2009. Fulani knowledge of the ecological impacts of *Khaya senegalensis* (Meliaceae) foliage harvest in Benin and its implications for sustainable harvest. Economic Botany 63:256–270.

Gaoue, O. G., and T. Ticktin. 2010. Effects of harvest of nontimber forest products and ecological differences between sites on the demography of African mahogany. Conservation Biology 24:605–614.

Ghimire, S. K., O. Gimenez, R. Pradel, D. McKey, and Y. Aumeeruddy-Thomas. 2008. Demographic variation and population viability in a threatened Himalayan medicinal and aromatic herb *Nardostachys grandiflora*: matrix modelling of harvesting effects in two contrasting habitats. Journal of Applied Ecology 45:41–51.

Ghimire, S., D. McKey, and Y. Aumeeruddy-Thomas. 2005. Heterogeneity in ethnoecological knowledge and management of medicinal plants in the Himalayas of Nepal: implications for conservation. Ecology and Society 9(3):6.

Govindachari, T. R., and G. N. K. Kumari. 1998. Tetranortriterpenoids from *Khaya senegalensis*. Phytochemistry 47:1423–1425.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169–1194.

Guedje, N. M., J. Lejoly, B.-A. Nkongmeneck, and W. B. J. Jonkers. 2003. *Population dynamics* of *Garcinia lucida* (Clusiaceae) in Cameroonian Atlantic forests. Forest Ecology and Management 177:231–241.

Guedje, N. M., P. A. Zuidema, H. During, B. Foahom, and J. Lejoly. 2007. Tree bark as a non-timber forest product: the effect of bark collection on population structure and dynamics of *Garcinia lucida* Vesque. Forest Ecology and Management 240:1–12.

Horvitz, C. C., J. Ehrlen, and D. Matlaga. 2010. Context dependent pollinator limitation in stochastic environments: can increase seed set overpower the cost of reproduction in an understory herb? Journal of Ecology 98:268–278.

Horvitz, C. C., S. Tuljapurkar, and J. B. Pascarella. 2005. Plant–animal interactions in random environments: Habitat-stage elasticity, seed predators, and hurricanes. Ecology 86:3312–3322.

Jonzen, N., J. Ripa, and P. Lundberg. 2002. A theory of stochastic harvesting in stochastic environments. American Naturalist 159:427–437.

Joyal, E. 1996. The palm has its time: an ethnoecology of *Sabal uresana* in Sonora, Mexico. Economic Botany 50:446–462.

Keay, R. W. J. 1989. Trees of Nigeria. Clarendon Press Oxford, Oxford, UK.

King, M. 1997. Fisheries biology: assessment and management. Blackwell Science, Oxford, UK.

Knight, T. M., H. Caswell, and S. Kalisz. 2009. Population growth rate of common understory herb decreases non-linearly across a gradient of deer herbivory. Forest Ecology and Management 257:1095–1103.

Koons, D. N., J. B. Grand, B. Zinner, and R. F. Rockwell. 2005. Transient population dynamics: relations to life history and initial population state. Ecological Modelling 185:283–297.

Lompo, M., J. B. Nikiema, I. P. Guissou, A. J. Moes, and J. Fontaine. 1998. The topical antiinflammatory effect of chloroform extract from *Khaya senegalensis* stem barks. Phytotherapy Research 12:448–450.

Maron, J. L., and E. Crone. 2006. Herbivory: effects on plant abundance, distribution and population growth. Proceedings of the Royal Society B 273:2575–2584.

Martinez-Ramos, M., N. P. R. Anten, and D. D. Ackerly. 2009. Defoliation and ENSO effects on vital rates of an under-storey tropical rain forest palm. Journal of Ecology 97:1050–1061.

Menges, E. S., and P. F. Quintana-Ascencio. 2004. Population viability with fire in *Eryngium cuneifolium*: deciphering a

decade of demographic data. Ecological Monographs 74:79–99.

Menges, E. S. P. F. Quintana-Ascencio, C. W. Weekley, and O. G. Gaoue. 2006. Population viability analysis and fire return intervals for an endemic Florida scrub mint. Biological Conservation 127:115–127.

Mode, C. J. 1988. On statistically assessing critical population size of an endangered species in a random environment. Journal of Mathematics Applied in Medicine and Biology 5:147–166.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.

Morris, W. F., et al. 2008. Longevity can buffer plant and animal populations against changing climatic variability. Ecology 89:19–25.

Muellner, A. N., R. Samuel, S. A. Johnson, M. Cheek, T. D. Pennington, and M. W. Chase. 2003. Molecular phylogenetics of Meliaceae (Sapindales) based on nuclear and plastid DNA sequences. American Journal of Botany 90:471–480.

Nakatani, M., S. A. M. Abdelgaleil, H. Okamura, T. Iwagawa, A. Sato, and M. Doe. 2000. Khayanolides A and B, new rearranged phragmalin limonoid antifeedants from *Khaya senegalensis*. Tetrahedron Letters 41:6473–6477.

Nantel, P., D. Gagnon, and A. Nault. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. Conservation Biology 10:608–621.

Nault, A., and D. Gagnon. 1993. Ramet demography of *Allium tricoccum*, a spring ephemeral, perennial forest herb. Journal of Ecology 81:101–119.

Normand, D., and P. Sallenave. 1958. Caracteristiques et proprietes des acadjous (*Swietenia* et *Khaya*). Bois et Forets des Tropiques 59:43–52.

Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. Journal of Ecology 63:459–481.

Olmsted, I., and E. R. Alvarez-Buylla. 1995. Sustainable harvesting of tropical trees: demography and matrix models of two palm species in Mexico. Ecological Applications 5:484–500.

Peloquin, C., and F. Berkes. 2009. Local knowledge, subsistence harvests, and social-ecological complexity in James Bay. Human Ecology 37:533 – 545.

Peres, C. A., et al. 2003. Demographic threats to the sustainability of Brazil nut exploitation. Science 302:2112–2114.

Petit, S. 2003. Parklands with fodder trees: a Fulße response to environmental and social changes. Applied Geography 23:205–225.

Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Science USA 95:213–218.

Pinard, M. 1993. Impacts of stem harvesting on populations of *Iriartea deltoidea* (Palmae) in an extractive reserve in Acre, Brazil. Biotropica 25:2–14.

Poysa, H., J. Elmberg, G. Gunnarsson, P. Nummi, and K. Sjoberg. 2004. Ecological basis of sustainable harvesting: is the prevailing paradigm of compensatory mortality still valid? Oikos 104:612–615.

Silva, J. F., J. Raventos, H. Caswell, and M. C. Trevisan. 1991. Population responses to fire in a tropical savanna grass *Andropogon semiberbis*: a matrix model approach. Journal of Ecology 79:345–356.

Silvertown, J. 2004. Sustainability in a nutshell. Trends in Ecology and Evolution 19:276–278.

Silvertown, J., M. Franco, I. Pisanty, and A. Mendoza. 1993. Comparative plant-demography-relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. Journal of Ecology 81:465–476.

Sletvold, N., and K. Rydgren. 2007. Population dynamics in *Digitalis purpurea*: the interaction of disturbance and seed bank dynamics. Journal of Ecology 95:1346–1359.

Steinsaltz, D., S. Tuljapurkar, and C. Horvitz. *In press*. Derivatives of the stochastic growth rate. Theoretical Population Biology.

Svenning, J. C., and M. J. Macia. 2002. Harvesting of *Geonoma macrostachys* Mart. Leaves for thatch: an exploration of sustainability. Forest Ecology and Management 167:251–262.

Ticktin, T. 2004. The ecological implications of harvesting non-timber forest products. Journal of Applied Ecology 41:11–21.

Ticktin, T., P. Nantel, F. Ramirez, and T. Johns. 2002. Effects of variation on harvest limits for Nontimber Forest species in Mexico. Conservation Biology 16:691–705.

Tuljapurkar, S., and C. V. Haridas. 2006. Temporal autocorrelation and stochastic population growth. Ecology Letters 9:327–337.

Tuljapurkar, S., C. C. Horvitz, and J. B. Pascarella. 2003. The many growth rates and elasticities of populations in random environments. American Naturalist 162:489–502.

Tuljapurkar, S., and C. Istock. 1993. Environmental uncertainty and variable diapause. Theoretical Population Biology 43:251–280.

Turner, N. J., M. B. Ignace, and R. Ignace. 2000. Traditional ecological knowledge and wisdom of Aboriginal peoples in British Columbia. Ecological Applications 10:1275–1287.

Van der Voorta, M. E., and J. B. McGraw. 2006. Effects of harvester behavior on population growth rate affects sustainability of ginseng trade. Biological Conservation 130:505–516.

Zuidema, P. A., H. de Kroon, and M. J. A. Werger. 2007. Testing sustainability by prospective and retrospective demographic analyses: Evaluation for palm leaf harvest. Ecological Applications 17:118–128.