

Defoliation by pastoralists affects savanna tree seedling dynamics by limiting the facilitative role of canopy cover

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Abstract. Recurrent tree defoliation by pastoralists, akin to herbivory, can negatively affect plant reproduction and population dynamics. However, our understanding of the indirect role of defoliation in seedling recruitment and tree–grass dynamics in tropical savanna is limited. In West African savanna, Fulani pastoralists frequently defoliate several fodder tree species to feed livestock in the dry season. We investigated the direct and indirect effects of recurrent defoliation of African mahogany (*Khaya senegalensis*) by Fulani people on seedling (<2 cm basal diameter) and sapling dynamics in West Africa using four years of demographic data on seedling and sapling density, growth, and survival, coupled with fruit production and microhabitat data over the same time period. Tree canopy cover facilitated seedlings but had negative effects on sapling growth possibly via intraspecific competition with adult plants. Interspecific competition with grasses strongly reduced seedling survival but had a weak effect on sapling growth. Fire reduced seedling survival and weakly reduced growth of seedlings and saplings, but did not affect sapling survival. These results indicate that the effect of fire on seedlings and saplings is distinct, a mechanism suitable for an episodic recruitment of seedlings into the sapling stage and consistent with predictions from the demographic bottleneck model. Defoliation affected seedling density and sapling growth through changes in canopy cover, but had no effect on seedling growth and sapling survival. In the moist region, sapling density was higher in sites with low-intensity defoliation, indicating that defoliation may strengthen the tree recruitment bottleneck. Our study suggests that large-scale defoliation can alter the facilitative role of nurse trees on seedling dynamics and tree–sapling competition. Given that tree defoliation by local people is a widespread activity throughout savanna–forest systems in West Africa, it has the potential to affect tree–grass coexistence. Incorporating the influence of large tree defoliation into existing models of savanna dynamics can further our understanding of tree–grass coexistence and improve management. A rotating harvest system, which allows seedlings to recruit episodically, or a patchwork harvest, which maintains some nursery trees in the mosaic, could help sustain seedling recruitment and minimize the indirect effects of harvest.

Key words: African mahogany; canopy cover; Fulani pastoralists; *Khaya senegalensis*; nontimber forest product harvest; nurse tree; recurrent defoliation; relative growth rate; savanna–gallery forest matrix; seedling survival; tree recruitment; West Africa.

INTRODUCTION

The mystery of tree–grass coexistence in savannas has challenged ecologists for decades. Savannas are composed of virtually continuous grass cover with sparse and scattered trees, but they occur within a matrix of grasslands, thickets, and woodlands, including gallery forests (Bond 2008). The distribution of savanna and closed forest in moderate rainfall, low-seasonality climates is determined by the frequency of disturbance events, especially fire, to which seedlings are particularly vulnerable (Higgins et al. 2000, Bond 2008, Gignoux et

al. 2009, Staver et al. 2011). The demographic bottleneck model of savannas (Higgins et al. 2000) suggests that fire, water availability, and competition between grasses and trees limit tree recruitment. Episodic recruitment of trees during good years maintains tree presence in unfavorable years until another recruitment event (storage effect), promoting tree–grass coexistence (Chesson and Huntly 1989, Bond 2008, Staver and Bond 2014). Recently, there has been renewed interest in the role of herbivory by medium and large herbivores in tropical savanna tree–grass dynamics, especially in African savannas, where browsing by wild and domestic herbivores interacts with fire to limit tree density and facilitate tree–grass coexistence (Higgins et al. 2000, Bond 2008, Staver et al. 2009). West African savannas, which are established on less productive soils than East and Southern African savannas (Bationo et al. 2007), also experience recurrent and large-scale fodder tree-

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branch-logging by Fulani pastoralists during critical dry season. This recurrent defoliation, by reducing canopy cover, could further alter tree–grass dynamics.

Tree canopy cover can modulate the effects and extent of fire and herbivore activity, but the nature of these interactions is not always clear and our understanding of the effect of large-scale, human-mediated defoliation of savanna trees on tree–grass coexistence is limited. Adult trees can facilitate the establishment of woody seedlings through lower frequency and intensity of fire, a more humid microclimate, higher nutrients, lower temperatures, and lower biomass of herbaceous competitors (Belsky et al. 1989, Scholes and Archer 1997, Siemann and Rogers 2003, Gómez-Aparicio et al. 2005, Holdo 2005, Dohn et al. 2013, Vadigi and Ward 2013, Caldeira et al. 2014). The facilitative effects of adult trees are especially important for seedlings, which are most vulnerable to fire, drought, herbivory, and competition with grasses (Hoffmann 2000, Holdo 2005, Gignoux et al. 2009, Vadigi and Ward 2013, Staver and Bond 2014). Seedlings are killed by fire; saplings, though they often survive fire, suffer reduced growth, which prevents them from becoming adults (Higgins et al. 2000, Bond 2008). Because of the importance of positive feedback between adult trees and woody recruitment, defoliation of tree canopies could have serious implications for tree persistence in savannas and adjacent forests. Defoliation, by reducing canopy cover, increases light penetration in the understory and favors grass growth, which in turn will increase fire frequency. Reduction in canopy cover will also expose seedlings to increased light irradiance and higher evapotranspiration (Anderson et al. 2001, Gómez-Aparicio et al. 2005). Previous studies show that recurrent defoliation can reduce fruit production (seed source) and seedling recruitment and can negatively affect population dynamics (Gaoue and Ticktin 2008, 2010, van Lent et al. 2014). However, studies of the indirect effects of tree defoliation on savanna dynamics are rare. We investigate the direct and indirect effects of large-scale defoliation by local people on the dynamics of seedlings in gallery forest–savanna matrix.

Across savannas and dry forests in West Africa, several trees species (e.g., *Khaya senegalensis*, *Azelia africana*, *Pterocarpus erinaceus*, *Balanites aegyptiaca*) are defoliated frequently to feed livestock in the dry season (Petit 2003, Gautier et al. 2005, Gaoue and Ticktin 2007, Jurisch et al. 2012). Indigenous Fulani, who are migratory cattle-herders, climb large fodder trees and prune small branches to feed to their cattle, especially in the dry season, resulting in up to 100% defoliation of the tree (Gaoue and Ticktin 2007). Such harvest of nontimber forest products (NTFP) by local people has economic and cultural importance (Bawa et al. 2004, Ticktin 2004) and has shaped this tropical landscape for several decades (Petit 2003, Gaoue and Ticktin 2007, Jurisch et al. 2012, 2013). Elucidating direct and indirect effects of adult defoliation on

seedlings and saplings can advise managers of this critical and heavily used resource by illuminating short-term recruitment dynamics that are essential for medium-term population viability.

We studied the effects of recurrent defoliation by the Fulani on the dynamics of African mahogany *Khaya senegalensis* (Meliaceae) seedlings and saplings in Benin (West Africa). *K. senegalensis* is a key component of woodlands and gallery forests and serves as a nursery tree for woody species in the savanna (Azihou et al. 2013b). Gallery forests are narrow and therefore have high light penetration and support significant grass cover, resulting in similar dynamics, including frequent fires, in both the savanna and the narrow belt of gallery forest. We hypothesize that defoliation impacts seedling and sapling dynamics directly by reducing reproduction and seed source (e.g., decrease in seed number) and thus seedling density, and indirectly through effects on microhabitat (e.g., woody understory cover, grass cover, etc.), fire regime, and facilitative canopy cover. Understanding the drivers of seedling and sapling dynamics of this species can shed light on the ecology of tree dynamics in savannas.

MATERIALS AND METHODS

Study design

We studied populations of *Khaya senegalensis* in Benin (6–12°50' N, 1–3°40' E; West Africa), where it grows in the drier northern Sudanian region (9°30'–12' N) and the moist central Sudano-Guinean region (7°30'–9°30' N; Fig. 1). *K. senegalensis* is a valuable timber species and is important not only as cattle fodder (leaf harvest), but also as a medicinal plant (bark harvest). *K. senegalensis* is a large (30 m high, 3 m circumference), shade intolerant, semi-deciduous tree and produces thousands of wind-dispersed seeds (Gaoue and Ticktin 2008). In the drier Sudanian region, which receives 800–1100 mm of rain annually and has a 145-d growing season, *K. senegalensis* grows in gallery forests, where there is greater moisture availability. In the moist Sudano-Guinean region, which receives 1100–1300 mm of annual precipitation over a 200-d growing season, we included sites in woodlands and dense dry forest, as well as in gallery forests (for more information see Gaoue and Ticktin 2008).

In 2004, we surveyed a total of 29 geographically distinct populations of *K. senegalensis* across the study area and estimated their size and harvesting intensity by Fulani pastoralists (see Gaoue and Ticktin 2010). These populations were separated by 15–300 km with an average tree density of 43.16 ± 7.23 stems/ha (mean \pm SE; Gaoue et al. 2014). We categorized these 29 populations into two groups based on harvest intensity (low vs. high) within each of the two ecological regions. From this set of populations, we randomly selected three sites per region with high harvest intensity and three with low harvest intensity (Fig. 1). At high-harvest-intensity sites, typically >50% of trees are at least

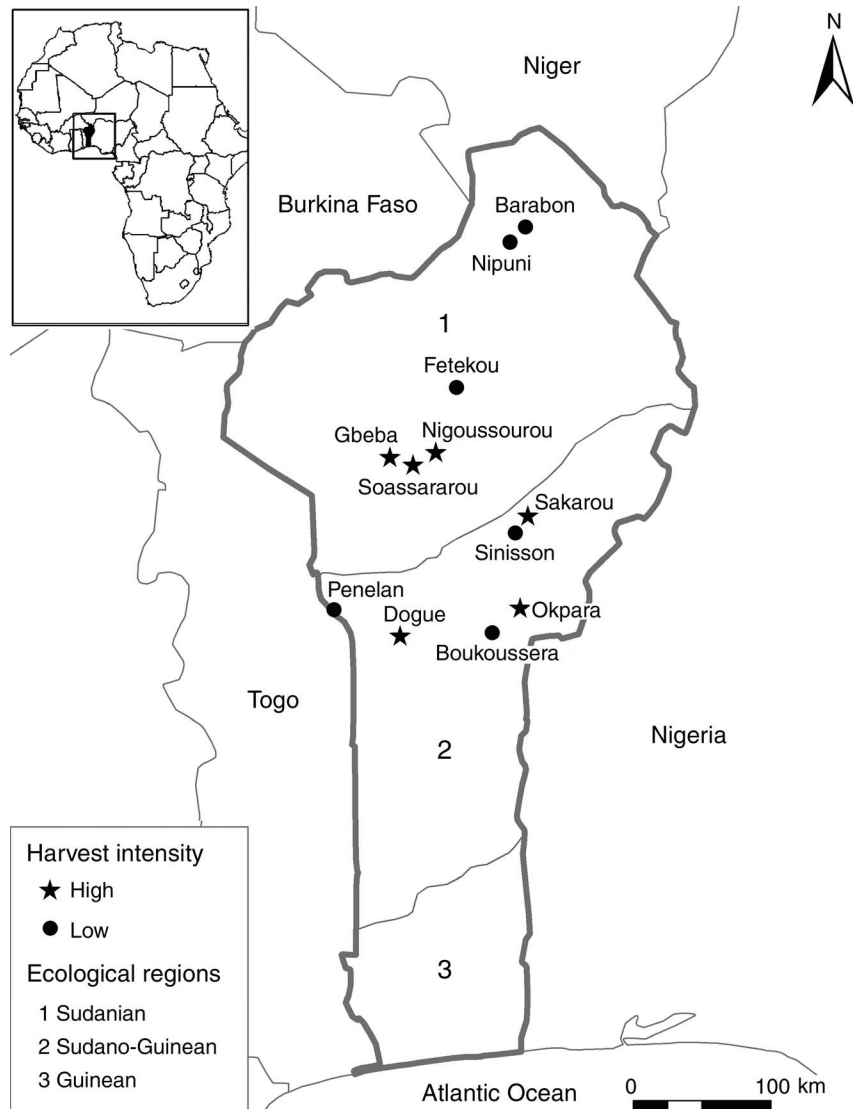


FIG. 1. Map of the study populations of African mahogany (*Khaya senegalensis*) in Benin, West Africa. Six populations were studied in the moist Sudano-Guinean region and six in the dry Sudanian region. In each region, half of the sites have high-intensity recurrent foliage and bark harvest by local pastoralists (stars) and half have low harvest intensity (circles).

partially defoliated and $>10\%$ of trees debarked. Low-harvest-intensity sites are often locally or nationally protected and have $<5\%$ of trees defoliated and $<10\%$ of trees debarked. Defoliated trees often lose $\geq 80\%$ of their foliage and harvest occurs year-round (Gaoue and Ticktin 2007). We established 1-ha plots in each population and revisited yearly from 2004 to 2007 as part of a demographic study of *K. senegalensis* (Gaoue and Ticktin 2010). All adult trees were tagged with round, numbered aluminum tags and both size and harvest intensity were measured annually for each individual. If any individual tags were lost, they were replaced at the beginning of each yearly census. Trees in these populations have been harvested by Fulani pastoralists for decades and harvest continued through-

out our surveys. Thus, we expect our surveys to capture the results of long-term harvest pressure.

Seedling demography and microhabitats

In each population, 10 subplots of 10×10 m were established at the four corners and the center of each half of the 1-ha plot to monitor seedlings and saplings. For this analysis, we used only *K. senegalensis* individuals with a basal diameter of <6 cm, and based on previous work on this species (see Gaoue and Ticktin 2010), we distinguished seedlings (basal diameter < 2 cm, typically under two years old) from saplings (basal diameter ≥ 2 cm). Once yearly from 2004 to 2007, all seedlings and saplings (mean \pm SD, 8 ± 12 individuals; range, 0–83) in the subplots were tagged and basal

diameter and height were measured. Survival and growth in subsequent years was determined by revisiting tagged individuals. Newly recruited seedlings were defined as those that had not been found in a previous census and had a diameter ≤ 1 cm and a height ≤ 0.5 m. The total fruit produced in each population was also visually estimated each year (Gaoue and Ticktin 2008). One of our populations (Penelan; Fig. 1), which had previously experienced low harvest intensity, was logged in 2005, affecting two of the ten subplots at that site. Therefore, we excluded data from these two subplots, from 2005 to 2007, from the analyses, leaving 118 subplots in total.

From 2005 to 2007, additional microhabitat data were collected in each subplot, including visual estimates of the percent cover of grass and percent woody understory cover. Fire is common in the savannas of Benin and often extends into the gallery forests, therefore we also measured the percentage of the subplot area that had been burned by ambient fires in the previous year. Total canopy cover was recorded in 2006 and 2007, but was not significantly different by year (ANOVA, $P = 0.22$), so we averaged canopy cover across years and used the mean value for each subplot for all analyses. All of these microhabitats data estimates were taken by O. G. Gaoue for the whole study period (2004–2007) to maintain consistency between plots and across years.

Data analysis

To investigate the effects of region and harvesting intensity on microhabitat characteristics and the effects of region, harvesting intensity, and microhabitat characteristics on seedling dynamics, we used (generalized) linear mixed-effects models (Bolker et al. 2009) in the packages *lme4*, *nlme*, and *glmmADMB* (Fournier et al. 2012) in R, version 3.1.1 (R Development Core Team 2014). We modeled the microhabitat variables, percentage of subplot-area burned ($n = 351$ observations), grass cover ($n = 350$), woody cover ($n = 349$), and canopy cover ($n = 118$), as proportions using a beta regression. Plots with a proportion of 0 or 1 were adjusted slightly (± 0.0001) because a beta regression cannot process values of 0 or 1 (Ferrari and Cribari-Neto 2004). Microhabitat models included region, harvest intensity, the interaction between region and harvest, and year as fixed effects and included population as a random effect.

To investigate seedling dynamics, we modeled three response variables and modeled seedlings and saplings separately: density (newly recruited seedlings, $n = 345$ subplots across years; small seedlings, $n = 342$ subplots where diameter was measured; saplings, $n = 335$ subplots), relative growth rate (RGR; seedlings, $n = 863$ individuals that survived and for which both previous and present diameter was measured; saplings, $n = 330$ individuals), and survival (seedlings, $n = 1660$ individuals; saplings, $n = 335$ individuals). RGR was calculated as the log of the ratio between two successive basal diameters. We began with a fully parameterized

model that included the interactions between region and harvest, region and grass cover, and region and woody understory cover. We included percentage of the subplot burned and percent canopy cover as fixed effects and both population and subplot within population as random effects. When modeling newly recruited seedling density, we also included the fruit produced by a population in a given year, in order to account for the effect of seed supply. When modeling RGR, we included an interaction between harvest intensity and year. We also included year in the model of seedling survival, but did not include it in our density models, because there was no graphical evidence for temporal variation. To model survival, we also included the total number of seedlings in the subplot, to test for negative conspecific density dependence, and previous basal diameter, to account for higher probability of survival in larger individuals. All continuous variables were standardized to facilitate the interpretation of regression coefficients (Schielzeth 2010). To model survival and RGR, we used a mixed-effects model of individual seedling/sapling data with population and subplot as random effects, as in the density models. We initially included individual ID as a random effect in these models to account for repeated measurements on the same individuals, but this term did not explain any additional variance and so was removed to simplify the model and improve estimation of other terms.

For each response variable, different variance and distribution structures were tested and the model structure with the lowest AIC_c (Akaike's information criterion corrected for small sample sizes) was selected. For seedling and sapling density models, we constructed Poisson models; where data were overdispersed, we also tested negative binomial and zero-inflated models. A few subplots had very high newly recruited seedling density ($n = 3$) or sapling density ($n = 7$). Although high recruitment events are interesting, the values extend too far beyond the rest of the data to be accurately modeled, so we excluded them from the analysis. Survival was modeled using a binomial distribution. For RGR, we tested heterogeneous variance structures and used a Gaussian distribution.

Including the fully parameterized models, we generated up to 25 candidate models for each response variable based on the terms and interactions of interest. The optimal model was chosen from among the candidate models using an information theoretic approach. For each variable, we selected as the final model the most complex model with a delta AIC_c of less than two in order to include all potentially important terms, while reducing model complexity to facilitate more accurate estimation of model terms. We calculated bootstrapped ($n = 1000$) confidence intervals for the effect sizes of the final model of sapling density, seedling RGR, and seedling and sapling survival in the package *boot*. For models of new seedling recruit density and overall seedling density, which were modeled in

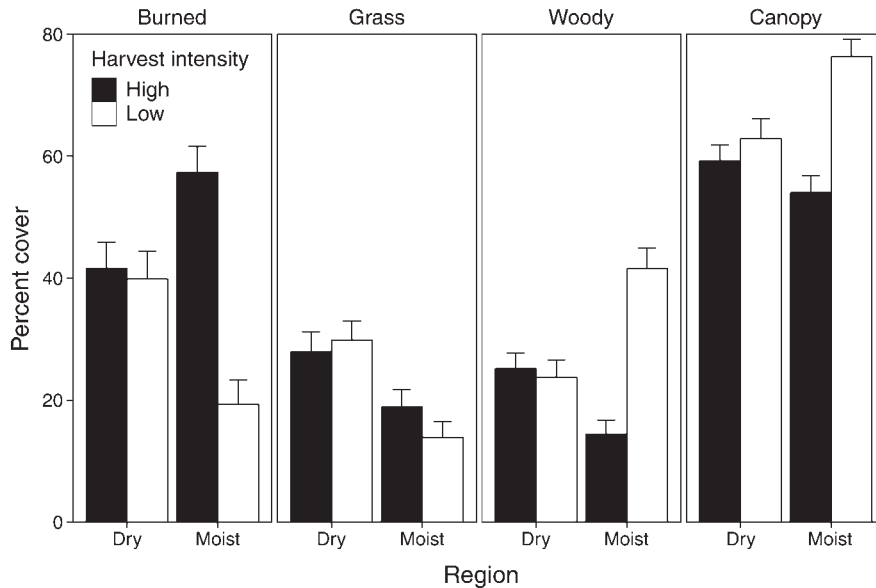


FIG. 2. Microhabitat characteristics of each region (dry, Sudanian, moist Sudano-Guinean) at different harvest intensities, including percentage of the area burned, percent grass cover, percent woody shrub cover, and percent canopy cover, measured in subplots within each of 12 populations of *Khaya senegalensis*. Bars represent mean + SE across populations. In generalized linear mixed-effects models of each microhabitat variable, there was a significant region and harvest interaction term in models of woody cover and canopy cover, and the models indicated a significant effect of region on grass cover.

glmmADMB, we used the post hoc Markov chain Monte Carlo (MCMC) function of AD Model Builder (*available online*),⁵ using 10 000 MCMC iterations with a burn-in of 2000 iterations. This MCMC method uses a flat prior to estimate credible intervals from the posterior distribution of the coefficients (Fournier et al. 2012). When we modeled the RGR of saplings, the choice of a final model was not clear, as many models had a ΔAIC_c of less than two. In this case, we used the zero method of model averaging based on model AIC_c values in the R package MuMIn to create an averaged final model with confidence intervals. Graphs were produced with ggplot2 (Wickham 2009) and present the effect size, which estimates the influence of the predictor and is the model coefficient when the predictor variables are standardized (Schielzeth 2010).

RESULTS

Microhabitat varied across regions and harvesting intensities

In the moist Sudano-Guinean region, populations with low harvest pressure had on average 50% more tree canopy cover and twice the understory woody cover of heavily harvested populations (Fig. 2). Harvest did not affect microhabitat in the dry region (Fig. 2). The variance attributed to the random effect of population was low ($\sigma^2 = 0.32, 0.01, 0.24,$ and 0.39 for burned area, grass cover, woody cover, and canopy cover, respectively). However, there was high variation in microhabitat

between populations in the moist region with low harvest, where two populations had virtually no fire because of a wet microclimate and active management by local people. This variation makes the effect of harvest in the wet region difficult to estimate and means that these coefficients, though large, are not significantly different from zero in the model of fire extent (Fig. 3).

Seedling and sapling density

Seedling density was greater in the low harvest intensity populations than in heavily harvested populations across regions and years, and sapling density was greater in populations with low harvest intensity across years in the moist Sudano-Guinean region. The effect of harvest on new seedlings, however, was not significant (Appendix A: Table A1; Appendix B: Fig B1). Population-level fruit production also had no significant effect on new seedling density (Fig. 4) and more variance was ascribed to population ($\sigma^2 = 0.87$) than to subplot ($\sigma^2 = 0.39$). Seedling density increased with decreasing fire and increasing canopy cover (Fig. 4), both of which are characteristic of low harvest intensity populations (Fig. 2). Both population and subplot had large random effect variances for the model of seedling density ($\sigma^2 = 1.16$ and 1.35 , respectively). In contrast, there was no significant effect of abiotic microhabitat factors on sapling density (Table A1), with only marginal support for a negative effect of fire (Fig. 4). Sapling density was highly variable by subplot ($\sigma^2 = 4.81$), but population did not explain any further variance ($\sigma^2 = 0.00$).

⁵ <http://admb-project.org>

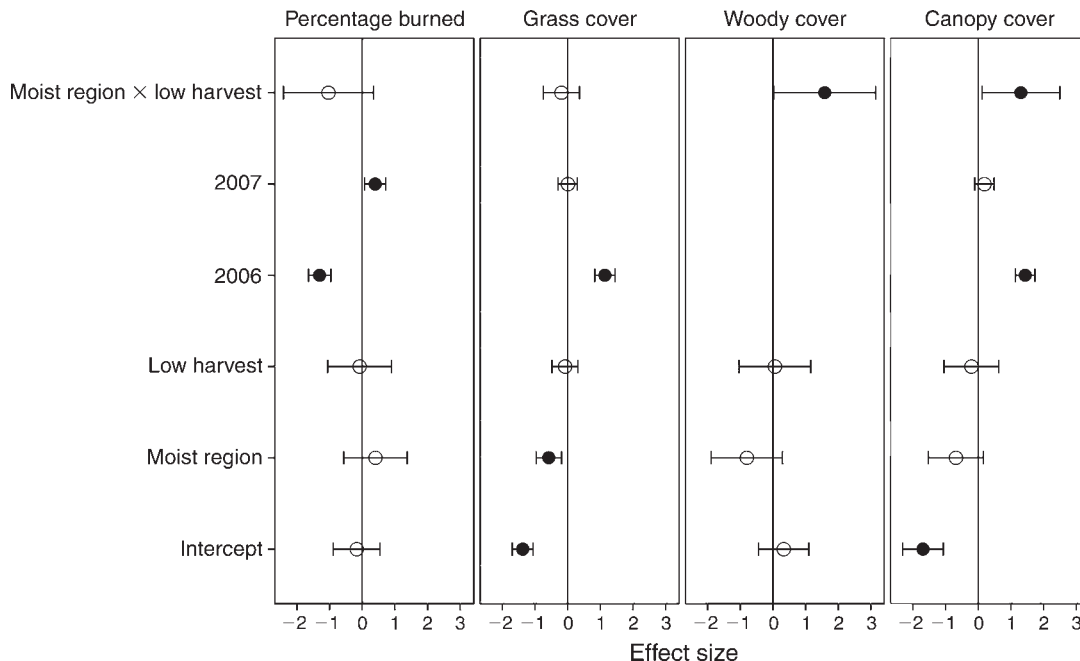


FIG. 3. Effect size and 95% confidence intervals calculated from the approximate SE for fixed effects in generalized linear mixed-effects models of the microhabitat characteristics of 10 × 10 m plots in 12 populations of *Khaya senegalensis* measured over three years, with the exception of canopy cover, which was averaged over two years. Solid circles indicate significant variables, where the confidence intervals do not overlap zero. Empty spaces occur when the term was not included in that model.

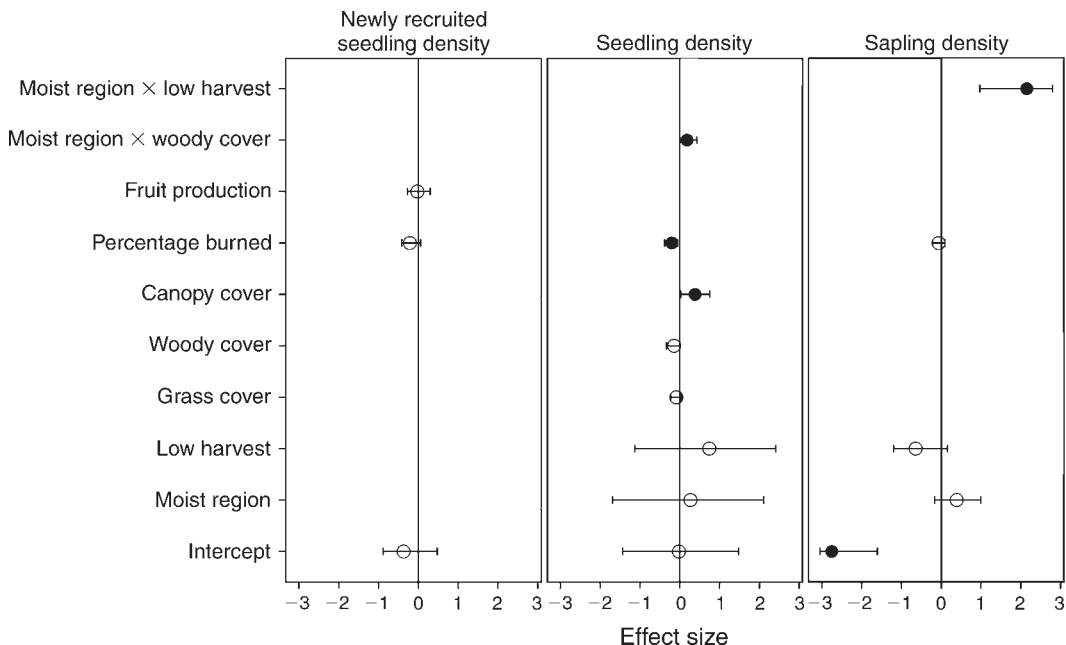


FIG. 4. Effect size and Markov chain Monte Carlo 95% credible intervals (new seedling density and seedling density) or 95% bootstrapped confidence intervals (CI; sapling density only) for fixed effects in the final reduced generalized linear mixed-effects models of the density of *Khaya senegalensis* seedlings and saplings (no./100 m²) across 12 populations measured over three years. Models include new seedling density, seedling density (<2 cm basal diameter), and sapling density (>2 cm basal diameter). Solid circles indicate significant variables, where the credible or confidence intervals do not overlap zero. Empty spaces occur when the term was not included in that final model.

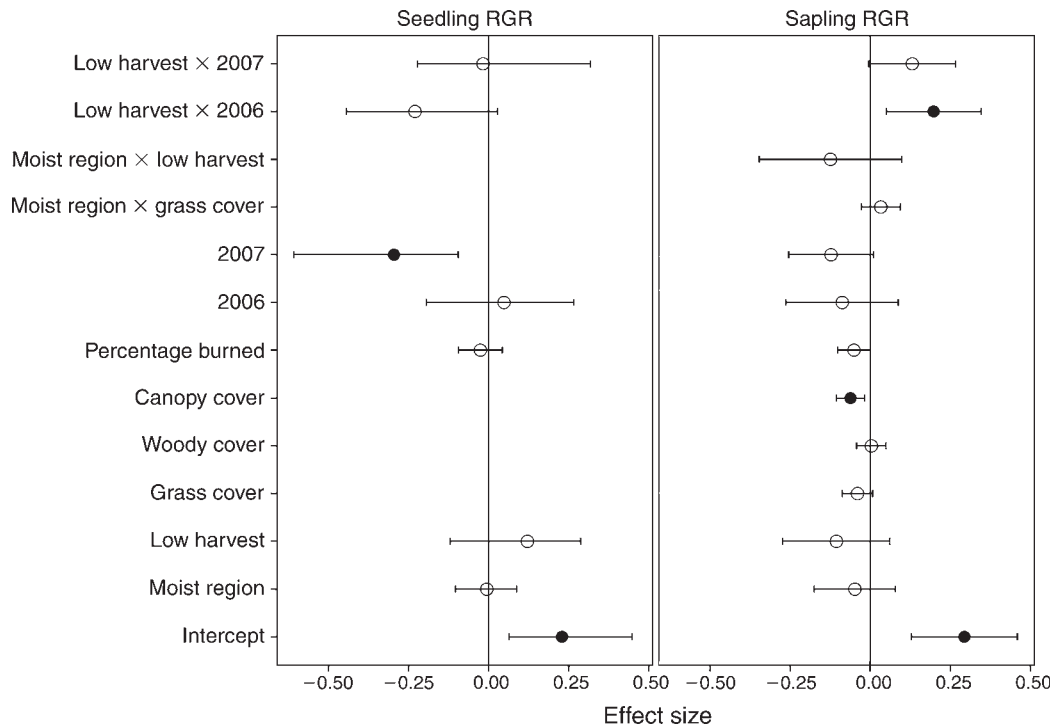


FIG. 5. Effect size and 95% CI for fixed effects in the final linear mixed-effects model of relative growth rate (RGR) of *Khaya senegalensis* seedlings and saplings monitored across 12 populations over four years. Confidence intervals for seedling relative growth rate (RGR) are 95% bootstrapped CI. Confidence intervals for sapling RGR are from model averaging across a suite of candidate models with $\Delta AIC_c < 2$. Solid circles indicate significant variables, where the CI do not overlap zero. Empty spaces occur when the term was not included in that final model.

Relative growth rate and survival

The effect of harvest on relative growth rate (RGR) varied between years and microhabitat affected sapling, but not seedling, RGR (Fig. 5, Table A2). Harvesting had a negative effect or no effect on seedling RGR in most years. In contrast, the effect of harvesting was positive for sapling RGR in most years, especially in the dry region, and saplings in low harvest populations did not grow in several years (Fig. B2). This harvest effect may be mediated by differences in microhabitats; canopy cover decreased sapling RGR and fire had a weak negative effect on RGR in both saplings and seedlings (Fig. 5). Random effects of population and subplot had little effect on models of RGR for seedlings ($\sigma^2 = 0.09$, 0.06 respectively) and saplings ($\sigma^2 < 0.001$ and $\sigma^2 = 0.06$, respectively).

Seedling survival was higher in the moist Sudano-Guinean region, while sapling survival was consistently high across regions and harvesting intensities (Appendix: Fig. B3). Seedling survival was negatively affected by fire and grass cover, but increased with higher densities of conspecific seedlings (Fig. 6) and was partly explained by population ($\sigma^2 = 1.04$; subplot $\sigma^2 = 0.23$). Sapling survival was not significantly influenced by harvest, region or microhabitat (Table A3) and was

largely explained by subplot ($\sigma^2 = 1.19$, population $\sigma^2 = 0$).

DISCUSSION

Harvest of the tropical forest tree *K. senegalensis* as fodder for livestock results in large-scale defoliation of adult trees with effects on seedling and sapling dynamics through decreases in adult canopy cover, reduced shrub cover and reduced fire frequency (Fig. 7). We did not find evidence that defoliation impacts seedling recruitment through changes in seed number or viability. This study provides further evidence for the role of facilitation by adult trees, fire, and changes across tree ontogeny in determining tree seedling establishment in a savanna-gallery forest matrix.

Defoliation affects seedlings through microhabitat

Contrary to other recent studies (van Lent et al. 2014), our analysis did not find evidence for impacts on seedling dynamics through fruit production. Although defoliation by harvest does reduce fruit production (Gaoue and Ticktin 2008), newly recruited seedling density was not a function of total fruit produced per population and this species does not form a seed bank that could contribute to future recruitment (O. G. Gaoue, *unpublished data*). This suggests that, even in harvested populations, seedling establishment is limited

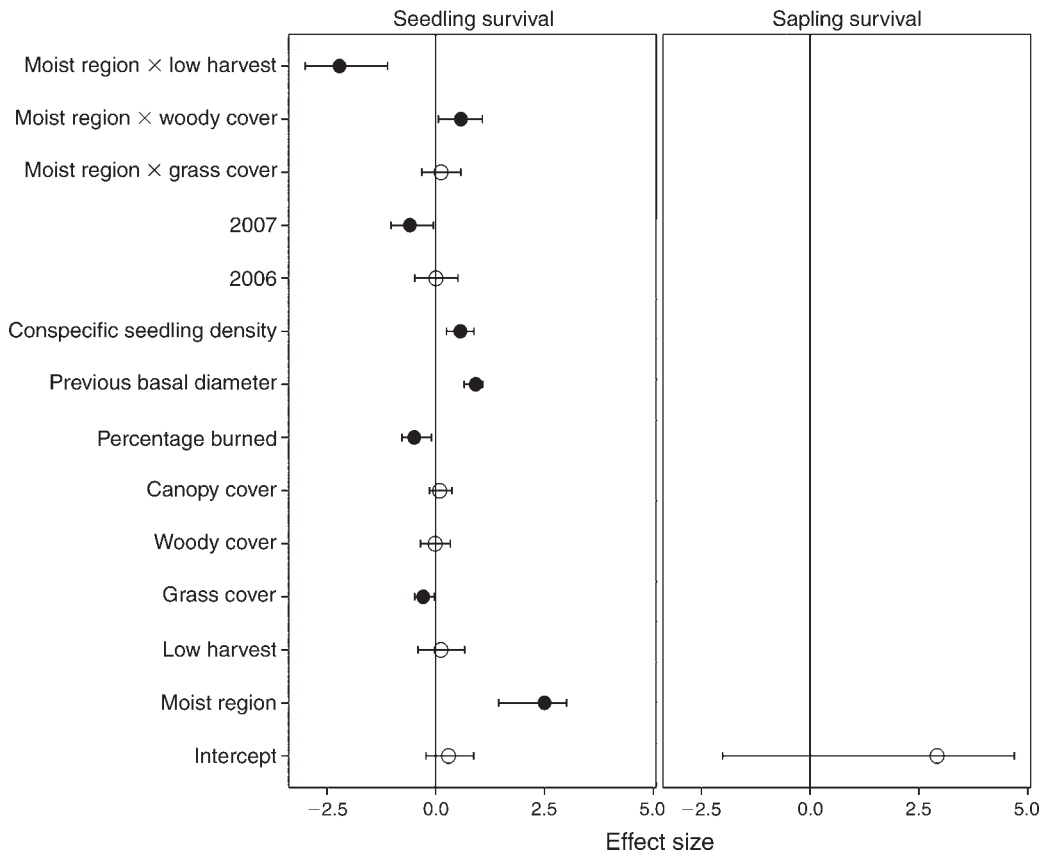


FIG. 6. Effect size and 95% bootstrapped CI from the final reduced model for *Khaya senegalensis* seedling survival across 12 populations in two regions and under different harvest regimes. Solid circles indicate significant variables, where the CI do not overlap zero. Empty spaces occur when the term was not included in that final model.

by safe sites and by disturbances such as fire, rather than by seed availability (Grubb 1977, Turnbull et al. 2000, Uriarte et al. 2010) and that harvest impacts seedling dynamics through changes in seedling survival, rather

than changes in recruitment. Furthermore, we did not find evidence of conspecific density-dependent mortality (Janzen 1970, Connell 1971), but instead found a positive association between conspecific seedling density

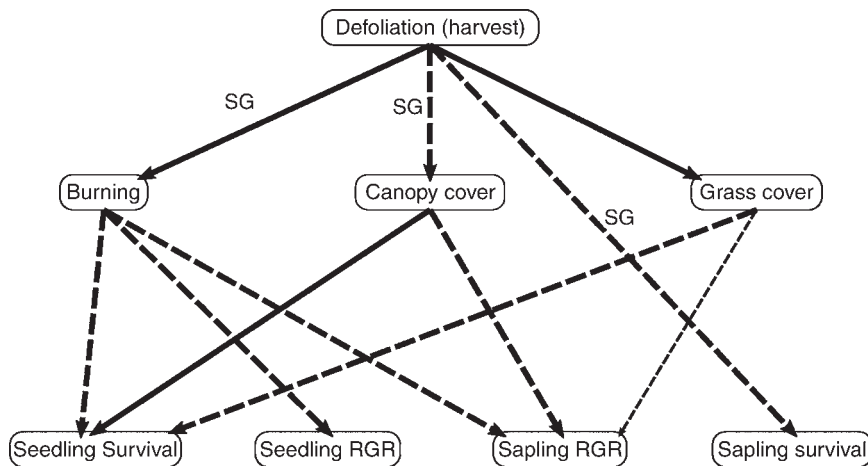


FIG. 7. Conceptual diagram of the microhabitat-mediated effects of defoliation of *Khaya senegalensis* on seedling and sapling RGR and survival. Solid lines indicate positive effects and dashed lines indicate negative effects. The thin dashed line from grass cover to sapling RGR indicates a weak effect; SG indicates that the effect is only evident in the moist Sudano-Guinean region.

and seedling survival (Azihou et al. 2013b). This implies that seedling survival is driven by abiotic conditions and abundance of conspecific seedlings is primarily an indication of good conditions.

Consistent with safe-site limitation, we found that harvested populations have altered microhabitat conditions, which may contribute to lower seedling densities in harvested populations. Because canopy leaves and branches are harvested by the Fulani pastoralists, populations with higher harvesting intensity have lower mean canopy cover at the subplot level than those with low harvesting intensity, especially in the moist Sudano-Guinean region. Harvested populations in the moist region also have lower woody understory cover and a greater extent burned than some low-harvest sites. Since burning negatively affects seedling survival, while canopy cover promotes seedling survival, the net effect is lower seedling densities in harvested populations and lower seedling survival with harvest in the drier region (Fig. 7). Another study in our study area found seedlings, but not saplings, of *K. senegalensis* under isolated trees in a savanna matrix, further demonstrating the importance of forest conditions on the transition from seedlings to saplings (Azihou et al. 2013b).

Sapling densities are much higher in the moist region without harvest, but microhabitat characteristics are not significant predictors of sapling density. This pattern may be driven by particularly low fire extent in low harvest populations in the moist region (Fig. 2), or because more mesic conditions allow seedlings to persist and transition to the sapling stage. Water availability appears to be higher in sites with low harvest intensity in the moist Sudano-Guinean region (O. Gaoue, *personal observation*) and fires are less frequent, especially in Boukoussera, the site with the greatest density of saplings. In this case, harvest intensity may be a proxy for other human impacts, including fire, but the absence of such effects in the drier Sudanian region suggests that these impacts are weak, or that they are sub-additive in the drier region.

By accounting for fire and canopy cover at the subplot level, we can separate these effects from other human activities associated with harvest that may affect seedling and sapling dynamics. Associated impacts could include damage to seedlings and saplings as a result of trampling or branch fall during harvest, but cattle rarely graze *K. senegalensis* seedlings and saplings, and harvesters do not clear or manipulate the environment around harvested trees, with the exception of seasonal fires. Furthermore, in our mixed models the harvest term rarely has a strong effect, indicating that differences between high and low harvest intensity populations is best accounted for by microhabitat characteristics.

Facilitation, fire, and savanna dynamics

Our study further illuminates facilitative and competitive interactions between tree seedlings or saplings and

both grasses and adult trees. Canopy cover, including the canopy of an individual tree, can benefit seedlings by providing a microhabitat with lower evaporation, increased nutrients from leaf litter and animal activity, and lower impacts from fire compared to open grassland (Belsky et al. 1989, Vetaas 1992, Scholes and Archer 1997, Hoffmann 2000, Siemann and Rogers 2003, Gómez-Aparicio et al. 2005, Holdo 2005, Vadigi and Ward 2013, Caldeira et al. 2014). However, adult trees can also compete with juveniles for water, nutrients and light (Holmgren et al. 1997, Anderson et al. 2001, Vadigi and Ward 2013, Bacelar et al. 2014). Our study of *K. senegalensis* revealed a facilitative effect of canopy cover on seedling survival and density. By contrast, canopy cover reduced sapling growth, perhaps through competition for light or water resources. Furthermore, high grass cover reduced survival of *K. senegalensis* seedlings, presumably through competition with grasses, possibly for water (Belsky 1994, Davis et al. 1998, Kraaij and Ward 2006, Riginos 2009, Vadigi and Ward 2013). For saplings, grass cover weakly reduces RGR, but has no effect on survival, suggesting that the strength of competition with grasses decreases across ontogeny. Some studies, however, have found that competition with grasses can reduce growth even for trees up to 4 m tall (Riginos 2009).

Fire has long been proposed as a key limit on the success of tree establishment in savannas (Scholes and Archer 1997, Bond 2008, Staver et al. 2011, Murphy and Bowman 2012), where the vulnerability of tree seedlings to fire is expected to play a large role in maintaining diversity and codominance of trees and grasses in these ecosystems through nonequilibrium, demographic-bottleneck models (Higgins et al. 2000, Sankaran et al. 2004). Previous work in our study region has documented low seedling to sapling transitions in many gallery forest species, including *K. senegalensis* (Azihou et al. 2013b), and has suggested that fire may play a key role in restricting these species to gallery forest in dry regions (Azihou et al. 2013a). Consistent with these predictions, the extent of burning was a component of the final model for all response variables tested here except sapling survival, underscoring the importance of fire in driving seedling dynamics in this mesic savanna system. *K. senegalensis* seedlings recruited at higher densities into plots with low burning, and fire had its strongest effect on the density of seedlings under 2 cm basal diameter, where it reduced survival and therefore seedling density. Density of new recruits (~6 months old) was less strongly affected, probably because of less exposure to fire. Density of saplings (>2 cm basal diameter) was only weakly affected by fire and there was no evidence of an effect on sapling survival. This is consistent with previous studies, which have demonstrated that woody saplings can survive fire or resprout readily following fire (Hoffmann and Solbrig 2003, Gignoux et al. 2009, Lawes et al. 2011). Fire has a weak negative effect on relative growth rates of both seedlings

and saplings. This result is consistent with models of tree-grass dynamics that describe a barrier at the sapling stage, where frequent fires cause stem death or shrinkage and prevent saplings from reaching sufficient height to escape damage from fire and become reproductive adults (Higgins et al. 2000, Bond 2008).

CONCLUSIONS

Using *Khaya senegalensis*, a tropical gallery forest-savanna tree which is commonly defoliated as a result of harvest as a non-timber forest product (NTFP), we demonstrate the importance of fire and facilitation by adult trees in regeneration through seedling and sapling growth and survival. Fire, as predicted for savannas, has a negative effect on tree seedlings with the greatest effect on small seedlings and a decreasing effect on saplings. Adult trees play an important facilitative role for seedlings, increasing seedling survival and density, but compete with saplings for resources, resulting in decreased sapling growth. Because defoliation removes the canopy, it diminishes the facilitative role of adults and results in lower seedling densities and survival. This indicates that shade is a key mechanism of facilitation in the mesic savanna, likely through the creation of more humid microclimates.

While most studies of NTFP harvest have focused on direct effects of harvest on plant population growth parameters, few have been able to identify indirect effects of harvest on other life stages. Here we demonstrate indirect effects of defoliation on seedlings in a mesic savanna-gallery forest matrix. The Fulani almost completely defoliate a tree when harvesting, in order to maximize their gain for the risk of tree climbing. This means that harvested trees are poor facilitators for small seedlings, but may present an opportunity for sapling growth. A rotating harvest system, which allows seedlings to recruit episodically or a patchwork harvest which maintains some nursery trees in the mosaic could help sustain seedling recruitment and minimize the indirect effects of harvest. When combined with burning practices that minimize damage to seedlings, especially by restricting burns in the gallery forest, these management strategies could increase recruitment of *K. senegalensis* in this region.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-0953.1.sm>

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.j21n1>