

# Defoliation and bark harvesting affect life-history traits of a tropical tree

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## Summary

1. Selectively harvesting whole individuals in managed populations (e.g. fisheries, hunting) has substantial effects on life expectancy and age at maturity. Although demographic rates of trees are impacted by recurrent harvest of plant organs (e.g. fruit, leaf, bark) known as non-timber forest products, the effect of such harvesting on life-history traits is less explored.

2. Here, we investigate how different strategies of foliage and bark harvest by local people affect life expectancy and age at maturity of *Khaya senegalensis* across two climatic regions in West Africa. We compare elasticities of life expectancy to perturbation of vital rates to the elasticities of population growth rate, emphasizing how the two kinds of elasticity address distinct biological issues and management goals.

3. Life expectancy was shorter and reproduction delayed in the dry than in the moist region, indicating a cost of drought to life-history traits. Harvesting at constant rates only affects (increased) life expectancy in the moist region and (reduced) age at first reproduction in the dry region.

4. Models in which harvest intensity varies stochastically over time show results similar to those with constant harvesting rate. However, there is an interactive effect of harvest on life-history traits between regions. Increasing harvesting pressure accelerates maturity and reduces life expectancy in the dry region but delays reproduction and increases life expectancy in the moist region. This indicates that stochasticity magnifies the effect of harvesting on life-history traits.

5. With the notable exception of heavily harvested populations in the moist region, life expectancy is more elastic to survival of early rather than late life stages. This pattern contrasts with the elasticity of population growth rate; the latter is more elastic to survival of late rather than early life stages.

6. *Synthesis.* Our results suggest that plant harvesting can affect life-history traits but in different ways across an environmental gradient. Failure to account for stochasticity in harvesting rate can mask some of these effects. Our results also indicate that processes driving plant life expectancy, at least for long-lived species, may differ from those driving population dynamics.

**Key-words:** age at first reproduction, age-from-stage models, *Khaya senegalensis*, matrix models, non-timber forest product harvest, plant life expectancy, plant population and community dynamics, sensitivity of life expectancy

## Introduction

The role of recurrent disturbance (e.g. fire, hurricanes, episodic herbivory) in shaping the spatial and temporal dynamics of ecosystems and populations has long been of interest to

ecologists (Sousa 1984; Fraterrigo & Rusak 2008). Within this context, the potential evolutionary impact of anthropogenic disturbance, including recurrent harvest of select individuals from wild populations (as in fisheries and hunting), has increasingly drawn the attention of evolutionary ecologists (Darimont *et al.* 2009). This type of harvest mimics predation. The focus has been on the fact that humans often harvest phenotypically interesting individuals, and thus directly select on a wide array of traits, from morphological to life history,

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of wild plants and animals that are exploited (Allendorf & Hard 2009; Darimont *et al.* 2009).

Another type of harvest from wild populations is the removal of detachable products known as non-timber forest products (e.g. fruits, leaves, resins, bark) from individual plants that are left standing (Silvertown 2004). This type of harvest mimics herbivory or grazing, both of which have the potential for acting as a selective force on a host (Strauss & Agrawal 1999; Maron & Crone 2006). The effect of this type of harvest on host traits has been largely ignored, although it is no less likely to result in altered distributions of morphological and life-history traits (McGraw 2001; Law & Salick 2005). In particular, defoliating plants is likely to produce negative effects on annual survival and growth (Endress, Gorchov & Noble 2004; Martínez-Ramos, Anten & Ackerly 2009) with direct consequences for how long it takes organisms to achieve reproductive size as well as how many years they are expected to live. The response to defoliation is often habitat dependent (Strauss & Agrawal 1999; Wise & Abrahamson 2007). This paper addresses the life-history consequences of harvest for a tropical tree whose bark and foliage are harvested by indigenous people as source of fodder and medicine.

The demographic consequences of harvesting non-timber forest products have been quantified in several studies using the asymptotic populations growth rate,  $\lambda$  (Schmidt *et al.* 2011). However, the effects of harvest on the timing of key events in the life cycle (e.g., age at maturity, longevity) are as much, if not more, of interest for management of a stand that local people expect to continue to use. For example, a harvest-induced increase in the age at maturity (delay in reproduction) or reduction in life expectancy could translate into significant reduction in lifetime yield of non-timber products (e.g. fruits, resin, leaves). From a management perspective, local people who depend upon harvest of non-timber forest products for their livelihood may choose to manage these resources not just for population persistence, but also for longer life expectancy and early reproduction of individual organisms, depending upon the socio-economic objectives. Therefore, identifying the demographic processes driving changes in life expectancy is an important but under-investigated issue. For management seeking to increase population growth rate and life expectancy at the same time, a comparative sensitivity analysis can help identify potential conflicts and trade-offs among management strategies.

In this paper, we employ age-from-stage matrix modelling (Caswell 2001; Tuljapurkar & Horvitz 2006) to elucidate how both fixed and variable harvesting of non-timber forest products can affect life expectancy and time to maturity. The analysis is based on Markov chain theory; essentially, it involves following the dynamics of the number and of stage structure for a cohort of newborns over time. The lifetime trajectory of each individual is modelled as a sample path. This approach has been used to study the longevity of plants with contrasting life histories under different environmental regimes (Morris *et al.* 2008; Metcalf *et al.* 2009). The sensitivity of life expectancy is a new type of analysis that answers an

important, but distinct question from sensitivity analysis of population growth (Steiner *et al.* 2012).

Specifically, we focus on how defoliation and bark harvesting by indigenous people affect life expectancy and age at first reproduction of African mahogany, *Khaya senegalensis* (Meliaceae), in two ecological regions (dry versus moist) in Benin, West Africa. The bark (for medicine) and foliage (for cattle fodder) of African mahogany have been repeatedly harvested by indigenous people. Harvesters often target large reproductive individuals and harvest takes place at a very high intensity (Gaoue & Ticktin 2007). Harvesting foliage to feed cattle during the dry season involves cutting a large proportion of leafy branches (> 80%) out of the canopy of those individual trees selected for harvest (Fig. 1). Chronic defoliation and bark removal have significant demographic consequences, including a significant reduction in reproduction and a negative impact on leaf economics and on population growth rate (Gaoue & Ticktin 2008, 2010; Gaoue, Sack & Ticktin 2011), with the magnitude of the effects varying by climatic region.

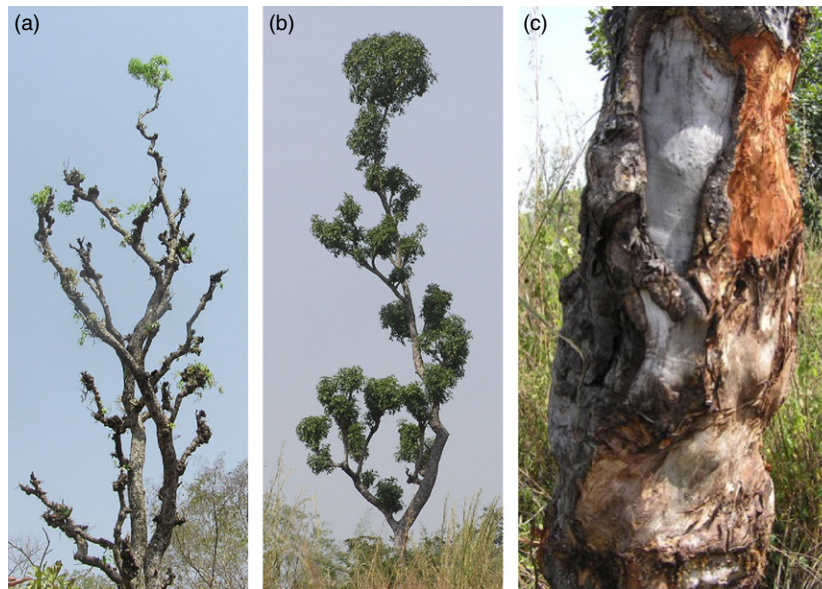
In this paper, we investigate (i) whether harvesting non-timber forest products affects life expectancy and age at first reproduction, (ii) whether these effects differ between habitats, (iii) whether the elasticity pattern of life expectancy is similar to that of population growth and (iv) whether temporally varying harvest intensity has stronger effect on these life-history traits than fixed-rate harvest intensity.

## Materials and methods

### STUDY SYSTEM

*Khaya senegalensis* is a tropical tree distributed in Africa across multiple habitats, from gallery forests to savanna woodland (Normand & Sallenave 1958; CTFT 1988). It is a semi-deciduous, shade-intolerant monoecious tree with wind-dispersed flat-winged seeds and insect-pollinated small white hermaphrodites flowers (CTFT 1988). *K. senegalensis* is one of the first timber species exported from Africa during the colonial era (Normand & Sallenave 1958). Remnant standing individuals and populations are heavily harvested across West Africa for foliage and bark.

Populations of *K. senegalensis* are found in two contrasting ecological regions in Benin (6°10' N and 12°50' N and 1°E and 3°40'E, West Africa). The Sudanian region is dry with lower rainfall, fewer rainy months and higher mean temperature than the moist Sudano-Guinean region. Details about the ecological differences between the dry and moist regions are provided elsewhere (Gaoue & Ticktin 2007, 2010). *Khaya senegalensis* only occurs in gallery forest in the dry region whereas in the moist region, it is found also in dense dry forest and woodland. We established our study populations to sample across the range of these differences in habitat and harvest intensity. Over 4 years (2004–2007), we collected data on diameter at breast height (dbh), survival, foliage and bark harvesting intensity, fruit and seed production of *K. senegalensis* individuals (with dbh  $\geq$  5 cm), in 12 1-ha permanent plots equally distributed between the dry and moist regions in Benin. We collected similar data on seedling and saplings (< 5 cm dbh), in 5 10 m  $\times$  10 m subplots established within each plot. We linked population-level seedling density in a given year to population fruit production in previous year to estimate population



**Fig. 1.** *Khaya senegalensis* is defoliated by Fulani to feed their cattle during the dry season. (a) Most harvested individuals lose at least 80% of their foliage. (b) Frequently defoliated individuals do not always recover their original canopy volume. (c) Bark removal serves for medicinal purposes; some individuals experience severe bark stripping.

fertility. For each population, we estimated the per cent of trees harvested (pruned and/or debarked). We categorized each population into one of three levels of harvest intensity (low, medium or high) depending on the proportion of trees harvested for foliage and bark. Populations with fewer than 25% of trees harvested were classified as low harvest (**L**); medium-harvest populations (**M**) were those with 25–50% of trees harvested, and high-harvest populations (**H**) had more than 50% of trees harvested. In the moist region, we surveyed

by harvest intensity to obtain three matrices **L**, **M** and **H** in each region.

#### LIFE EXPECTANCY AND AGE AT FIRST REPRODUCTION

The general form of *K. senegalensis* population projection matrix **A** written as a function of lower-level vital rates (survival,  $\sigma_i$ , growth,  $\gamma_{ij}$ , shrinkage,  $\rho_{ji}$ , fertility,  $\phi_i$ ) was as follows:

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

three low-, two medium- and one high-harvest populations; while in the dry region, there were three low-, one medium- and two high-harvest populations.

We defined 5 life stages using the basal diameter for seedlings and saplings and dbh for juvenile and adults: seedlings (basal diameter <2 cm), saplings (2–5 cm), juveniles (5–20 cm), small reproductive (20–40 cm) and large reproductive adults (dbh  $\geq$ 40 cm). The cut-offs for these life stages were selected based on previous results about the biology (seedling survival, minimum reproductive size, size-specific fruit production data) of the study species. We observed that individuals with <2 cm diameter do not often survive drought and fire. Only individuals with diameter greater than 5 cm were tall enough to be measured at breast height. Reproducing individuals are often >20 cm dbh, but most individuals reproduced at about 40 cm dbh (see Gaoue & Ticktin 2008, 2010 for details). To estimate age at maturity, we assumed that all individuals with dbh  $\geq$ 20 cm are reproductive in both ecological regions. For each population and year, we built a  $5 \times 5$  stage-based projection matrix **A** (Caswell 2001). We averaged the elements of the projection matrices across populations and years

We split matrix **A**, an  $S \times S$  matrix (here the number of life stages  $S = 5$ ) into an  $S \times S$  transition matrix **Q** in which the fertility elements are replaced with zeros ( $\sigma_i\phi_i = 0$ ) so that **Q** represents transitions among stages of already existing individuals, and an  $S \times S$  fertility matrix **F** which has all matrix entries equal zero except the fertility elements,  $\sigma_i\phi_i$ , so that it represents only the production of new individuals. We calculated life expectancy in a constant harvest scenario, for each of the six **Q** matrices (two climatic regions  $\times$  three harvest intensities), by determining how much time an individual is expected to spend in each stage before dying following Cochran & Ellner (1992) (see detailed method of calculation in Appendix S1, Supporting Information).

Calculating life expectancy when harvest intensity varies stochastically over time requires a Markov chain model for the harvest dynamics, essentially a model of environmental dynamics, where each state of the environment corresponds to one of three harvest intensities: low, medium and high. To generate plausible temporal sequences of harvest intensities for a given population, we created 36 different 3-state Markov chains. Each chain simulates a specific

management option and harvesting pressure. 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. Each Markov chain was characterized by a return time to high harvest, that is, the average number of years between two consecutive high-harvest years (Appendix S2). The return times for the 36 Markov chains ranged from 1 to 99 years; details are presented elsewhere (Gaoue, Horvitz & Ticktin 2011).

We then construct a model that includes environmental dynamics and life-stage transitions in each state of the environment to determine the time that an individual is expected to remain alive in the context of a dynamic harvesting environment. Since all individuals are born into one specific harvest environment or another, specified as  $\alpha$ , we calculate the average life expectancy and stage durations for all individuals born in harvest environment  $\alpha$  using a new stage duration matrix,  $\mathbf{N}_\alpha$ , where one is calculated for each of the  $K = 3$  harvesting intensities  $\alpha$  given by:

$$\mathbf{N}_\alpha = \mathbf{I} + \tilde{e}(\tilde{\mathbf{I}} - \mathbf{m})^{-1}\tilde{\mathbf{Q}}_\alpha, \quad \text{eqn 2}$$

is an  $SK \times SK$  identity matrix,  $\tilde{e}$  is a block matrix made up of a row of  $K$  blocks where each block is  $\mathbf{I}$ ;  $\tilde{\mathbf{Q}}_\alpha$  is a block matrix made up of a column of  $K$  blocks, where each block is an  $S \times S$  matrix and only the  $\alpha$ th block is nonzero and represents the corresponding  $\mathbf{Q}$  matrix; and  $\mathbf{m}$  is the  $SK \times SK$  megamatrix (see detailed calculation in Appendix S3) that combines population and environment-level dynamics (Pascarella & Horvitz 1998; Tuljapurkar & Horvitz 2006). We note that  $\mathbf{N}_\alpha$  is different from the stage duration matrix  $\mathbf{N}$  previously calculated for constant environments (see Appendix S1).

For a scenario in which the harvest intensity remains constant, we calculate the expected age at first reproduction as the mean first-passage time from the seedling stage (stage 1) to the first reproductive stage (stage 4), conditional on reaching this stage before death (Cochran & Ellner 1992; Caswell 2001). We obtain the expected age at first reproduction for populations experiencing stochastic variation in harvest intensity by using the large block matrix that encapsulates the dynamics of environment together with the dynamics of stage transitions within each state of the environment as above (see Appendix S4 for detailed method), following Metcalf *et al.* (2009).

#### SENSITIVITY OF LIFE EXPECTANCY

To compare the elasticity patterns of life expectancy with that of population growth rate, we begin our analysis of the elasticity of life expectancy to perturbation of lower-level vital rates by first determining the sensitivity of the life expectancy to perturbation of matrix elements  $q(i, j)$ . According to recent work by Steiner *et al.* (2012), the sensitivity of the elements of the stage duration matrix  $\mathbf{N}$  (see Appendix S1) to perturbation of the elements of the transition matrix is given by (see details in Appendix S5)

$$\frac{\partial(N(k, l))}{\partial q(i, j)} = N(k, i)N(j, l). \quad \text{eqn 3}$$

The first factor on the right-hand side of eqn (3) reflects what individuals starting in stage  $i$  are going to do (how much time they will stay in stage  $k$ ) before they die, and the second factor reflects where individuals visiting stage  $j$  are coming from (how many visits to this destination stage will be made from starting stage  $l$ ). This equation emphasizes the dependency of each element of the fundamental matrix on all elements of the transition matrix.

Steiner *et al.* (2012) further provide the sensitivity of total life expectancy conditional on surviving to stage  $k$ ,

$$\frac{\partial(\eta(k))}{\partial q(i, j)} = \eta(i)N(j, k). \quad \text{eqn 4}$$

To obtain the sensitivity of the life expectancy of newborns to perturbation of matrix elements, we set  $k = 1$ . For the sensitivity of remaining life expectancy of those that have reached the reproductive stage, stage 4 in our example, we set  $k = 4$ . Similarly to eqn (3), the first factor in eqn (4) reflects how many years individuals in stage  $i$  are expected to live, and the second factor again reflects where individuals seen in stage  $j$  come from (the number of visits to stage  $j$  for those who start in stage  $k$ ). We note that the sensitivity of life expectancy of newborns was derived by Caswell (2009) independently; his formulation involves a vec-permutation method. Steiner *et al.*'s method yields the same result as Caswell's for life expectancy of newborns, but additionally provides sensitivities for the conditional life expectancy of any stage and is easy to interpret biologically.

We used the chain rule to obtain the sensitivity of life expectancy of newborns, and the remaining life expectancy of adults reproductive to perturbation of vital rates as follows.

$$\frac{\partial\eta(k)}{\partial\theta(i, j)} = \frac{\partial\eta(k)}{\partial q(i, j)} \frac{\partial q(i, j)}{\partial\theta(i, j)}, \quad \text{eqn 5}$$

where  $\theta$  is a  $13 \times 1$  vector of vital rates and the corresponding elasticity to vital rates as

$$\eta(k)^{-1} \frac{\partial\eta(k)}{\partial\theta(i, j)} \theta(i, j). \quad \text{eqn 6}$$

We provide R code (see Appendix S6) to estimate age at first reproduction, life expectancy in constant or stochastic environments, and the sensitivity and elasticity of life expectancy to perturbation of projection matrix elements or lower-level parameters. We compared the elasticity of life expectancy to perturbation of vital rates with that of the population growth rate  $\lambda$ . The population growth rate was calculated as the dominant eigenvalue of the projection matrix  $\mathbf{A}$ . The elasticity of  $\lambda$  was calculated as described in Caswell (2001:232).

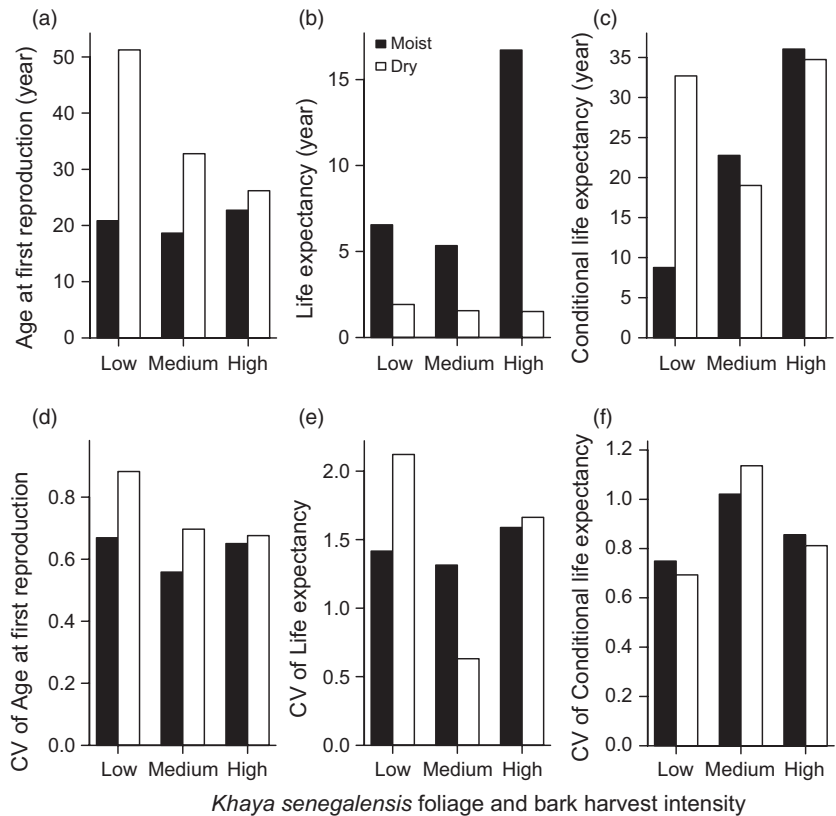
## Results

### EFFECTS OF HARVEST ON AGE AT FIRST REPRODUCTION AND LIFE EXPECTANCY

When harvest intensity is held constant over time, age at maturity varied from 19 years in the medium-harvest environment in the moist region to more than 50 years in low-harvest environment in the dry region (Fig. 2a). For a given harvest intensity, plants took longer to reach maturity in the dry region than in the moist region. In the moist region, age at maturity was relatively similar across harvest intensities, varying between 19 and 22 years. However, in the dry region, plants in environments that were less intensively harvested took almost twice as long to reach maturity compared to those that were in heavily harvested environments (Fig. 2a).

*Khaya senegalensis* lives longer in the moist region than in the dry region. A seedling in the moist region will live 8 years longer than a new recruit in the dry region (Fig. 2b). Harvesting at constant rate did not affect life expectancy in the dry region; however in the moist region it does, and heavy harvesting is associated with longer life: 10 years longer life in highly harvested environments than in lightly





**Fig. 2.** (a) Age at first reproduction (b) life expectancy and (c) remaining life expectancy conditional on reaching reproductive stage and their (d, e, f) coefficients of variation (CV) between low-, medium- and high-harvest populations in moist versus dry regions for constant harvesting rate over time.

harvested environments (Fig. 2b). Life expectancy conditional on passing the seedling stage, that is, the remaining life expectancy of saplings, is of importance in this study, given that seedling mortality rate is often high and individuals that escape this stage often live beyond the sapling stage. Saplings in the moist region are expected to live 12 years longer when in highly harvested environments compared to lightly harvested environments. The opposite trend was observed in the dry region where saplings are expected to die 5 years earlier in highly harvested environments than in lightly harvested environments.

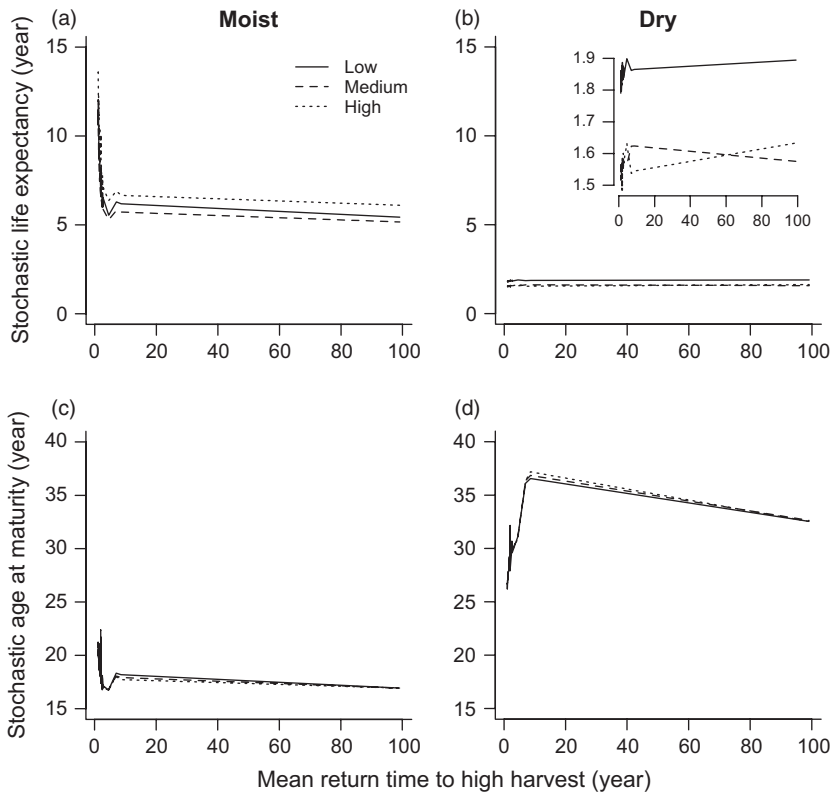
Conditional life expectancies of larger individuals differed between the two regions (Fig. 2c). In the moist region, individuals of *K. senegalensis* living in highly harvested forests live longer in general than in lightly harvested forests; this pattern is consistent across stages: conditional on reaching any size, expectation of further life is highest in highly harvested environments. In the dry region, the picture is more complicated and the effect of harvest on future life depends upon which stage the plants have already attained.

For models where harvesting intensity varied stochastically over time, variation in life expectancy (1.5–16 years) and age at first reproduction (17–38 years) is similar to what was found for models with constant harvesting intensity. Life expectancy was three- to sixfold higher in the moist region than in the dry region (Fig. 3a, b), while reproduction is delayed in the dry region more than in the moist region (Fig. 3c, d). Similarly to models of constant harvest, increasing harvesting pressure increased life expectancy in the

moist region while reducing age at first reproduction in the dry region. In addition, there was an interactive effect of harvest on life-history traits between regions. Increasing harvesting pressure sped up maturity (Fig. 3d) and reduced life expectancy (Fig. 3b) in the dry region but delayed reproduction (Fig. 3c) and increased longevity (Fig. 3a) in the moist region. Variation in life expectancy and age at first reproduction was low for a wide range of return time (20–100 years) and only increased when harvesting pressure is below the threshold of 5 years mean return time to high harvest.

#### ELASTICITY OF LIFE EXPECTANCY TO PERTURBATION OF VITAL RATES

Life expectancy is more elastic to perturbation of survival than to growth or retrogression (Fig. 4). Elasticity values differ between ecological regions and with harvesting intensity within each region. Life expectancy in the dry region is only elastic to perturbation of early life survival (seedling 's1', sapling 's2' and juvenile 's3'; Fig. 4d, e, f). In contrast, life expectancy in the moist region is elastic to perturbation of various vital rates (Fig. 4a, b, c). For example, perturbation of the survival of small reproductives (Fig. 4a) positively affects life expectancy in the moist region but not in the dry region (Fig. 4d). Perturbation of the growth of large reproductives negatively affects life expectancy in the moist region (Fig. 4b), while it has no effect in the dry region (Fig. 4e). Across regions, life expectancy is elastic to perturbation of



**Fig. 3.** Life expectancy (a, c) and age at first reproduction (b, d) with increasing mean return time to high harvest in moist and dry regions for stochastically variable harvesting rate over time. Inset in (b) shows detailed variation in life expectancy with harvesting pressure. Each line represents the initial harvesting intensity in which cohorts were born (low-, medium- or high-harvest populations).

survival and growth of seedlings regardless of harvest intensity, but this is not true for the other life-history stages (Fig. 4 a–e). In the moist region, the elasticity structure is dominated by survival of early life stages (seedlings, saplings, juveniles) in the low-harvest environments, whereas it is dominated by survival of late life stages (juveniles, small adults) in the highly harvested environment (Fig. 4a). The survival of juvenile also dominates the elasticity in lightly harvested environments in the dry region. In highly harvested environments, life expectancies are equally elastic to perturbation of sapling and juvenile survival. This pattern of elasticity of life expectancy contrasts with that of the population growth rates to perturbation of vital rates (Fig. S2). The population growth rate was more elastic to perturbation of the survival of reproductive adults (s4, s5) particularly in medium- and high-harvest populations.

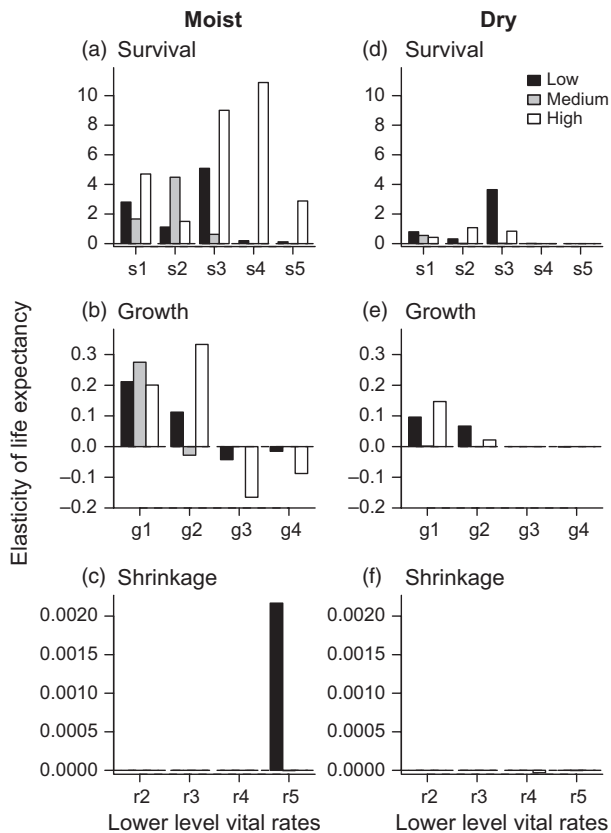
## Discussion

We used age-from-stage modelling to investigate how life-history parameters are affected by the intensity and frequency of harvest of non-timber forest products in two ecological regions. Previous studies that have used age-from-stage models for plant populations provided new insights into how light dynamics affect life span and the rate of forest turnover (Metcalfe *et al.* 2009), and the role of longevity in buffering temporal stochasticity in climate (Morris *et al.* 2008). Our study is the first, to our knowledge, to use these methods to analyse how anthropogenic disturbance affects plant life expectancy and age at first reproduction.

## EFFECTS OF HARVEST ON LIFE-HISTORY TRAITS

The effects of harvesting whole individuals on life-history traits have been investigated in the context of fisheries and game hunting, where individuals with particular phenotypes (such as large size) are selectively removed from wild populations (e.g. Allendorf & Hard 2009; Darimont *et al.* 2009). These studies show that harvesting leads to population changes in trait distributions, especially a reduction in mean body size and concomitant reduction in mean size or age at maturity accompanied by an increase in early reproductive investment. Defoliation and bark removal from standing individuals is distinct from selectively removing individuals from populations. Our study contributes new insights into the role that recurrent anthropogenic perturbations may play in shaping plant life-history traits. We specifically highlight the influence of stochastic variation in the sequence of perturbation and show how it magnifies the effect of harvest on mean age at maturity and life expectancy.

At constant harvesting rates, heavily harvested populations reproduce at an earlier age than do low-harvest populations in the more stressful environment (dry region) without an apparent cost to life expectancy. These heavily harvested populations in the dry region also have the highest reproductive effort (Gaoue & Ticktin 2008) but with no positive effect on population dynamics (Gaoue & Ticktin 2010). Our result is consistent with predictions from life-history theory that selection will favour early reproduction in stressful environments (Miller, Tenhumberg & Louda 2008; Darimont *et al.* 2009), but do not support the prediction that there is a trade-off between reproductive effort and longevity. The lack of impact



**Fig. 4.** Elasticity of life expectancy to perturbation of stage-specific (a, d) survival rates (s1: seedling, s2: sapling, s3: juvenile, s4: small adult, s5: large adult) (b, e) growth (g1, g2, g3, g4) and (c, f) shrinkage (r2, r3, r4, r5) for constant harvesting rate over time differed between populations with differing harvest intensity (low, medium or high) and also between the (a, b, c) moist versus (d, e, f) dry region.

of harvesting at constant rates on life expectancy in the dry region may be explained by the fact that life expectancies are already very low in this region, and the impact of additional perturbation is not significant to be detected under a deterministic model.

Similar to the effects of harvesting at constant rates, for models with stochastically variable harvesting intensity, increasing harvesting pressure reduces age at first reproduction in the dry region and increases life expectancy in the moist region. However, in addition, increasing harvesting pressure accelerates maturity and reduces life expectancy in the dry region but delays reproduction and increases life expectancy in the moist region. This suggests that modelling harvesting as stochastically variable over time magnifies the effect of harvesting on life-history traits in a way that the deterministic model failed to reveal. Our results in the moist region are consistent with the theoretical prediction that in uncertain environments, delayed reproduction and increased longevity will be favoured (Tuljapurkar 1990; Koons, Metcalf & Tuljapurkar 2008). However, in our system, the nature of this trade-offs greatly depends on the ecological conditions in which harvesting is taking place. The fact that this prediction does not hold in the dry region may indicate that in uncertain

environment, when the ecological conditions are stressful, the effect of harvest on life-history traits may be similar to that in constant environment due to compounding effect of multiple source of stress (harvest, drought, stochasticity). Although we compare our results to theoretical predictions from life-history theory, questions remain about whether the changes in age at first reproduction or life expectancy for our study species in constant or stochastic environments can be interpreted as harvest-induced adaptations to maximize population fitness. *Khaya senegalensis* is a long-lived tree species and has been harvested, at high intensity, by indigenous *Fulani* people only since the great drought of the 1970s (Gautier, Bonnerat & Njoya 2005). For this short time scale, it is less likely that this long-lived species has adapted to harvesting. Instead, these changes in life-history traits are the result of a phenotypic plasticity.

#### ELASTICITY OF LIFE EXPECTANCY VS. POPULATION GROWTH RATE

Life expectancy in the dry region was less elastic to perturbation of vital rates than it was in the moist region. This may explain the lack of impact of harvest on life expectancy in the dry region. In contrast to findings by Caswell (2009) that life expectancy of the long-lived right whale was more elastic to perturbation of mature female survival, we found that life expectancy was most elastic to survival of early life stages. In previous work on the same species, Gaoue & Ticktin (2010) and Gaoue, Horvitz & Ticktin (2011) found that population growth rate was most elastic to perturbation of survival of late life stages in constant (Fig. S2) and stochastic environments. Such a pattern of elasticity of population growth rates is common in long-lived species (Silvertown *et al.* 1993; Morris *et al.* 2008). It has been proposed that this pattern is maintained through selection pressure favouring the maintenance of the long-term investment in biomass (Petit & Hampe 2006). General patterns of elasticity for life expectancy in long-lived organisms are as yet not known. However, given that life expectancy is the mean age at death of newborns, it is expected that life expectancy is more elastic to survival of early life stages. Our study is, to our knowledge, one of the few to analyse the elasticity of life expectancy to perturbation of vital rates (see Steiner *et al.* 2012).

#### IMPLICATIONS FOR SUSTAINABLE MANAGEMENT

A growing number of studies have provided evidence that plant harvest has ecological consequences at the population (Ghimire *et al.* 2008; Martínez-Ramos, Anten & Ackerly 2009) and ecosystem levels (Ticktin 2004), therefore implying that this activity, carried out by millions of local people across the world (Bawa *et al.* 2004), may be a key factor in forest dynamics. Our results show that harvesting impacts on population dynamics may be coupled with effects on life-history traits. The difference in elasticity patterns between these two parameters (population growth rate and life expectancy) suggests that to achieve both increased longevity and population

growth rate, it is critical to focus not just on improving the survival of reproductive individuals, as it would be suggested whether the focus were solely on growth rate, but also on the survival of non-reproductive individuals. For *K. senegalensis*, this is even more critical for populations experiencing additional stress from drought.

The phenotypic changes caused by harvest may have significant implications for the ecological and economic sustainability of non-timber forest product harvest. For example, if, as we found for *K. senegalensis* in the moist region, chronic harvest leads to delayed reproduction, this could affect lifetime yields for species that are exploited for their fruits or seeds, for example *Bertholletia excelsa* (Zuidema & Boot 2002), *Sclerocarya birrea* (Emanuel, Shackleton & Baxter 2005). However, the effect of delayed reproduction on lifetime yield will depend upon the degree to which this is compensated by the associated increase in longevity observed. In the specific case of our study species and in stochastic harvesting context, our results indicate that a mean return time to high harvest of 5 years or less is necessary to induce changes in longevity or age at maturity.

Overall, our study emphasizes the need to account for the heterogeneity in ecological conditions in modelling the impact of perturbation (e.g. herbivory, grazing or harvesting non-timber forest products) on life history or on population dynamics, given that the response of populations may be context dependent. Most studies of the impact of harvesting of non-timber forest products have failed to account for spatial variation in environmental conditions and temporal stochasticity in harvest intensity (Ticktin 2004; Gaoue, Horvitz & Ticktin 2011). Finally, beyond the sustainability of harvest, results from our study have broader implications for the impacts of other (non) human-related perturbation such as grazing, herbivory and fire. Specifically, defoliation of fodder trees by indigenous *Fulani* people to feed their cattle as reported in our study is comparable to grazing, with the difference that the *Fulani* help bring the browse close to the herbivore. This type of defoliation is also comparable to herbivory and as reported for population dynamics, it is reasonable to hypothesize that the effect of harvest on life-history traits reported in our study mirrors some of the responses of plants population to grazing and herbivory. Similar studies on the effects of disturbance and climate change on life-history traits are needed to allow a synthesis of how this may vary across life forms, phylogenetic relatedness and type of organs harvested. In addition to habitat heterogeneity, individual level variation in individual quality (caused in our case by heterogeneity in harvesting intensity) can affect the population-level estimates of life-history parameters (Vindenes, Engen & Sæther 2008; Zuidema *et al.* 2009). Although we did not account for this source of variation in this paper, future studies could analyse how integrating demographic heterogeneity may provide further understanding of the role of harvest on life-history dynamics. This can be done using integral projection modelling (Ellner & Rees 2006) where individual harvesting intensity and response can be explicitly accounted for.

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## Supporting Information

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

**Appendix S1.** Estimating life expectancy in constant environments using stage duration matrix.

**Appendix S2.** Method to estimate return times to high harvest using stage duration matrix **N**.

**Appendix S3.** Building megamatrix **m**, which combines population and environment dynamics.

**Appendix S4.** Age at first reproduction in constant and stochastic environments.

**Appendix S5.** Method to calculate the sensitivity of life expectancy to perturbation of vital rates.

**Appendix S6.** R script to estimate life-history parameters in constant or stochastic environments.

**Data S1.** Markov chains used to simulate different management strategies in stochastic models.

**Data S2.** *Khaya senegalensis* vital rates in two ecological regions and three harvesting intensity.

**Figure S1.** Sensitivity of stage-specific life expectancies to perturbation of matrix elements.

**Figure S2:** Elasticity of population growth rate to perturbation of lower-level vital rates.