

No effects of fire, large herbivores and their interaction on regrowth of harvested trees in two West African savannahs

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Abstract

Theory and empirical evidence for the impacts of fire and herbivory in savannahs is well established – they are top-down disturbances that maintain savannahs in disequilibrium states away from potential tree cover. In African savannahs, the demand for fuelwood is extremely high, so tree harvest likely also has an impact, both directly and indirectly, on tree cover, density and biomass. Many savannah trees resprout vigorously from the base after harvest. However, harvested trees regenerate as saplings susceptible to fire and browsing, so harvest may have important demographic consequences. Here, we report the effects of tree harvest, and its interaction with fire and herbivory, on savannah dynamics by analysing woody regrowth following a harvest in arid Sahelian and mesic Guinean savannahs in Mali, West Africa. Tree harvest resulted in an overall reduction in wood production per tree compared to growth in nonharvested trees. Regrowth, either biomass or height, did not differ among fire and herbivory treatments. Our results suggest that the resprouting abilities that savannah trees have evolved to cope with frequent fire are essential for surviving tree harvest and subsequent disturbance. In these savannahs, regrowth is rapid enough in the first growing season to escape the impact of dry season fires.

Key words: fire, herbivory, Mali, savannah, tree harvest, West Africa

Résumé

La théorie et les preuves empiriques de l'impact des feux et de l'herbivorie dans les savanes sont bien établies – ce sont des perturbations en cascade qui maintiennent les savanes dans un état instable en l'empêchant de former une couverture arborée. Dans les savanes africaines, la demande de bois de feu est extrêmement élevée, et la collecte d'arbres a donc probablement aussi un impact, direct et indirect, sur la couverture, la densité et la biomasse des arbres. De nombreux arbres de savane rejettent vigoureusement de la base après la coupe. Mais les arbres coupés repoussent en jeunes plants susceptibles de brûler ou d'être mangés de sorte que la collecte peut avoir des conséquences démographiques importantes. Nous signalons ici les effets de la collecte d'arbres et de son interaction avec les feux et l'herbivorie sur la dynamique des savanes en analysant la repousse ligneuse après une collecte dans des savanes arides sahéliennes et mésiques guinéennes du Mali, en Afrique de l'Ouest. La collecte d'arbres aboutit à une réduction globale de la production de bois par arbre, comparée à la croissance chez les arbres non récoltés. La repousse, en biomasse et en hauteur, ne différait pas entre traitement par le feu ou par l'herbivorie. Nos résultats suggèrent que les capacités de repousse que les arbres de la savane ont développées pour répondre aux feux fréquents sont essentielles pour survivre aux collectes de bois et aux perturbations qu'elles entraînent. Dans ces savanes, la repousse lors de la première saison de croissance est assez rapide pour échapper aux impacts des feux de saison sèche.

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Introduction

Top-down disturbances are essential for determining and maintaining the savannah biome (Sankaran, Ratnam & Hanan, 2004; Bond, 2008). In particular, fire and herbivory act to maintain savannah systems in a state of disequilibrium where bioclimatic potential tree cover is rarely attained (Sankaran *et al.*, 2005; Staver, Archibald & Levin, 2011b). However, other top-down forces exist that may contribute to the codominance of trees and grasses in tropical savannahs. Tree harvest for fuelwood in African savannahs is an under-explored and potentially important disturbance due to the large annual demand. Tree harvest may play a direct role in savannahs via tree removal, but may also amplify the well-known impacts of fire and herbivory (Tredennick & Hanan, 2015).

Fire is likely the most important driver of savannah structure beyond climatic constraints (Bucini & Hanan, 2007; Staver, Archibald & Levin, 2011a). The impact of fire is observed at landscape and regional scales, but the direct effect of fire operates at the tree population level by reducing recruitment rates (Higgins, Bond & Trollope, 2000) more than through removal of adult tree biomass (Hanan *et al.*, 2008). Many savannah tree species are able to resprout vigorously when top-kill occurs during fire; a key functional trait that reduces mortality and provides an opportunity for rapid recovery of adult populations (Bond & Midgley, 2001; Hoffmann, Orthen & Nascimento, 2003; Hoffmann *et al.*, 2012; Clarke *et al.*, 2013). But, the 'Bottleneck Hypothesis' suggests recurrent fire increases tree sapling mortality, thus decreasing recruitment rates of trees to adult size-class (Higgins, Bond & Trollope, 2000; Sankaran, Ratnam & Hanan, 2004).

The impact of tree harvest is likely to contrast that of fire because harvest generally impacts adults, not seedlings. The removal of adult trees during harvest results in resprouting of cut individuals – individuals now potentially caught as saplings in the fire (Bond, 2008) and browse traps (Staver & Bond, 2014) as saplings. While tree harvest does result in a net loss of biomass from savannahs, the indirect effect of harvest by interacting with fire may also be important at the population and community levels (Tredennick & Hanan, 2015).

The effects of herbivory on savannah tree structure are less general, often depending upon feeding type (grazing

versus browsing) and how herbivore disturbance interacts with fire. Grazing can reduce grass fuel loads, thereby increasing sapling recruitment while reducing sapling–grass competition (Holdo *et al.*, 2009; Riginos, 2009; February *et al.*, 2013). However, browsing results in loss of biomass and can inhibit reproduction of adult trees and reduce sapling survival and growth directly (Augustine & McNaughton, 2004; Staver *et al.*, 2009; Moncrieff *et al.*, 2011; Staver & Bond, 2014) or indirectly through an interaction with fire (Staver *et al.*, 2009; Staver & Bond, 2014).

In African savannahs, it is clear that climate, top-down disturbances and the interactions of these factors determine landscape scale tree cover. But how does tree harvest for fuelwood, an essential ecosystem service in rural Africa (Arnold, Köhlin & Persson, 2006), modify these interactions? Recent modelling work predicts that tree harvest can have a large impact at forest-savannah and savannah-grassland ecotones, but within savannah the effects should be minimal because savannah trees can resprout (Tredennick & Hanan, 2015). But, even with the ability to resprout, a negative impact of fire on regrowth after harvest is expected.

Here we report a 4-year manipulative study on the isolated and interactive effects of tree harvest, fire and herbivory conducted in two savannah sites in Mali, West Africa – one semi-arid South Sahelian site and a mesic North Guinean site. In 2008, we deployed fully factorial experimental structures at each site that included fire and herbivory exclusion. We harvested trees in 2010 and measured woody regrowth in 2011 and 2013 to test three hypotheses:

- 1 In the absence of herbivory, fire will have a depressing effect on regrowth (biomass and height) after harvest because of top-kill of shoots by fires.
- 2 The effect of fire will be smaller in plots with herbivory because grassy fuel loads will be reduced and fires less intense.
- 3 In isolation, the presence of herbivory will have a positive impact on regrowth (biomass and height) after harvest if dominated by grazers (e.g. cattle), by reducing grass competition, but a negative impact if dominated by browsers (sheep and goats).

Although not a formal hypothesis, we expected larger treatment effects for re-growing trees we measure in 2013 relative to 2011 because treatment effects may not emerge after just one growing season.

Materials and methods

Study area

The study was conducted at two sites that bookend the savannah tropical rainfall gradient across Mali, West Africa (Fig. 1a). Both sites are underlain by similar silty-sand soils. Mean annual precipitation is 577 mm year⁻¹ at Lakamané and 1,132 mm year⁻¹ at Tiendéga (mean annual precipitations calculated for 1981–2010 from the CRU TS3.10 Dataset; Harris *et al.*, 2014).

Field sites were established in designated State Forests and Grazing Lands where they are protected from agriculture and other development, but not from fuel-wood harvest, fire or herbivory by domestic herbivores.

Tree cover at Tiendéga is approximately 60% and at Lakamané is approximately 12%. The most common large grazers are domestic mixed herds of cattle, sheep and goats – large wild herbivores are effectively absent. The herds at Tiendéga are primarily cattle, while at Lakamané herds are predominately mixtures of sheep and goats. Herbivory varies temporally and spatially as herds migrate south to north in the wet season (late June–August). All sites are under some constant herbivory throughout other months. Other herbivores include termites and small rodents. Ambient fire return time is approximately 2 years at Tiendéga and 1 year at Lakamané. However, we imposed annual burns in our fire treatment plots.

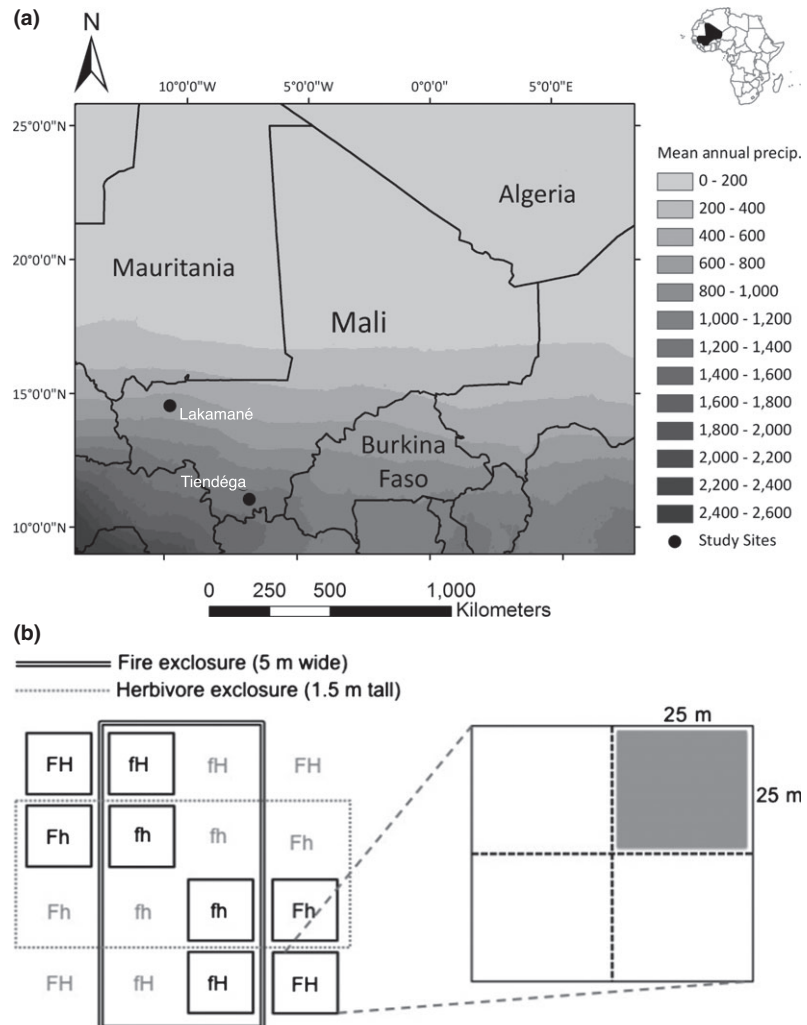


Fig 1 (a) Map of Mali, West Africa, showing locations of the two study sites (Tiendéga in the South; Lakamané in the North) and broad trends in mean annual precipitation. (b) The experimental layout at each site. *F* = fire present; *f* = fire excluded. *H* = large herbivores present; *h* = large herbivores excluded. As described in the main text, a 25 × 25 metre plot in two of four treatment replicates was used for this study.

Treatments and wood harvest simulation

At each of the sites, a replicated 2×2 factorial plot design with fire (*F*)/no fire (*f*) and large herbivore (*H*)/no large herbivore (*h*) treatments was established in 2008 (Fig. 1b). Four replicate plots (50×50 m each) were deployed at each site. The control (fire and herbivory, *FH*) allows for grazing of all large herbivores in the area and fire at ambient levels. Herbivore exclosures (fire/no fire and no herbivory; *Fh* and *fh*) are fenced with 1.5 m wire-mesh fencing with 8 cm mesh size that excludes all domestic and larger wild herbivores (but not rodents or small mammals). Fire exclosures (no fire and herbivory/no herbivory; *fH* and *fh*) were established using 5 m fire breaks cleared of all small trees and most large trees, all shrubs and all herbaceous cover. Firebreaks were re-cleared at the end of each rainy season. The herbivory treatments (*FH* and *fH*) were open to grazing at ambient levels to mimic grazing and browsing pressure in the surrounding savannah matrix. Fire treatments (*FH* and *Fh*) were burned annually in December.

To implement the fuelwood harvest simulation in each treatment, we first delineated a 25×25 m plot in two of four treatment plots for each treatment (Fig. 1b). The plots were chosen based on the availability of 10 or more individuals of the preferred fuelwood species (as identified by local knowledge) at each site. While species selection was not random, our study better reflects reality by focusing on the tree species actually used for fuelwood. Between the two plots, we selected 20 individuals that were tagged at the base and given unique identification numbers. We chose *Deterium microcarpum* Guill. and Perr. ($n = 20$ per treatment) at Tiendéga and *Combretum glutinosum* Perr. ($n = 20$ per treatment) at Lakamané. Tree selection was haphazard, but the sample reflected the size structure of the tree community at each site. We only selected trees with diameters at the base greater than or equal to 2 cm.

We harvested trees under each combination of fire and herbivory. Before harvesting we took baseline measurements of basal diameter and height to develop allometric relationships between those variables and biomass, and also to assess the relationship between initial biomass and subsequent regrowth. Trees were cut 10 cm from the soil surface using bow saws. All tree biomass was removed from the site after harvest. After initial harvest during the peak-growing season of 2010, biomass regrowth was harvested and measured at peak-growing season (July–August) in 2011 ($t_{\text{harv}} + 1$) for one subset of

harvested trees and just after the growing season (October–November) in 2013 ($t_{\text{harv}} + 3$) for another subset of harvested trees. A random and equal sample of trees (10 per treatment per year at each site) was measured in each observation year (2011 and 2013). This means that for trees in fire plots (*FH* and *Fh*), those measured in 2011 grew through one dry season fire, while those measured in 2013 grew through three annual dry season fires.

We measured woody biomass regrowth in 2011 and 2013. In 2013, we measured the heights of trees harvested in 2010 but not re-harvested for biomass measures in 2011. For the biomass measures, all biomass associated with a harvested tree was collected and we separated leaf and wood biomass to obtain wet weights of wood. Subsamples of wood were taken and dried at 100°C to account for water-content contribution to wet weights taken in the field. Species-specific dry:wet weight ratios were applied to all wet weights to convert to dry biomass. Data on wet weight samples for Lakamané were damaged in a storm in 2013. Thus, for the 2013 data from Lakamané, we use a dry:wet weight ratio of 0.5 (near the value from 2011 of 0.52) and we performed a sensitivity analysis to ensure our results are robust to changes in the dry:wet weight ratio (See Fig. S2). Importantly, the loss of this data does not impact our statistical tests for treatment effects.

We used nonharvested trees (hereafter, ‘control trees’) in the no fire/no herbivory plots (*fh*) as controls to measure annual wood growth in the absence of harvest or other disturbance. At each site, we selected 20 trees distributed throughout the four *fh* plots that matched the species chosen for harvest. We measured initial circumference and installed dendrometer bands to measure wood growth. We measured dendrometer band change each year (2011, 2013) during peak-growing season.

Data analysis

To convert diameter and height measures to estimates of biomass, we used an allometric relationship (see Tredennick, Bentley & Hanan, 2013 and Fig. S1). We used the model to estimate initial aboveground wood biomass of harvested trees before harvest, initial biomass of control trees and biomass of control trees in 2011 and 2013. Regrowth biomass of harvested trees was measured directly.

Our analysis focuses on annual wood biomass change, defined as relative growth rate (*rgr*) for control (nonharvested) trees and relative regrowth rate (*rrgr*) for harvested trees. We calculated *rgr* for control trees as:

$$rgr_t = \frac{\ln(B_t) - \ln(B_{initial})}{year_t - year_{initial}} \quad (1)$$

and $rrgr$ for harvested trees as

$$rrgr_t = \frac{\ln(B_t + B_{initial}) - \ln(B_{initial})}{year_t - year_{initial}} \quad (2)$$

where rgr_t and $rrgr_t$ are relative growth and relative regrowth rates for measurement year t , B_t is wood biomass at year t , and $B_{initial}$ is initial wood biomass measured in 2010. The term $year_t - year_{initial}$ simply accounts for the number of years between measurements so that rgr and $rrgr$ are consistent per year rates. Note that in Eq. 2 B_t represents the woody regrowth of a harvested tree.

To estimate the effects of fire and herbivory on $rrgr$ at each site, we analysed the biomass data using factorial ANOVA. We fit a model with plot ID as a random effect, but based on AIC chose not to use the mixed model for our analysis (Table S1). We used the 'lm' procedure in the program R (2012) to fit the models. We report F - and P -values from the 'ANOVA' function in R applied to the 'lm' models. We also performed two-way ANOVAs to compare harvested tree biomass regrowth versus control tree wood growth using the 'aov' procedure in R and performed *post hoc* Tukey's tests when applicable using the 'TukeyHSD' procedure in R. For all analyses, $rrgr$ and rgr were log-transformed to meet model assumptions of normal residuals and homoscedasticity. All reported statistics refer to log-transformed $rrgr$ and rgr , but in the figures, we show nontransformed values.

We tested for treatment effects on postharvest heights in 2013 using ANOVA. Height was log-transformed to meet model assumptions. We used logistic regression to estimate the probability of a tree growing to a specific escape height 3 years after harvest as a function of initial tree size. We focused on escape heights of 1, 2 and 3 m because these reflect the range relevant to escaping the effects of fire and herbivory (Bond & Midgley, 2001; Bond, 2008; Staver & Bond, 2014).

All code and data to reproduce our results are archived and available as release v1.0 on GitHub at <http://github.com/atredennick/HarvestExperiment/releases/tag/v1.0>.

Results

Tree harvest depressed woody growth relative to control (nonharvested) trees at both sites (Fig. 2). On average, control tree relative growth rates were 6.9 times greater

than harvested trees in Tiendéga. In Lakamané, control trees relative regrowth rates were three times greater than harvested trees. Mortality of harvested trees was low (Table 1). Per cent mortality did not appear to differ among treatments, years or sites.

Fire and herbivory had little effect on postharvest regrowth (Fig. 3). We failed to detect any significant effects of fire, herbivory or their interaction at either site and in both years (Table 2). Given the lack of statistically strong treatment effects, we do not report effect sizes of herbivore and fire exclusion on tree relative regrowth rates (but the magnitude of effects can be visually interpreted in

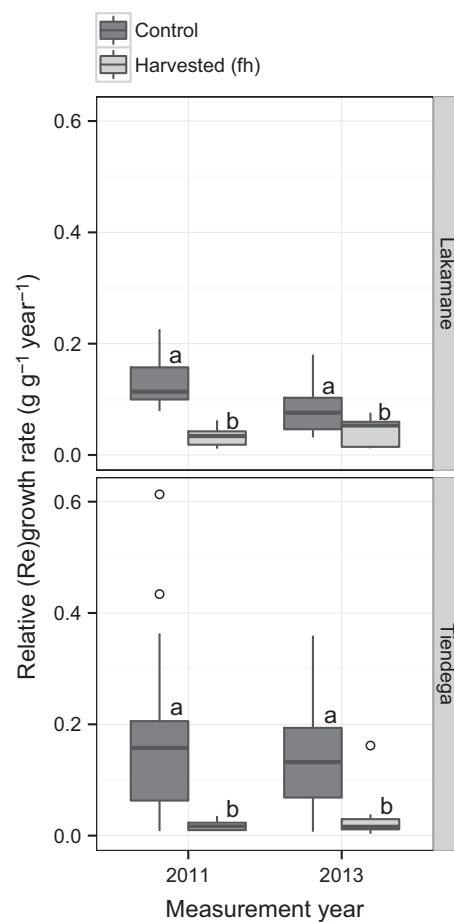


Fig 2 Box plots comparing relative (re)growth rates by site for control (growth rates) and harvested trees (regrowth rates) across both measurement years. Letters denote statistically significant ($P < 0.1$) pairwise comparisons from *post hoc* Tukey's HSD tests. Growth rates are expressed per unit aboveground wood biomass of trees in 2010 (prior to cutting in harvested treatments; see Eqs. 1 and 2).

Site	Percent mortality		
	2011	2013	Years combined
Tiendéga	2.5% (1/40)	5% (2/40)	3.75% (3/80)
Lakamané	0% (0/38)	5.4% (1/37)	1.3% (1/75)

Table 1 Per cent mortality of harvested trees each measurement year. The raw number of dead trees out of the total sample is shown in the parentheses

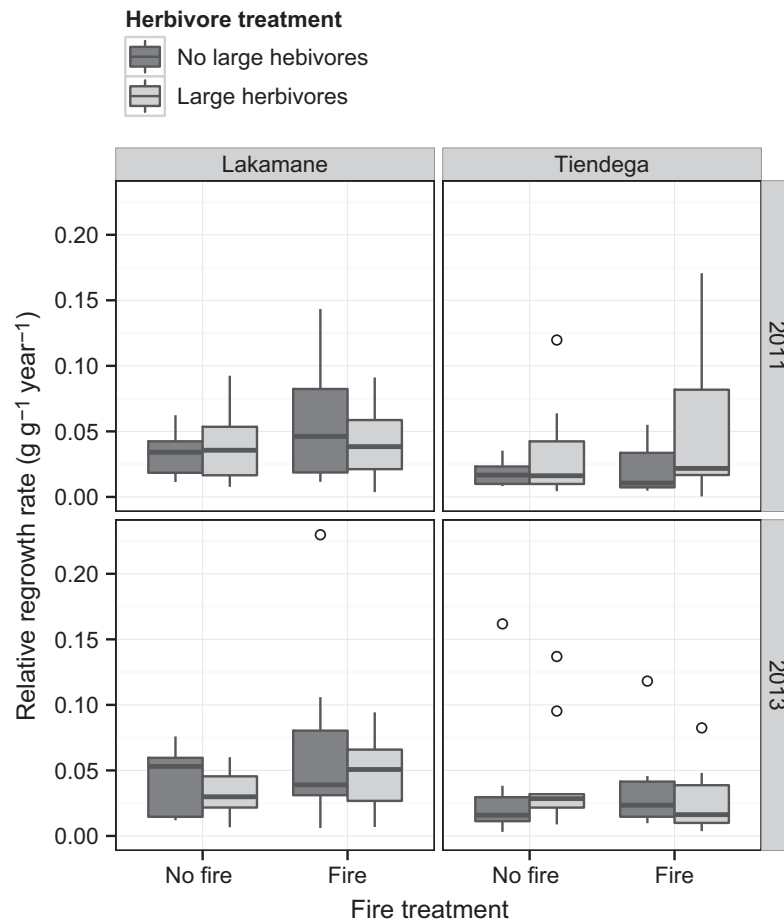


Fig 3 Box plots of relative biomass regrowth rates (*rrgr*) 1 year (2011) and 3 years (2013) after harvest for each treatment at each site. There are no strong statistical differences among treatments within each year (see Table 1). We tested for interactions between treatments and the year harvested, but found no statistically important interaction effects.

Fig. 3). When pooled among treatments, mean *rrgr* at Lakamané was 0.04 (SD = 0.03) and 0.05 (SD = 0.04) in 2011 and 2013, respectively. At Tiendéga, mean *rrgr* across all treatments was 0.03 (SD = 0.04) and 0.03 (SD = 0.04) in 2011 and 2013, respectively. *rrgr* did not differ significantly between years at either site ($P = 0.6$ and 0.3 for Lakamané and Tiendéga, respectively; see Supporting Information for sensitivity of these tests to the dry:wet ratio).

There were no significant treatment effects on tree height 3 years after harvest ($P = 0.38$ at Tiendéga, $P = 0.39$ at Lakamané; Fig. 4a). Average height at Tiendéga was 2.12 m

(SD = 0.71) and at Lakamané was 1.74 m (SD = 0.66). Initial tree biomass is a significant predictor of the probability that a tree will reach 2 and 3 m 3 years after harvest in Tiendéga ($P = 0.004$ and $P = 0.023$, respectively) and for 2 m in Lakamané ($P = 0.022$) (Fig. 4b,c).

Discussion

Savannah trees resprout vigorously. While this trait likely evolved by natural selection in response to frequent fires in savannahs (Bond & Midgley, 2001; Shackleton, 2001), it also benefits trees that are harvested for fuelwood (Shack-

Table 2 Results from the factorial ANOVA for the effects of herbivore and fire exclusion on postharvest biomass regrowth (*rrgr*) one and 3 years after harvest. Measurement periods are denoted as in the main text where $t_{\text{harv}} = 2010$. Statistical tests result from running an ANOVA ('ANOVA') on the results from a linear model ('lm') in the program R

Measurement Period	Site	n ^a	Fire		Herbivory		Fire × Herbivory	
			$F_{1,n-3}$	<i>P</i>	$F_{1,n-3}$	<i>P</i>	$F_{1,n-3}$	<i>P</i>
$t_{\text{harv}} + 1$	Tiendéga	38	0.024 ^b	0.879 ^b	0.446	0.509	0.024 ^b	0.879 ^b
	Lakamané	37	0.611	0.44	0.318	0.577	0.379	0.542
$t_{\text{harv}} + 3$	Tiendéga	38	0.097	0.758	0.048	0.828	2.65	0.113
	Lakamané	36	0.88	0.355	0.175	0.679	0.076	0.785

^aSample sizes may be different from those in Table 2 because we excluded dead trees and one observation with an unreliable estimate of initial biomass.

^bDue to rounding, these values appear similar but actually differ. Their equal values as represented in the table are not typos.

leton, 2001). Indeed, we observed near-zero mortality after harvest (Table 1). This is unsurprising because work in a South African savannah reported similar results (Shackleton, 2001). But unexpectedly, relative regrowth rate and height of harvested trees did not differ among the fire and herbivore treatments. We expected that woody regrowth in fire plots would be lower because of shoot mortality in fires. However, we found no support for an interaction between harvest and fire, or for any of the other hypotheses advanced in the Introduction (Table 2, Fig. 4a).

For the herbivore treatments, it is possible that grazing by cattle has very little impact, either through reduced grass competition or reduced fuel loads, on postharvest regrowth. Other experiments have shown that the direct effect of browsers is much greater than the indirect effects of grazers (Staver & Bond, 2014). Thus, it is not surprising that at the grazer-dominated mesic site (Tiendéga), we found no effect of herbivory, especially because our treatments only ran for 3 years. The indirect effects of grass-tree competition and increased fuel loads may emerge over time.

A positive effect of browsing release in Lakamané, where goats and sheep dominate herds, should have been immediate. Yet we found no statistical support for an herbivore effect (Table 2, Fig. 4a). The most likely explanation is that harvested trees regrow very quickly and are able to escape from the 'browse trap' within 1 year (Staver & Bond, 2014) (Fig. 4). Thus, harvested trees are able to regrow rapidly and avoid disturbance impacts, unlike seedlings and saplings growing from seed. One possible mechanism is that belowground carbohydrate storage contributes a larger fraction to growth after harvest than current photosynthesis. Thus, browsing of leaves would not affect re-growing trees as much as those growing from seed.

The lack of an effect on *rrgr* or height by excluding fire is more perplexing. Decades of work in savannah systems point towards fire reducing tree growth rates, so why did we not observe a positive effect of fire exclusion here? It is likely that postharvest saplings simply grow faster than saplings growing from seed. In that case, postharvest saplings are able to escape the firetrap quickly by drawing on large stores of belowground carbohydrates (Hoffmann, Orthen & Nascimento, 2003; Hoffmann, Orthen & Franco, 2004). We found evidence of this as initial tree size was a good predictor of a tree reaching escape heights (Fig. 4 b,c). By growing fast, postharvest saplings avoid subsequent top-kill during the dry season.

Most other work on savannah tree demographics has not considered the effect of tree harvest (but see Zida *et al.*, 2007). Thus, the insight that fire can maintain the savannah state by limiting sapling-to-adult transitions is constrained to systems where the saplings that have grown from seed or resprouted from a sapling top-killed by a previous fire. In other words, coppice saplings growing from the rootstock of large trees may have faster growth rates than even the fastest growing 'regular' saplings (those from seed or regrowth from saplings). In our previous work, we assumed equal growth rates among 'new' and 'harvested' saplings (Tredennick & Hanan, 2015). Clearly, this assumption needs to be refined. To do so will require comparative studies of sapling growth rates when grown from seed and across a size spectrum at the time of harvest.

Another surprising result is that biomass regrowth at the mesic site (Tiendéga) was not consistently greater than at the arid site (Lakamané), although we cannot test this statistically since at the site level we only have $N = 2$. Even though the species differ among the sites, based on climate constraints alone, we expected regrowth to be consistently

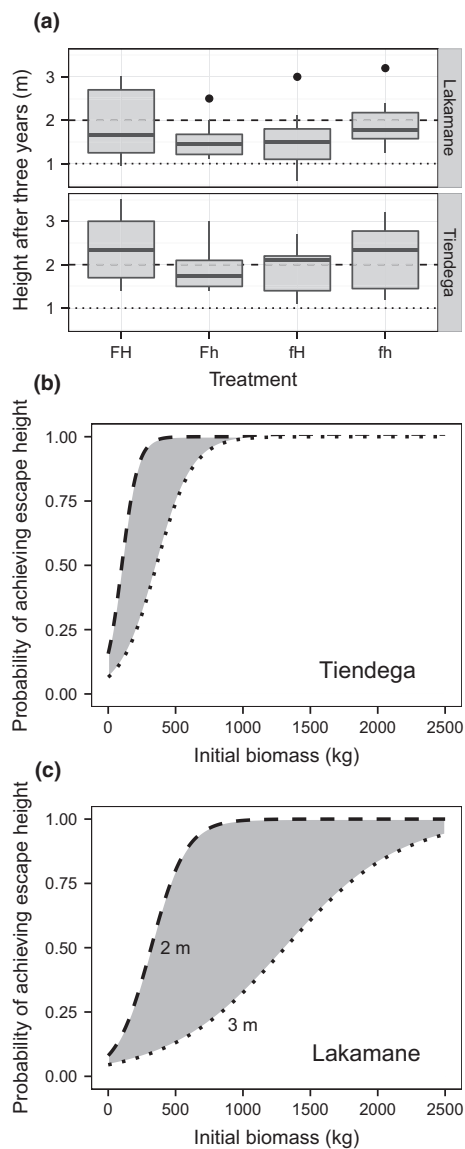


Fig 4 Box plots of harvested tree heights after 3 years (a) and results from logistic regression estimating the probability of reaching an escape height (2 or 3 metres) after 3 years as a function of preharvest tree size (b and c). In a, there are no statistical differences among treatments. In c, only the regression for a 2 metre escape height has initial biomass as significant, but we still show the 3 metre regression for context.

greater at the mesic site. However, there are many factors that may interact with precipitation to inhibit regrowth in mesic savannahs relative to arid savannahs, like competition for light with adult trees (Iponga, Milton & Richardson, 2008) or competition with grass (Riginos, 2009) and

tree roots (Sea & Hanan, 2012) for soil water. Understanding the susceptibility of regenerating trees to fire and herbivory will require disentangling those interacting resource-based drivers.

Nonharvested trees grew at faster rates than harvested trees in these two savannahs (Fig. 2), in line with other studies on growth rates in savannah trees after disturbance (Holdo, 2006). But, we found little evidence that presence of fire and large herbivores, or both, affects postharvest regrowth of trees in semi-arid and mesic savannahs of West Africa. Savannah trees resprouting after harvest are able to draw on large nutrient stores held in substantial root systems. Thus, their growth rates are rapid, allowing them to escape the impacts of disturbance quickly. The timing of disturbance is likely important for determining the success and magnitude of postharvest regrowth.

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Supporting information

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

Appendix S1 Converting diameter measurements to biomass using allometric models.

Appendix S2 Assessing impact of dry:wet weight ratio on statistical results.

Appendix S3 Model selection for statistical tests of treatment effects.

Figure S1 Fitted regression of $\log(\text{Biomass}) \sim \log(\text{Diameter})$.

Figure S2 Results of our simulation test for bias induced by the wet:dry weight ratio.

Table S1 AIC scores from model selection with and without subplot ID as a random effect.