

Transient dynamics reveal the importance of early life survival to the response of a tropical tree to harvest

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Summary

1. Exploitation of non-timber forest products can contribute to the alleviation of poverty. However, overexploitation can also lead to species decline. Studies on the sustainability of harvest often use stationary population growth rates to assess harvesting effects. For such frequently harvested systems, transient analysis can provide new insights into the response of populations to harvest.

2. To test the prediction that the effect of harvest differs between transient and asymptotic phases, I used four years of demographic data to compare the impact of harvesting bark and foliage on the short- and long-term dynamics of African dry zone Mahogany *Khaya senegalensis* in West Africa.

3. The effect of harvest was stronger in the short term than in the long term, particularly in the moist region. Patterns of transient elasticities also differed from the elasticities of long-term growth rates to perturbation of vital rates. Survival at early life stages was more important for short-term dynamics than for long-term population dynamics.

4. *Synthesis and applications.* This study illustrates that using the asymptotic growth rates to assess the impact of harvest may underestimate the short-term effects of harvest. Short-term management plans based on the elasticity analysis of long-term growth rates will be suboptimal given the relative importance of the survival of non-reproductive stages for population dynamics in the near term. Managers should use results from elasticity analysis of both long-term and short-term population dynamics to develop more realistic management plans.

Key-words: African mahogany, ecological harvesting impacts, ecosystem services, matrix models, non-timber forest products, plant population dynamics, transient elasticity analysis

Introduction

Harvesting non-timber forest products has served as a valuable source of food and medicine for local people world-wide for several thousands of years (Costanza *et al.* 1997; Godoy *et al.* 2000). Exploitation of these resources can generate income and potentially contribute to poverty alleviation (Shackleton *et al.* 2007). However, frequent harvest at high intensity can lead to population decline, reduce community diversity and jeopardize the ability of future generations to benefit from these ecosystem services (Moegenburg & Levey 2002; Peres *et al.* 2003; Ticktin 2004). To assess the sustainability of harvesting non-timber forest products, a growing number of studies have used stage-structured matrix projection models (Caswell 2001) to estimate the effects of harvesting on the long-term population growth rate λ , and its elasticity to changes in popu-

lation vital rates (Gaoue, Horvitz & Ticktin 2011; Klimas *et al.* 2012; Pinard 1993; Ticktin *et al.* 2002; Zuidema, de Kroon & Werger 2007). Elasticity analyses for long-term population growth rates revealed that for long-lived species such as trees, manipulating the survival of adult reproductive individuals is the most significant process to induce a desirable effect on long-term population growth rates (Schmidt *et al.* 2011): increasing trends for endangered species or decreasing dynamics for invasive species. Although such elasticity analysis (see de Kroon, Van Groenendael & Ehrlén 2000) has been widely used as an important management tool, it has surprisingly focused mostly on the long-term (rather than the short-term) response of populations to perturbation (Crone *et al.* 2011).

Using the elasticity of long-term population growth rates to inform management actions and sustainable harvest plans, which are often designed for the short term (≤ 10 years), can be misleading (Ezard *et al.* 2010). These systems, which are frequently and heavily harvested for non-

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timber forest products (e.g. Gaoue & Ticktin 2007; Moe-nenburg & Levey 2002), may not reach a long-term equilibrium (Hastings 2004). Non-timber forest products harvesting, like any perturbation that leads to loss of biomass, often changes population vital rate and also constantly changes population structure which will depart from the stable stage distribution (Haridas & Tuljapurkar 2007). As a result, it is expected that short-term dynamics in harvested populations will differ from long-term population dynamics (Hastings 2004; Stott, Hodgson & Townley 2012b). Furthermore, given that changes in population size over the short term are mostly due to change in the survival rate of early life stages, transient elasticity analysis may reveal unique patterns with significant implications for short-term management (Ezard *et al.* 2010; Miller & Ten-humberg 2010; Stott, Hodgson & Townley 2012b; Tremblay, Raventos & Ackerman 2015). Transient elasticities can be temporally dynamic (Haridas & Tuljapurkar 2007; Yearsley 2004). For example, Maron, Horvitz & Williams (2010) showed that the relative importance of fertility for transient growth of the invasive *Cynoglossum officinale* varies over time and between native and invasive ranges, oscillating in one environment and phasing each other in another. Understanding the temporal dynamics of transient elasticity to fertility can inform adaptive management actions such as the timing of releasing biological control agents to better limit fertility over time (see also Kidd & Amarasekare 2012; McMahon & Metcalf 2008).

Here, I investigate whether the effects of non-timber forest product harvest on population dynamics differ in the near term (transient dynamics) versus the long term (asymptotic dynamics). I examined the patterns of the elasticity of both the short- and long-term population growth rate to perturbation of vital rates. This allows me to assess whether the demographic mechanisms that are likely to influence population response to harvest are the same at these two different temporal scales. Given that population response to harvest can be mediated by abiotic factors (Gaoue & Ticktin 2010; Mandle & Ticktin 2012), I compared population dynamics in two contrasting ecological regions that differ in rainfall, habitat diversity and soil conditions (see Gaoue & Ticktin 2007, 2008). This study illustrates that the effect of harvest is stronger in the short term than over the long term, and that the elasticity patterns differed as well, with survival at early life stages more important for short-term dynamics than for long-term population dynamics. These results suggest clear management strategies for the sustainable harvest of wild plants.

Materials and methods

STUDY SYSTEM

Khaya senegalensis (Meliaceae) is a tree that can attain 35 m in height and is naturally distributed in the dry areas of West Africa. Foliage of *K. senegalensis* is bitter and serves as a medicine as well as an important browse for cattle in West

Africa. During the dry season when herbaceous pastures are scarce, *Fulani* herdsman prune fodder trees to feed their cattle. The intensity of foliage harvest is high (Gaoue & Ticktin 2007) with most individual trees losing more than 80% of their crown. A given tree may be harvested for fodder and for its bark by local communities. The impact of both foliage and bark harvest on the reproduction and dynamics of *K. senegalensis* populations has been extensively documented elsewhere (Gaoue & Ticktin 2008, 2010; Gaoue *et al.* 2013).

I studied the effects of foliage and bark harvesting on 12 populations of *K. senegalensis* in two ecological regions of Benin (West Africa) over four years (2004–2007). The two regions differ in their annual rainfall, habitat diversity and soils. The Sudano-Guinean region (7°30′–9°30′N, hereafter ‘moist’) experiences higher annual rainfall (1100–1300 mm), lower temperature (25–29 °C), a longer growing season (200 days) and a higher diversity of habitats for *K. senegalensis* (savanna, woodland, dry dense forest and gallery forests) than the Sudanian region (hereafter ‘dry’, located at 9°30′–12°N, with 800–1100 mm rainfall, 24–31 °C temperature, a growing season that last 145 days, and dominated by woodland and gallery forests). Further details on the ecological differences between these regions are reported in Gaoue & Ticktin (2007, 2008).

I used the percentage of trees harvested for foliage and bark to classify populations into low and high harvest categories. Harvested individuals were mostly reproductive trees with often >80% of their branches harvested and <25% trunk bark removed. High harvest populations (**H**) 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 [SD] = 17.69% [7.32]). Low harvest populations (**L**) had <25% of trees harvested for foliage (mean = 4.80% [3.16]) and <10% of trees debarked (mean [SD] = 9.71% [5.20]) (Gaoue & Ticktin 2007, 2010).

MATRIX PROJECTION MODEL

I collected demographic data from the 12 populations using 1-ha plots for each population (two adjacent subplots of 0.5 ha, separated by the river bed when the population was in a gallery forest) (Gaoue & Ticktin 2010). For each individual of *K. senegalensis* within the plots, I measured diameter at breast height (DBH) or basal diameter (for individuals <1.3 m high) to estimate yearly growth (or shrinkage). I also recorded individual survival from one year to another and counted the number of fruits they produced. For each reproducing tree, I randomly sampled 10 fruits to count the number of seeds produced per fruit and estimate the total individual seed production. Ten subplots of 10 m × 10 m were used to estimate the density of new seedlings in each population. I estimated fertility of a given population as the ratio of the number of new seedlings produced in a given year and the number of seeds produced by the population in the previous year. To build *K. senegalensis* projection matrices, I classified individual trees in each population into five life stages using their basal diameter (for seedlings and saplings) and DBH (for juvenile and adults): seedlings (diameter at base <2 cm), saplings (2–5 cm), juveniles (5–20 cm), small reproductive (20–40 cm) and large reproductive adults (DBH ≥ 40 cm).

Data on survival (σ_i), growth (γ_{ij} or shrinkage ρ_{ji}) and fertility (ϕ_i) were used to build a 5 × 5 stage-structured summary matrix **A** for each harvest intensity (low and high) in each ecological

region (dry and moist) by pooling data across populations and years. Matrix **A** comprises all of the information on the dynamics of the populations in one time step and was used to estimate various transient and asymptotic growth rates and their elasticity matrices. The general form of **A** for *K. senegalensis* populations is:

$$\mathbf{A} = \begin{pmatrix} \sigma_1(\mathbf{1} - \gamma_{12}) & \sigma_2\rho_{21} & \mathbf{0} & \sigma_4\phi_4 & \sigma_5\phi_5 \\ \sigma_1\gamma_{12} & \sigma_2(\mathbf{1} - \gamma_{23} - \rho_{21}) & \sigma_3\rho_{32} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \sigma_2\gamma_{23} & \sigma_3(\mathbf{1} - \gamma_{34} - \rho_{32}) & \sigma_4\rho_{43} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \sigma_3\gamma_{34} & \sigma_4(\mathbf{1} - \gamma_{45} - \rho_{43}) & \sigma_5\rho_{54} \\ \mathbf{0} & \mathbf{0} & \mathbf{0} & \sigma_4\gamma_{45} & \sigma_5(\mathbf{1} - \rho_{54}) \end{pmatrix}$$

To determine the transient and long-term growth rates and understand the relative importance of survival, growth and fertility to changes in population dynamics, I developed stage-based matrix projection models (Caswell 2001):

$$n(t+1) = \mathbf{A}n(t), \quad \text{eqn 1}$$

where **A** is a 5×5 lower-level projection matrix (it represents **L** and **H**), $n(t)$ is a 5×1 vector of the number of individuals in each of the five life stages in year, $n(t+1)$ is the population vector in the following year $t+1$. The column sum of each vector $n(t)$ and $n(t+1)$ represents $N(t)$ and $N(t+1)$, the total population size at time t and $t+1$, respectively.

TRANSIENT AND ASYMPTOTIC DYNAMICS

Long-term dynamics

The dominant eigenvalue λ of matrix **A** is the long-term population growth rate. It is a measure of the average demographic quality of the environment for *K. senegalensis* 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 period. I calculated the elasticity of λ to perturbation of vital rates (survival, growth and fertility) following Caswell (2001): $(\theta/\lambda)(\partial\lambda/\partial\theta)$.

Transient dynamics

Several metrics of transient dynamics (population momentum, damping ratio, reactivity, amplification envelope, transient growth and population size) have been proposed along with their sensitivity to perturbation of vital rates (Caswell 2007; Koons *et al.* 2005). A thorough discussion about the advantages and issues related to each of these metrics can be found in Stott, Townley & Hoggson (2011). In this paper, I used the average transient growth rate $r(t_1, t_2)$ as the metric of transient dynamics to facilitate comparisons with the long-term growth rate, λ . A critical point of discussion on transient dynamics is the time period during which a given population should be projected (see Maron, Horvitz & Williams 2010; Stott, Townley & Hoggson 2011). Given that the goal of the transient

analysis here is to understand the dynamics of the populations in a time period more relevant to management, I analysed transient dynamics over 10 years. Management plans are often designed for 5–10 years and re-evaluated after each period (Ezard *et al.* 2010). I calculated the average transient growth rate $r(t_1, t_2)$ by projecting the population over 10 years using

eqn (1):

$$r(t_1, t_2) = \frac{1}{t_2 - t_1} \log \frac{N(t_2)}{N(t_1)}, \quad \text{eqn 2}$$

with initial population vector $n(0)$ equal to the average observed population structure over the 4-year study. Transient dynamics are sensitive to initial population structure (Haridas & Tuljapurkar 2007; Stott, Townley & Hoggson 2011; Stott, Hoggson & Townley 2012b). One could use different $n(0)$ (dominated by adults, or by seedlings, or stable stage distribution) to test how initial conditions may change transient dynamics. Initial population structures that are dominated by reproductive adults will lead to a transient growth rate that is greater than the long-term growth rate (amplification); in contrast, a slower transient growth rate is expected (attenuation) when the initial population structure is dominated by immature individuals (Stott, Hoggson & Townley 2012b). However, given that what is of interest to management in this study is the response of the system from its current state, I used the mean observed population structures for each region and harvest intensity combination over 4 years.

To be able to compare the values of r with those of λ , I used the exponential of r . The transient sensitivity $dr(t_1, t_2)/d\theta^T$ to perturbation of vital rates, $\theta_i = \{\sigma_i, \gamma_{ij}, \rho_{ji}, \phi_i\}$, was calculated following Caswell (2007):

$$\frac{dr(t_1, t_2)}{d\theta^T} = \frac{1}{t_2 - t_1} \left(\frac{\mathbf{c}^T}{N(t_2)} \frac{dn(t_2)}{d\theta^T} - \frac{\mathbf{c}^T}{N(t_1)} \frac{dn(t_1)}{d\theta^T} \right), \quad \text{eqn 3}$$

where T denotes the transpose operation, and \mathbf{c}^T is a column vector of 1. The elasticity of transient growth rate r to perturbation of vital rates was calculated as:

$$r(t_1, t_2)^{-1} \frac{dr(t_1, t_2)}{d\theta} \text{diag}(\theta), \quad \text{eqn 4}$$

where $\text{diag}(\cdot)$ represents the diagonal matrix with zeros everywhere else but the diagonal which has θ . All the computations were done in R (R Core Team 2012). Example R code is available in Appendix S1 (Supporting Information) and posted on GitHub and detailed population level projection matrices are available from the Dryad Digital Repository (Gaoue 2015) to implement all these calculations.

EFFECTS OF HARVEST ON SHORT- AND LONG-TERM DYNAMICS

For each harvest intensity **L** and **H**, I determined λ , the long-term population growth rate, its elasticity to perturbation of vital rates, and the transient growth rate r and its elasticity. To test whether the effect of harvest is stronger in the short term than it is in the long term, I compared the differences in growth rates (between low and high harvest scenarios) for the asymptotic ($\Delta\lambda = \lambda_{\text{low}} - \lambda_{\text{high}}$) and the transient dynamics ($\Delta r = r_{\text{low}} - r_{\text{high}}$) from the deterministic model. To test whether the relative importance of vital rates varies between short-term versus long-term, I compared the elasticity of transient population growth rate with the elasticity of λ to perturbation of survival, growth and fertility for each life stage (seedling, sapling, juvenile, small and large adults). This allowed me to identify the vital rates and life stages that will be more responsive to managers seeking to improve *K. senegalensis* population growth rates in the short-term versus long-term and in each ecological region.

Results

The long-term population growth rates did not differ between dry and moist regions (Fig. 1a). However, populations in the dry region grew at a slower rate than those in the moist region even though these differences in growth rates are not statistically significant. The difference in population growth rates between ecological regions was greater during the transient phase for low harvested populations (Fig. 1b). Overall, the effect of harvest on long-term dynamics ($\Delta\lambda_{\text{low-high}}$) was smaller than that on near-term dynamics ($\Delta r_{\text{low-high}}$, Fig. 1c). In the moist region, the effect of harvest on transient dynamics was tenfold that on long-term population growth rates. However, in the dry region, the effect of harvesting on transient dynamics was minimal.

Across ecological regions, over the short term or long term, population growth rates were mainly sensitive to perturbation of survival (σ_i); the elasticity of population

growth rates to perturbation of growth (γ_{ij}) or life stage regression (ρ_{ji}) was negligible (Fig. 2). However, there were clear differences in the patterns of elasticity between the short- and long-term dynamics. In both regions, long-term growth rates were more sensitive to perturbation of the survival (σ_4 and σ_5) of late life stages (Fig. 2). Specifically, for high harvested populations, and in the dry region, long-term population growth rate was only sensitive to changes in the survival of reproductive individuals. Transient elasticities were more spread out between different life stages (Fig. 2d). Contrary to long-term growth rates, transient growth rates were also sensitive to changes in the survival of seedlings (σ_1) and saplings (σ_2), although this contrast in elasticity pattern was most noticeable in the dry region (Fig. 2c,d). In both ecological regions, transient dynamics were also sensitive to perturbation of fertility (ϕ_5).

Harvest did affect the magnitude of the elasticity of the asymptotic and transient growth rates to perturbation of survival (Fig. 2a–d). In the moist region, long-term growth rates in low harvest populations were less sensitive to perturbation of survival than they were for high harvest populations (Fig. 2a,b). Moreover, the asymptotic growth rates of low and high harvest populations were sensitive to the survival of different life stages, particularly in the moist region (Fig. 2d). In addition, even though short- and long-term elasticities to perturbation of growth were very small in most cases, they were more noticeable in low harvest populations in the moist region where plants are expected to experience less water stress (Fig. 2a). The asymptotic growth rates in high harvest populations were sensitive to perturbation of only late life stages (adults) survival and in low harvest populations, they were elastic to survival of all stages (Fig. 2a). These patterns were not noticeable for transient growth rates where in both regions, growth rates were more sensitive to survival of early life stages (sum of $\sigma_1, \sigma_2, \sigma_3$; Fig. 2) in high harvest populations (Fig. 2b,d) than in low harvest populations (Fig. 2a,c).

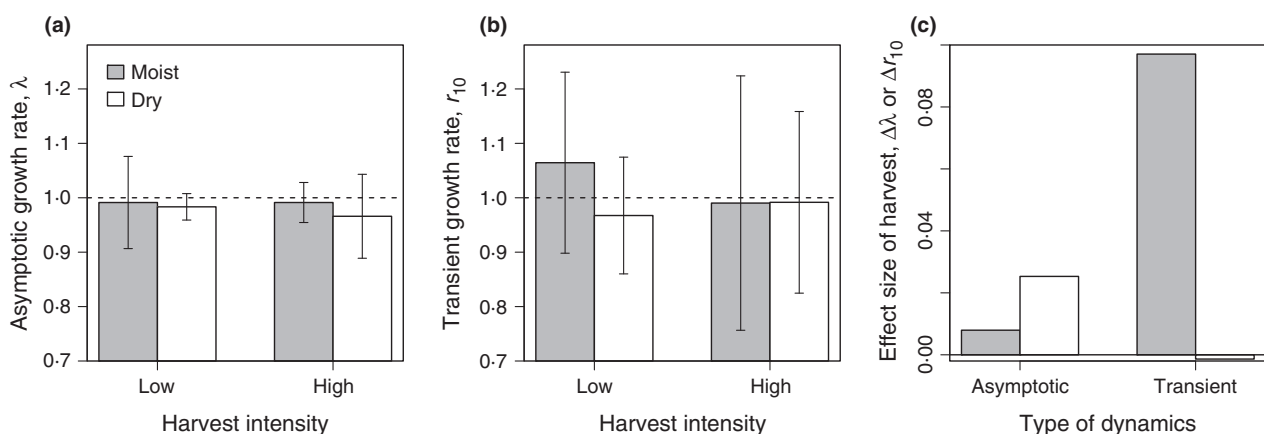


Fig. 1. Effect of *Khaya senegalensis*' bark and foliage harvest on the (a) asymptotic, λ ; (b) transient growth rates, r ; and (c) effect size of harvest for transient ($\Delta r_{\text{Low-High}}$) and asymptotic ($\Delta\lambda_{\text{Low-High}}$) population growth rates in two ecological regions (moist vs. dry).

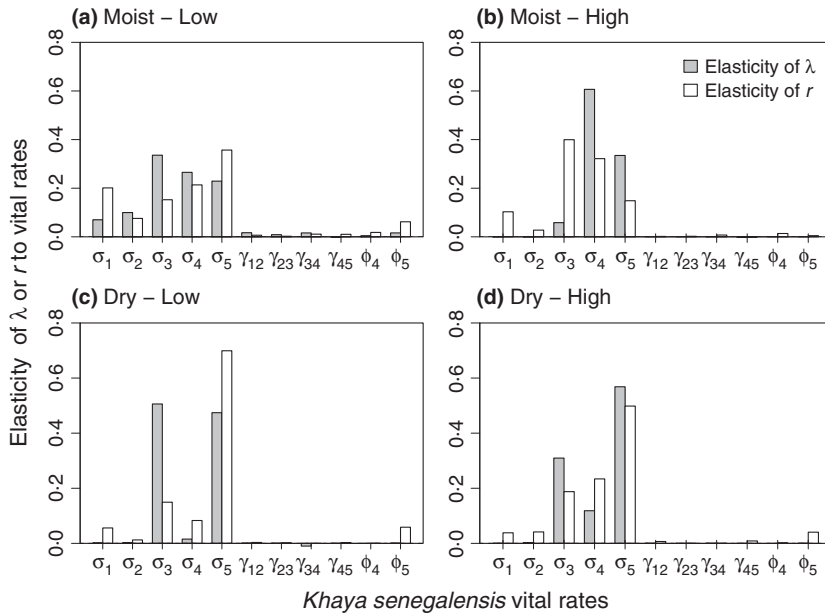


Fig. 2. Elasticities of *Khaya senegalensis* population asymptotic (grey bars), λ , and transient growth rates (white bars), r to perturbation of vital rates in two ecological regions (moist vs. dry) and two harvesting intensities (low vs. high). The vital rates σ_i , γ_{ij} and ϕ_i represent survival, growth and fertility rates, respectively, for the following life stages: seedlings ($i = 1$), saplings ($i = 2$), juveniles ($i = 3$), small ($i = 4$) and large ($i = 5$) adults.

Discussion

TRANSIENCE AND LONG-TERM GROWTH RATES

There is an extensive body of work on the ecological consequences of non-timber forest product (NTFP) harvest. Surprisingly, few of these studies have investigated the impacts of harvest in the near term for which management plans are often designed (e.g. Endress, Gorchov & Noble 2004; Ghimire *et al.* 2008; Groenendijk *et al.* 2012; Ticktin & Nantel 2004; Ticktin *et al.* 2012). Focusing on the long-term growth rate, most studies of the effect of NTFP harvest on population dynamics have discarded the transient dynamics (e.g. Holm, Miller & Cropper 2008). Previous work on transient dynamics of NTFP-harvested systems focused on simulating population growth rates over the short term, with the length of the transient period varying from a few years (Ticktin & Nantel 2004) to 100 years (Groenendijk *et al.* 2012). In this paper, I directly compared the effect of NTFP harvest on the short- versus long-term dynamics, and for the first time to my knowledge, analysed differences in the effects of NTFP harvest on transient and asymptotic elasticity patterns.

For *K. senegalensis*, transient growth rates were lower, but the effect of harvest on short-term population growth rates was nearly four times the size of the effect on long-term growth rates, particularly in the moist region. This is consistent with results found elsewhere on the effect of leaf harvest on palm species in Mexico (Endress, Gorchov & Noble 2004), and the effect of invasive species and mistletoes on *Phyllanthus* spp. in India (Ticktin *et al.* 2012), but these results differ from that of Maron, Horvitz & Williams (2010) who found no difference in the effect of disturbance on short- and long-term growth rates. The difference in the effect of

harvest on transient and asymptotic growth rates is potentially due to differences in recovery time. During the transient phase, populations are at the beginning of the recovery process and therefore experience a stronger effect of harvest on population abundance and growth rate. This reduced growth rate is due to lowered fruit production and seedling recruitment. It is expected that this effect of perturbation on the system will decrease over time, in the absence of further perturbations, and converge to the long-term effect. Similar results of greater effects of harvest and invasion on transient dynamics were reported elsewhere (see for a discussion Prasad *et al.* 2014; Ticktin *et al.* 2012, 2014). However, what was surprising in my results is the lack of significantly stronger effect of harvest on transient dynamics in the dry region where the study species already experiences harsher climatic conditions (Gaoue, Sack & Ticktin 2011).

Analysis of how the effects of harvest depend on climate or habitat is surprisingly rare, despite evidence that harvesting often takes place in heterogenous habitats (Klimas *et al.* 2012; Ticktin & Nantel 2004). This study shows that the effects of harvest on asymptotic (but not transient) dynamics were also greater in the dry region than in the moist region. Similar results were previously obtained for the same species (Gaoue & Ticktin 2010; Gaoue, Horvitz & Ticktin 2011), and other NTFP species. For example, the effect of simulated seed and timber harvest on *Carapa* in Brazilian Amazon was stronger in the dry (*terra firma*) than in the moist environment (Klimas *et al.* 2012). There was also an interaction between leaf harvesting and ENSO (El Niño Southern Oscillation) on the demography of *Chamaedorea* palm in Mexico (Martinez Ramos, Anten & Ackerly 2009). Rhizome harvest from the Himalayan medicinal herb *Nardostachys grandiflora* was more detrimental in dry

rocky outcrop habitats with poorer soils than in the wetter meadow (Ghimire *et al.* 2008). Results from these studies suggest that the limits for sustainable NTFP harvesting are drought-sensitive, with a tendency for wild plants to do worse when harvested in a context of multiple disturbances.

PATTERNS OF TRANSIENT ELASTICITY

For long-lived species, elasticity analyses often reveal that long-term population growth rates are most elastic to the survival of reproductive adults (Schmidt *et al.* 2011; Silvertown *et al.* 1993). Results from this study are consistent with this prediction. The disproportionate importance of the survival of late life stages for the long-term persistence of long-lived species is often explained by a long-term selection for high survival in these species (often slow growing) and a buffer against environmental variability (Morris *et al.* 2008). Therefore, a significant increase in the mortality of reproductive adults, which often have the highest reproductive value and the highest lifetime investment in biomass, can lead to population decline more strongly than an increased mortality of early life stages. However, consistent with other studies (e.g. Fox & Gurevitch 2000; Haridas & Gerber 2010; Miller & Tenhumberg 2010) transient elasticity for *K. senegalensis* showed a different pattern with the relative importance of survival of various life stages more evenly distributed than for asymptotic elasticities. This greater importance of early life stages to the dynamics in the near-term can be explained by the greater variation in early life survival. Therefore, population size post-disturbance is likely to be more affected by changes in the number of seedlings and saplings than changes in the density of mature individuals which often have high survival rates.

IMPLICATIONS FOR SUSTAINABLE MANAGEMENT

This study has direct implications for the sustainable harvest of wild plants that are often experiencing multiple stressors (Mandle & Ticktin 2012; Ticktin *et al.* 2012) as well as implications for a more realistic assessment of the ecological and evolutionary impacts of human activities. The emphasis on the importance of near-term dynamics for management may wrongly suggest that long-term population growth rates are less relevant for management. However, given that many species (although not specifically harvested) may be at their stable stage distribution (Williams *et al.* 2011), with a very short transient phase (Fox & Gurevitch 2000), it is important to consider both the short- and long-term goals of management. Consistent with results from this study, focusing solely on the asymptotic dynamics can generate misleading management suggestions (see also Ezard *et al.* 2010; Haridas & Gerber 2010; Miller & Tenhumberg 2010), yet the same is true for short-term dynamics. Using results from both the short- and long-term elasticity analysis would be a better option.

For *K. senegalensis*, large individuals are often harvested by local people and sustainable management effort based on asymptotic elasticities would focus on preserving mature individuals by limiting logging, or controlling hemiparasites that attack mature individuals in some populations (Gaoue & Ticktin 2007). However, in the short term (≤ 10 years), one of the threats faced by *K. senegalensis* is related to soil erosion in gallery forests where the species is most abundant. River and stream banks are constantly being eroded, and this poses a threat to seedlings and saplings that can be easily uprooted by grazing cattle when they occur on shallow soils. Another threat is related to drought and fire which can disproportionately affect seedling and sapling survival. Sustainable harvest of *K. senegalensis* in such an environment would require a strategy that addresses short-term threats that can affect early life stages (e.g. fire, drought, soil erosion) as well as the long-term threats associated with mature individuals (e.g. hemiparasites, logging). In previous studies, Gaoue & Ticktin (2010) and Gaoue, Horvitz & Ticktin (2011) recommended management plans for *K. senegalensis* which emphasized reducing the number of reproductive adults that are harvested rather than reducing harvesting intensity at the individual tree level. Furthermore, following recommendations from local *Fulani* harvesters (see also Gaoue & Ticktin 2009), these studies suggest the creation of *Fulani*-own plantation of fodder trees to reduce the harvesting pressure on wild populations of *K. senegalensis*. Results from this transient elasticity study suggest that in addition to these management recommendations, it is critical to establish anti-erosion measures and strictly limit fire in savanna adjacent to gallery forests where *K. senegalensis* is present. One way of implementing this will be to set early season fire along gallery forests to reduce future fuel load and therefore reduce the likelihood that fire will spread into the edge of these forests. These anti-fire and anti-erosion measures, by reducing soil movement into stream beds, will improve water conservation and increase soil moisture, both of which are critical for the survival and growth of *K. senegalensis* seedlings and saplings (Bufford & Gaoue 2015).

FUTURE DIRECTIONS FOR APPLIED ECOLOGICAL RESEARCH

Meta-analysis of the ecological impacts of non-timber forest products harvest failed to detect a globally strong effect on long-term population dynamics (Schmidt *et al.* 2011). For most study species, the effect of harvesting was weak, particularly for fruit-harvested species. Consistent with my results and many other referenced above, it is fair to ask if using transient growth rates, in lieu of the asymptotic growth rates, would have yielded stronger effects of harvest? Results from this study suggest that a lack of significant effect of harvest or other human activities in the long run should be supported with an in-depth analysis of the transient effects in order to avoid

drawing optimistic conclusions about management outcomes that may prove erroneous over time. Perturbation analyses such as the asymptotic and transient elasticity analyses performed in this study and elsewhere (see review in Crone *et al.* 2011) provide a linear estimate of the effect of perturbation on population dynamics (Stott, Hoggson & Townley 2012b). However, the response of population growth rate to perturbation can be strongly nonlinear (Dahlgren, Garcia & Ehrlen 2011; Stott, Hoggson & Townley 2012a; Tavener *et al.* 2011). Transfer function analysis which accounts for such nonlinearity and models the effects of multiple perturbations provides a more realistic alternative (Stott, Hoggson & Townley 2012a, b). Future studies on the transient response of populations to harvest should further test for the qualitative difference in management recommendations using transfer function analysis versus transient elasticity analysis. Similarly to most studies on the sustainability of NTFP harvesting, this study focuses only on the dynamics of harvested populations and not on the dynamics of the organs that are harvested. It is worth noting that future studies in this field should also focus on projecting the short- and long-term dynamics of the population productivity. For species that are harvested for fruit or seeds, this new approach will yield results that are directly usable for managers in planning management operations.

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Data accessibility

Khaya senegalensis mean projection matrices are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.mb1d0> (Gaoue 2015). The R script used to estimate the elasticities of short- and long-term population growth rates to perturbation of vital rates is available from Appendix S1 and GitHub at <https://github.com/ogaoue/Khaya-Transient-Elasticity.git>.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. R script to estimate transient elasticities. This is also available from GitHub <https://github.com/ogaoue/Khaya-Transient-Elasticity.git>.