Weak effects of fire, large herbivores, and their interaction on regrowth of harvested trees in two West African savannas

Andrew T. Tredennick[1], Moussa Karembé[2], Fadiala Dembélé[3], Justin Dohn[4], and Niall P. Hanan[5]

Postal addresses:
[1]Department of Wildland Resources, Utah State University, Logan, UT, USA
[2]Universite du Bamako, Bamako, Mali
[3]Institut Polytechnique Rurale du Katibougou, Katibougou, Mali
[4]Natural Resource Ecology Laboratory and Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, USA
[4]Geospatial Science Center of Excellence, South Dakota State University, Brookings, SD, USA

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Corresponding author: Andrew Tredennick (atredenn@gmail.com)

1

20 **Abstract**

21 Theory and empirical evidence for the impacts of fire and herbivory in savannas is well

22 established – they are top-down disturbances that maintain savannas in disequilibrium states

23 away from potential tree cover. In African savannas the demand for fuelwood is extremely high,

24 so tree harvest likely also has an impact, both directly and indirectly, on tree cover, density, and

25 biomass. Many savanna trees resprout vigorously from the base after harvest. However,

26 harvested trees regenerate as saplings susceptible to fire and browsing, so harvest may have

27 important demographic consequences. Here, we report the effects of tree harvest, and its

28 interaction with fire and herbivory, on savanna dynamics by analyzing woody regrowth

29 following a harvest in arid Sahelian and mesic Guinean savannas in Mali, West Africa. Tree

30 harvest resulted in an overall reduction in wood production per tree compared to growth in non-

31 harvested trees. Regrowth, either biomass or height, did not differ among fire and herbivory

32 treatments. Our results suggest that the resprouting abilities that savanna trees have evolved to

33 cope with frequent fire are essential for surviving tree harvest and subsequent disturbance. In

34 these savannas, regrowth is rapid enough in the first growing season to escape the impact of dry

35 season fires.

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Introduction

Top-down disturbances are essential for determining and maintaining the savanna biome (Sankaran, Ratnam & Hanan, 2004; Bond, 2008). In particular, fire and herbivory act to maintain savanna 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 co-dominance of trees and grasses in tropical savannas. Tree harvest for fuel, particularly in African savannas, represents an under-explored and potentially important disturbance due to the large annual demand in Africa and the density of human populations in savanna regions. Tree harvest may play an independent role in determining savanna tree cover through direct removal, but may also amplify the well-known impacts of fire and herbivory (Tredennick & Hanan, In Press).

Fire is likely the most important driver of savanna structure (i.e., tree cover and biomass) beyond climatic constraints (Bucini & Hanan, 2007; Staver, Archibald & Levin, 2011a). The impact of fire is observed at landscape and regional scales in savannas 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 savanna 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). In particular, the "Bottleneck Hypothesis" suggests recurrent fire increases tree sapling mortality, thus decreasing recruitment rates of trees to adult size-class (Higgins et al., 2000; Sankaran et al., 2004).

58   The impact of tree harvest, on the other hand, is likely to contrast that of fire because

59   harvest generally impacts adults but not seedlings. The removal of aboveground biomass of adult

60   trees during harvest, much like fire, results in resprouting of cut individuals – individuals now

61   potentially caught as saplings in the fire (Bond, 2008) and browse traps (Staver & Bond, 2014)

62   as saplings. Thus, while tree harvest does result in a net loss of biomass from savannas, the

63   indirect effect of harvest in terms of its interaction with fire may also be important at the

64   population and community levels (Tredennick & Hanan, In Press).

65   The effects of herbivory on savanna tree structure are less general, often depending upon

66   feeding type (grazing vs. browsing) and how herbivore disturbance interacts with fire. For

67   example, grazing can reduce grass fuel loads thereby increasing sapling recruitment while

68   reducing sapling–grass competition (Holdo et al., 2009; Riginos, 2009; February et al., 2013).

69   However, browsing results in loss of biomass and can, potentially, inhibit reproduction of adult

70   trees and reduce sapling survival and growth directly (Augustine & McNaughton, 2004; Staver

71   et al., 2009; Moncrieff et al., 2011; Staver & Bond, 2014) or indirectly through an interaction

72   with fire (Staver et al., 2009; Staver & Bond, 2014).

73   In African savannas it is clear that climate, top-down disturbances, and the interactions of

74   these factors are important in determining landscape scale tree cover or density. But how does

75   tree harvest for fuelwood, an essential ecosystem service in rural Africa (Arnold, Köhlin &

76   Persson, 2006), modify these interactions? Recent modeling work predicts that tree harvest can

77   have a large impact at forest-savanna and savanna-grassland ecotones, but within savanna the

78   effects should be minimal due to the resprouting ability of trees (Tredennick & Hanan, In Press).

79   Even with the ability to resprout, a negative impact of fire on regrowth after harvest is expected.

80   Here we report a four-year manipulative study on the isolated and interactive effects of

81   tree harvest, fire, and herbivory conducted in two savanna sites in Mali, West Africa – one semi-

82   arid South Sahelian site and a mesic North Guinean site. In 2008 we deployed fully factorial

83   experimental structures at each site that included fire and herbivory exclusion. We simulated tree

84   harvest in 2010. Our study focuses on woody regrowth (one year and three years post-harvest)

85   following the simulated harvest and how regrowth is impacted by herbivory, fire, and climate.

86   Based on our knowledge of savanna systems and our recent modeling work (Tredennick &

87   Hanan, In Press), we developed five hypotheses:

88   1. In the absence of herbivory, fire will have a depressing effect on regrowth

89   (biomass and height) after harvest due to the potential for top-kill of shoots by

90   fires.

91   2. The effect of fire will be smaller in plots with herbivory because grassy fuel loads

92   will be reduced and fires will be less intense.

93   3. In isolation, the presence of herbivory will have no impact on regrowth (biomass

94   and height) after harvest if dominated by grazers (e.g. cattle) but a direct negative

95   impact if dominated by browsers (sheep and goats).

96   4. The effects described in hypotheses 1 and 2 will be additive over time (larger

97   effects in 2013 relative to 2011).

98   5. On average, across treatments, regrowth will be greater in the mesic savanna

99   relative to the arid savanna.

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101 **Materials and Methods**

102 *Study Area*

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103   The study was conducted at two sites that bookend the savanna tropical rainfall gradient

104   across Mali, West Africa (Figure 1A). Both sites are underlain by similar silty-sand soils as

105   identified by local expert knowledge. Mean annual precipitation is 577 mm year^{-1} at Lakamané

106   and 1,132 mm year^{-1} at Tiendéga (mean annual precipitations calculated for 1981-2010 from the

107   CRU TS3.10 Dataset; Harris et al. 2014).

108   Each site receives varying degrees of fire, herbivory, and fuelwood harvesting. All field

109   sites were established in designated State Forests and Grazing Lands where they are protected

110   from agriculture and other development, but not from fuelwood harvest, fire, or herbivory by

111   domestic herbivores. Tree cover at Tiendéga is approximately 60% and at Lakamané is

112   approximately 12%. The most common large grazers are domestic mixed herds of cattle, sheep,

113   and goats – large wild herbivores are effectively absent. The herds at Tiendéga are primarily

114   cattle, while at Lakamané herds are predominately mixtures of sheep and goats. Herbivory varies

115   temporally and spatially as herds migrate south to north in the wet season (late June – August).

116   All sites are under some constant herbivory throughout other months. Other grazers include

117   termites and small rodents. Fire is an important disturbance at both sites and ambient fire return

118   time is approximately two years at Tiendéga and one year at Lakamané. However, we note

119   below that we imposed annual burns in our fire treatment plots.

120

121   *Treatments and wood harvest simulation*

122   At each of the sites, a replicated 2 × 2 factorial plot design with fire (*F*)/no-fire (*f*) and

123   large herbivore (*H*)/no large herbivore (*h*) treatments was established in 2008 (Figure 1B). Four

124   replicate plots (50 × 50 m each) were deployed at each site. The control (fire and herbivory, *FH*)

125   allows for grazing of all large herbivores in the area and fire at ambient levels. Herbivore

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126 exclosures (fire/no fire and no herbivory; *Fh* and *fh*) are fenced with 1.5 m wire-mesh fencing

127 with 8 cm mesh size that excludes all domestic and larger wild herbivores (but not rodents or

128 small mammals). Fire exclosures (no fire and herbivory/no herbivory; *fH* and *fh*) were

129 established using 5 m fire breaks cleared of all small trees and most large trees, all shrubs, and all

130 herbaceous cover. Firebreaks were re-cleared at the end of each rainy season. The herbivory

131 treatments (*FH* and *fH*) were open to grazing at ambient levels to mimic grazing and browsing

132 pressure in the surrounding savanna matrix. Fire treatments (*FH* and *Fh*) were burned annually

133 in December.

134   To implement the fuelwood harvest simulation in each fire/herbivory treatment we first

135 delineated a 25×25 m plot in two of four treatment plots for each treatment (Figure 1B). The

136 plots were chosen based on the availability of 10 or more individuals of the preferred fuelwood

137 species (as identified by local knowledge) at each site. While species selection was not random,

138 our study better reflects reality by focusing on the tree species actually used for fuelwood.

139 Between the two plots we selected 20 individuals that were tagged at the base and given unique

140 identification numbers. We chose *Deterium microcarpum* Guill. And Perr. ($n = 20$ per treatment)

141 at Tiendéga and *Combretum glutinosum* Perr. ($n = 20$ per treatment) at Lakamané. Tree selection

142 was haphazard, but the sample reflected the size structure of the tree community at each site. We

143 only selected trees with diameters at the base greater or equal to 2 cm.

144   We simulated tree harvest under each combination of fire and herbivory (*FH, fH, Fh*, and

145 *fh*). Before harvesting the trees we took baseline measurements of basal diameter to develop

146 allometric relationships between those variables and biomass, and also to assess the relationship

147 between initial biomass and subsequent regrowth. Trees were cut at 10 cm from the soil surface

148 using bow saws. All tree biomass was removed from the site following harvest. Following initial

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149   harvest during the peak-growing season of 2010, biomass regrowth was harvested and measured

150   at peak growing season (July – August) in 2011 (t_{harv} + 1) and just after the growing season

151   (October – November) in 2013 (t_{harv} + 3). A random and equal sample of trees (10 per treatment

152   per year at each site) was measured in each observation year (2011 and 2013). This means that

153   for trees in fire plots (*FH* and *Fh*), those measured in 2011 grew through one dry season fire,

154   while those measured in 2013 grew through three annual dry season fires.

155   We measured woody biomass regrowth in 2011 and 2013, and in 2013 we measured the

156   heights of trees harvested in 2010 but not re-harvested for biomass measures in 2011. For the

157   biomass measures, all biomass associated with a harvested tree was collected and we separated

158   leaf and wood biomass to obtain wet weights. Sub-samples of wood were taken and dried at 100°

159   C to account for water-content contribution to wet weights taken in the field. Species-specific

160   dry:wet weight ratios were applied to all wet weights to convert to dry biomass. Data on wet

161   weight samples for Lakamané were damaged in a storm in 2013. Thus, for the 2013 data from

162   Lakamané we use a dry:wet weight ratio of 0.5 (near the value from 2011 of 0.52) and we

163   performed a sensitivity analysis to ensure our results are robust to changes in the dry:wet weight

164   ratio (see Supplemental Information). Importantly, the loss of this data does not impact our

165   statistical tests for treatment effects.

166   We used non-harvested trees in the no fire/no herbivory plots (*fh*) as controls to measure

167   annual wood growth in the absence of harvest or other disturbance. At each site we selected 20

168   trees distributed throughout the four *fh* plots that matched the species chosen for harvest. We

169   measured initial circumference and installed dendrometer bands to measure wood growth. We

170   measured dendrometer band change each year (2011 and 2013) during peak growing season.

171   Throughout the rest of the text we refer to these as "control trees."

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Data analysis

To convert diameter and height measures to estimates of biomass we used allometric

relationships. We log-transformed the response variable (biomass) and the predictor variable

(diameter or height) because the data had a multiplicative error distribution (see Tredennick,

Bentley & Hanan, 2013). We compared candidate models using Akaike Information Criterion

(see Supplementary Information). The best model includes log(diameter) as the predictor

variable and is interspecific ($R^2 = 0.92$, $P < 0.0001$). We used the model to estimate initial

aboveground wood biomass of harvested trees immediately before harvest, initial biomass of

control trees, and annual biomass growth of control trees in 2011 and 2013 (see Supplementary

Information for details). Regrowth biomass of harvested trees was measured directly as

described above.

Our analysis focuses on annual wood biomass change, defined as relative growth rate

(*rgr*) of wood for control (non-harvested) trees and relative regrowth rate (*rrgr*) of wood for

harvested trees. We calculated *rgr* for control trees as

$$rgr_t = \frac{\ln(B_t) - \ln(B_{initial})}{year_t - year_{initial}} \quad [\text{Eq. 1}]$$

and *rrgr* for harvested trees as

$$rrgr_t = \frac{\ln(B_t + B_{initial}) - \ln(B_{initial})}{year_t - year_{initial}} \quad [\text{Eq. 2}]$$

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194   where rgr_t and $rrgr_t$ are relative growth and relative regrowth rates for measurement year t, B_t is

195   biomass at year t, and $B_{initial}$ is initial biomass measured in 2010. The term $year_t$ - $year_{initial}$ simply

196   accounts for the number of years between measurements so that rgr and $rrgr$ are consistent per

197   year rates. Note that in Eq. 2 B_t represents the regrowth of a harvested tree.

198   We aimed to determine the quantitative difference in regrowth attributable to fire,

199   herbivory, and their interaction, both overall and within sites. To estimate the effects of fire and

200   herbivory on $rrgr$ we analyzed the biomass data using factorial ANOVA at two levels: 1) data

201   pooled across sites but with a site random effect on the intercept (mixed effects model), and 2)

202   within-site. For the factorial ANOVAs, we used the 'lme4' package (Bates et al., 2014) in the

203   program R (2012) to fit the mixed effects model using the 'lmer' function and the 'lm' procedure

204   to fit the within-site models. We report F- and P-values from the 'anova' function in R applied to

205   the 'lmer' and 'lm' models. We also performed two-way ANOVAs to compare harvested tree

206   biomass regrowth vs. control tree wood growth using the 'aov' procedure in R and performed

207   post hoc Tukey's tests when applicable using the 'TukeyHSD' procedure in R. We used the same

208   approach to test for biomass regrowth differences between the two sites using pooled treatment

209   data. For all analyses, $rrgr$ and rgr were log-transformed to meet model assumptions of

210   normality of residuals and homoscedasticity. So all reported statistics and statistically significant

211   differences refer to the log-transformed version of $rrgr$ and rgr, but in the figures we show non-

212   transformed values.

213   We tested for treatment effects on post-harvest heights in 2013 using factorial ANOVA.

214   Height was log transformed to meet model assumptions. We also used logistic regression to

215   estimate the probability of a tree growing to a specific escape height three years after harvest as a

216   function of initial tree size. We focused on escape heights of 1, 2, and 3 meters because these

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217   reflect the range relevant to escaping the effects of fire and herbivory as reported elsewhere

218   (Bond & Midgley, 2001; Bond, 2008; Staver & Bond, 2014).

219   All code and data to reproduce our results has been deposited on Dryad (DRYAD LINK

220   HERE AFTER ACCEPTANCE) and archived at

221   http://atredennick.github.com/HarvestExperiment.

222

223 Results

224   Tree harvest depressed woody growth relative to that of non-harvested trees at both sites

225   (Figure 2). On average, non-harvested trees had relative growth rates that were 6.9 times greater

226   than harvested trees in Tiendéga. In Lakamané, non-harvested trees had relative regrowth rates 5

227   times greater than harvested trees. Mortality of harvested trees was low (Table 1). Percent

228   mortality did not differ among treatments, years, or sites.

229   Since we initiated annual fires, we know the fire treatments were effective. Herbivore

230   exclosures were also effective, as indicated by grass biomass being significantly greater within

231   herbivore exclosures relative to biomass outside of exclosures in 2010, 2011, and 2012 ($P < 0.05$

232   in all years at each site except for 2012 at Lakamané). Unfortunately, we do not have data on

233   grazer and browser use via dung counts. Fire and herbivory had little effect on post-harvest

234   regrowth (Figure 3). We failed to detect any significant effects of fire, herbivory, or their

235   interaction at both sites and in both years (Table 2). While not statistically significant, the effect

236   of fire is stronger at both sites in 2013 relative to 2011 (Table 2), giving some qualitative support

237   for our hypothesis that treatment effects would emerge over time. Given the lack of statistically

238   strong treatment effects we do not report effect sizes of herbivore and fire exclusion on tree

239   relative regrowth rates (but the magnitude of the effects can be visually interpreted in Figure 3).

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240 When we pooled *rrgr* among treatments, *rrgr* at Lakamané was greater than at Tiendéga

241 in 2011 ($P = 0.006$), but in 2013 *rrgr* was greater in Tiendéga ($P = 0.004$; but see Supplementary

242 Information for caveats about this test). *rrgr* at Tiendéga was greater in 2013 relative to 2011 (P

243 $= 0.001$; Figure 4). *rrgr* among years at Lakamané were likely similar (we do not provide a P

244 value due to the sensitivity of this test to the dry:wet weight ratio; see Supplementary

245 Information). See Supplementary Information for the effects of different dry:wet weight ratios in

246 Lakamané in 2013 on these statistical tests.

247 There were no significant treatment effects on tree height three years after harvest, but

248 average height was greater at Tiendéga than Lakamané ($P = 0.012$; Figure 4A). Initial tree

249 biomass is a significant predictor of the probability that a tree will reach 2 and 3 meters three

250 years after harvest in Tiendéga ($P = 0.004$ and $P = 0.023$, respectively) and for 2 meters in

251 Lakamané ($P = 0.022$) (Figure 4B,C).

252

253 Discussion

254 A defining trait of savanna tree species is their ability to resprout vigorously. While this

255 trait likely evolved by natural selection in response to frequent fires in savanna ecosystems

256 (Bond & Midgley, 2001; Shackleton, 2001), the same trait benefits savanna trees that are

257 harvested for fuelwood (Shackleton, 2001). Indeed, we observed near zero mortality after

258 harvesting savanna trees in two West African savannas (Table 1). This is unsurprising, as prior

259 work in a South African savanna reported similar results (Shackleton, 2001). More surprising is

260 that relative regrowth rate and height of harvested trees did not differ among treatments of fire

261 exclusion, large herbivore exclusion, or the exclusion of both fire and herbivores. Given that

262 recent modeling work suggests an important interaction between tree harvest and fire, we

263   expected that woody regrowth in fire plots would be lower because of shoot mortality in fires.

264   However, we found no support for an interaction between harvest and fire, or for any of the other

265   hypotheses advanced in the Introduction (Table 2, Figure 4A). Perhaps most surprisingly,

266   treatment effects did not emerge over time, at least statistically.

267   In the case of the herbivore treatments, it could be that grazing by cattle has very little

268   impact, either through reduced grass competition or reduced fuel loads, on post harvest regrowth.

269   Other experiments have shown that the direct effect of browsers is much greater than the indirect

270   effects of grazers (Staver and Bond, 2014). Thus, it is not surprising that at the grazer-dominated

271   mesic site (Tiendéga) we found no effect of herbivory, especially since our treatments only ran

272   for three years. More time may be required for the indirect effects of grass-tree competition and

273   increased fuel loads to emerge.

274   Contrary to the possible indirect effects of grazing, a positive effect of browsing release

275   in Lakamané, where goats and sheep dominate herds, should have been immediate. Yet we found

276   no statistical support for an herbivore effect (Table 2, Figure 4A). The most likely explanation is

277   that harvested trees regrow very quickly and are able to escape from the 'browse trap' within one

278   year (Staver and Bond, 2014) (Figure 4B,C). Three years after harvest the average height of

279   regrowing trees across all treatments at Lakamané was 1.74 meters (s.d. = 0.66) (Figure 4A).

280   Thus, as we discuss below for the case of fire, harvested trees are able to regrow rapidly and

281   avoid disturbance impacts, unlike seedlings and saplings growing from seed.

282   The lack of an effect on *rrgr* or height by excluding fire, either in the presence or absence

283   of herbivores, is more perplexing. Decades of work in savanna systems points toward the key

284   role of fire in limiting seedling and sapling transitions to larger size classes, so why did we not

285   observe a positive effect of fire exclusion here? It is likely that post-harvest saplings simply grow

286 faster than saplings growing from seed. In that case, post-harvest saplings are able to escape the

287 firetrap quickly by drawing on large stores of belowground carbohydrates (Hoffmann et al.,

288 2003; Hoffmann, Orthen & Franco, 2004). We found evidence of this since initial tree size was

289 a good predictor of a tree reaching specific escape heights (Figure 4B,C). By growing fast, post-

290 harvest saplings avoid subsequent top kill during the dry season. This scenario could occur

291 within a single growing season if the harvest event occurs early enough, or the scenario could

292 play out over two growing seasons: in the first season the tree is harvested, but remains virtually

293 dormant through the dry season fires, then can grow quickly in the subsequent growing season.

294 Therefore, even after three annual burns, for trees measured in 2013, we did not detect a fire

295 effect on regrowth (Table 2, Figure 4A).

296   Most other work on savanna tree demographics has not considered the effect of tree

297 harvest (but see Zida et al., 2007). Thus, the insight that fire can maintain the savanna state by

298 limiting sapling transitions to adult trees is constrained to systems where the saplings that are

299 negatively impacted by fire have grown from seed or have resprouted from a sapling partially or

300 completely top-killed by a previous fire. In other words, most work on this topic does not

301 consider that coppice saplings growing from the rootstock of large trees may have faster growth

302 rates than even the fastest growing "regular" saplings (those from seed or regrowth from

303 saplings). In our previous work we assumed equal growth rates among "new" and "harvested"

304 saplings (Tredennick & Hanan, In Press). Clearly this assumption needs to be refined. To do so

305 will require comparative studies of sapling growth rates when grown from seed and across a size

306 spectrum at time of harvest.

307   Another surprising result is that biomass regrowth at the mesic site (Tiendéga) was not

308 consistently greater than at the arid site (Lakamané). In fact, in the first year after harvest,

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309   biomass regrowth was statistically larger at the arid site. This runs counter to our naïve

310   hypothesis based on climate constraints alone (e.g., a positive relationship between growth rates

311   and precipitation). However, there are many factors that may interact with precipitation to inhibit

312   regrowth in mesic savannas relative to arid savannas, like competition for light with adult trees

313   (Iponga, Milton & Richardson, 2008) or competition with grass (Riginos, 2009) and tree roots

314   (Sea & Hanan, 2012) for soil water. And, we did find that heights three years after harvest were

315   greater in the mesic site than in the arid site (Figure 4A). Fully understanding the susceptibility

316   of regenerating trees to fire and herbivory will require disentangling those interacting resource-

317   based drivers.

318   To conclude, while fuelwood harvest decreases overall tree population wood-growth

319   rates in post-harvest years, we found little evidence that presence of fire and large herbivores, or

320   both, affect post-harvest regrowth of trees in semi-arid and a mesic savannas of West Africa. Our

321   findings are broadly consistent with work from Burkina Faso that also found no interaction

322   between tree harvest, fire, and grazing (Zida et al., 2007). Our work suggests that the effects of

323   disturbance, however small, are most important during the first year of growth after harvest.

324   Savanna trees resprouting after harvest are able to draw on large nutrient stores held in

325   substantial root systems. Thus, their growth rates are rapid, allowing them to escape the impacts

326   of disturbance quickly. The timing of disturbance is likely important for determining the success

327   and magnitude of post-harvest regrowth.

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418

419 **Tables**

420

421 **Table 1.** Percent mortality of harvested trees each measurement year. The raw number of dead

422 trees out of the total sample is shown in the parentheses.

423

Site	Percent mortality		
	2011	2013	Years combined
Tiendéga	2.5% (1/40)	2.5% (1/40)	2.5% (2/80)
Lakamané	0% (0/38)	5.4% (2/37)	2.7% (2/75)

424

425 **Table 2.** Results from the factorial ANOVA for the effects of herbivore and fire exclusion on

426 post-harvest biomass regrowth (*rrgr*) one and three years after harvest. Measurement periods are

427 denoted as in the main text where t_{harv} = 2010. Statistical tests result from running an ANOVA

428 ('anova') on the results from a linear model ('lm') in the program R.

Measurement Period	Site	n^c	Fire		Herbivroy		Fire × Herbivory	
			$F_{1,n-3}$	P	$F_{1,n-3}$	P	$F_{1,n-3}$	P
t_{harv} + 1	All[a]	75	0.062	na[b]	0.01	na[b]	0.061	na[b]
	Tiendéga	38	0.004	0.95	0.164	0.688	0.059	0.809
	Lakamané	37	0.053	0.819	1.482	0.232	2.207	0.146
t_{harv} + 3	All[a]	74	0.062	na[b]	0.01	na[b]	0.061	na[b]
	Tiendéga	39	0.327	0.571	0.749	0.393	0.723	0.401
	Lakamané	35	2.739	0.108	0.874	0.357	0[d]	1[d]

429 [a]To estimate the effects of fire and herbivory across both sites we used a mixed-effects model
430 with a site random effect on the intercept.
431
432 [b]P values are not statistically appropriate when computed based on mixed-effects models, so we
433 do not report them here. However, the very small F values indicate that the fire and herbivory
434 effects are not important.
435
436 [c]Sample sizes may be different from those in Table 2 because we excluded dead trees and one
437 observation with an unreliable estimate of initial biomass.
438
439 [d]These are values rounded to three digits.
440

441 **Figure Legends**

442 **Figure 1.** (A) Map of Mali, West Africa showing locations of the two study sites (Tiendéga in

443 the South; Lakamané in the North) and broad trends in mean annual precipitation. (B) The

444 experimental layout at each site. F = fire present; f = fire excluded. H = large herbivores present;

445 h = large herbivores excluded. As described in the main text, a 25 x 25 meter plot in two of four
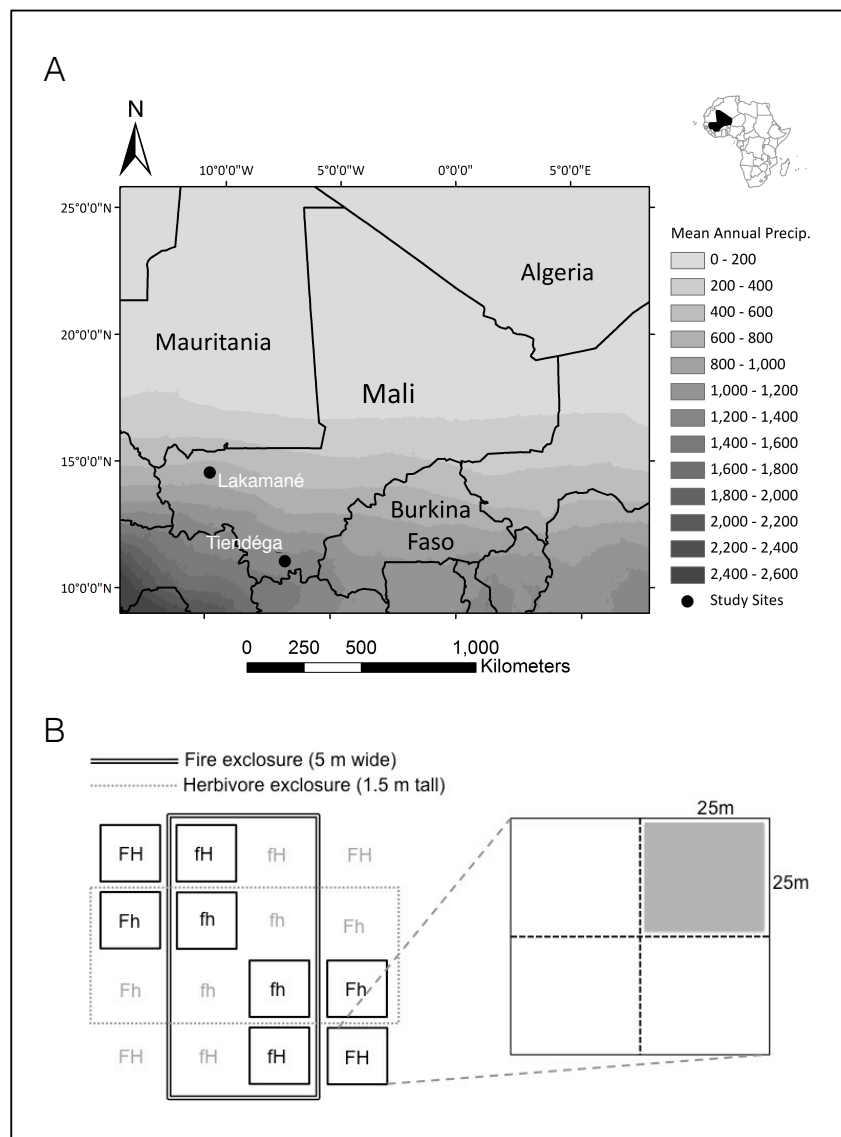
446 treatment replicates was used for this study.

447

448 **Figure 2.** Boxplots comparing relative (re)growth rates by site for control (growth rates) and

449 harvested trees (regrowth rates) across both measurement years. Letters denote statistically

450 significant ($P < 0.1$) pairwise comparisons from post-hoc Tukey's HSD tests. Growth rates are

451 expressed per unit aboveground wood biomass of trees in 2010 (prior to cutting in harvested

452 treatments; see Eqs. 1 and 2).

453
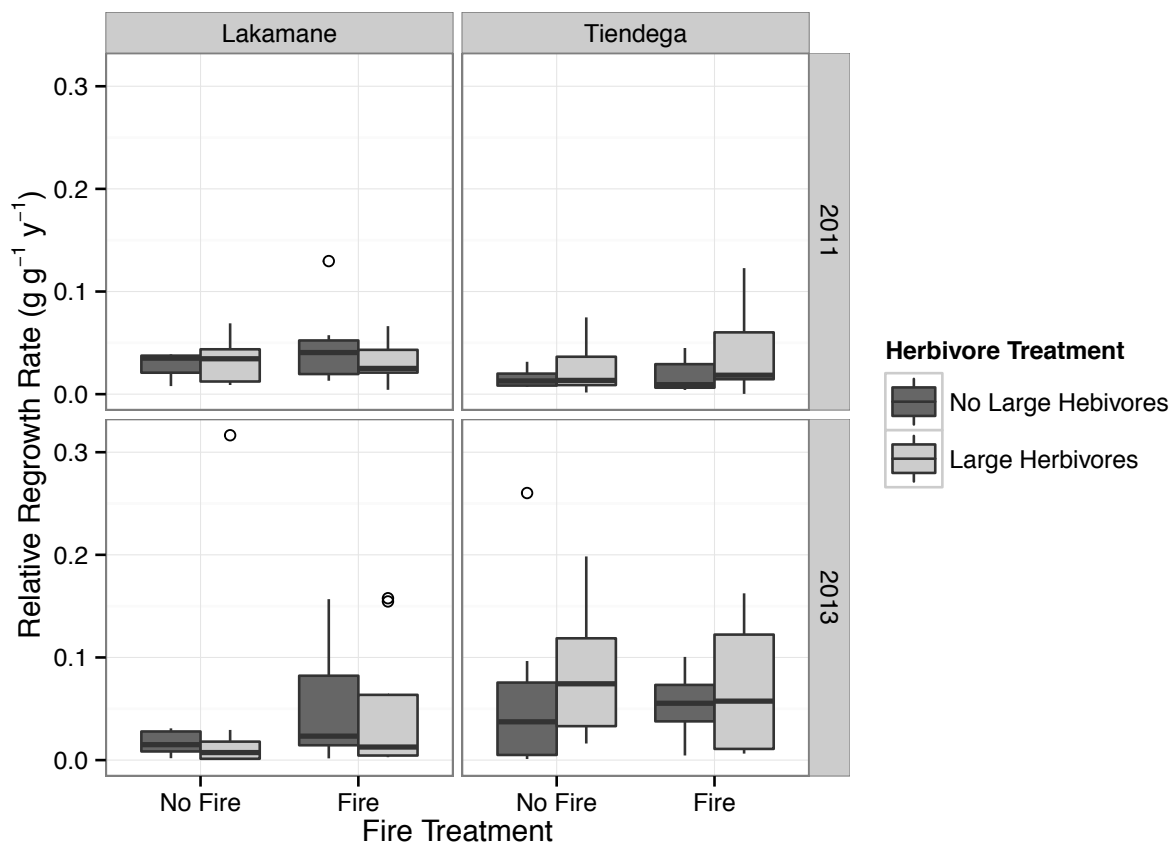
454 **Figure 3.** Boxplots of relative biomass regrowth rates (*rrgr*) 1 year (2011) and 3 years (2013)

455 after harvest for each treatment at each site. There are no strong statistical differences among

456 treatments within each year; however, treatment effects are further diminished by 2013 (see

457 Table 1). We tested for interactions between treatments and the year harvested, but found no

458 statistically important interaction effects.

459

460 **Figure 4.** Boxplots of harvested tree heights after three years (A) and results from logistic

461 regression estimating the probability of reaching an escape height (2 or 3 meters) after three

462 years as a function of pre-harvest tree size (B and C). In A, there are no statistical differences

463 among treatments, but average height after three years was greater in Tiendéga than in Lakamané

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464 ($P = 0.012$). In C, only the regression for a 2 meter escape height has initial biomass as

465 significant, but we still show the 3 meter regression for context.
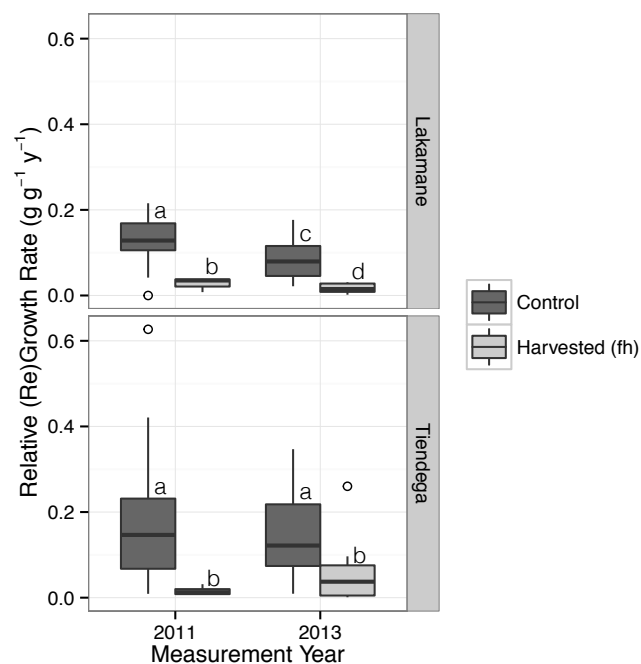
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Figure 1. (A) Map of Mali, West Africa showing locations of the two study sites (Tiendéga in

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 x 25 meter plot in two of four

treatment replicates was used for this study.

473

Figure 2. Boxplots 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).

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Figure 3. Boxplots 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; however, treatment effects are further diminished by 2013 (see Table 1). We tested for interactions between treatments and the year harvested, but found no statistically important interaction effects.

26

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years as a function of pre-harvest tree size (B and C). In A, there are no statistical differences

among treatments, but average height after three years was greater in Tiendéga than in Lakamané

($P = 0.012$). In C, only the regression for a 2 meter escape height has initial biomass as

significant, but we still show the 3 meter regression for context.

Supplemental Information for:
Weak effects of fire, large herbivores, and their interaction on regrowth of harvested trees in two West African savannas

Andrew T. Tredennick, Moussa Karembé, Fadiala Dembélé,
Justin Dohn, and Niall P. Hanan

### Supplemental Information 1: Assessing impact of dry:wet weight ratio on statistical results

There are two statistical tests in our paper that could be biased by an incorrect dry:wet wood ratio for Lakamané in 2013:

1. The comparison of relative regrowth rate between sites in 2013.
2. The comparison of relative regrowth rate between years in Lakamané.

Comparisons in Lakamané within the year 2013 are the same regardless of the dry:wet weight ratio because the ratio is constant among treatments within sites. To test the sensitivity of our statistical results for the two comparisons above we used a simple simulation where we performed the same statistical test after applying a range of dry:wet weight ratios to the wet weights observed in Lakamané. In the main text we base our conclusions on a dry:wet ratio of 0.5 – a value similar to the one estimated from the 2011 data in Lakamané, which was collected at nearly the same time of year.

Our simulation test shows that a statistical difference ($p < 0.1$) between Lakamané regrowth (pooled across treatments) and Tiendéga regrowth in 2013 occurs when the dry:wet weight ratio is less than 0.65 (Figure S1; open circles). For the comparison between years in Lakamané, a significant difference occurs when the dry:wet ratio is less than 0.54 (Figure S1; grey circles). Thus, we are confident in our conclusion that regrowth rates between sites in 2013 are statistically different, as reported in the main text. However, since the threshold for a significant difference between years in Lakamané is very near the dry:wet weight ratio we use, we are less confident in that result. Therefore, we do not report a significant difference between years in Lakamané in the main text.

We note that all statistical tests other than the two listed above are unaffected by this particular dry:wet weight ratio.
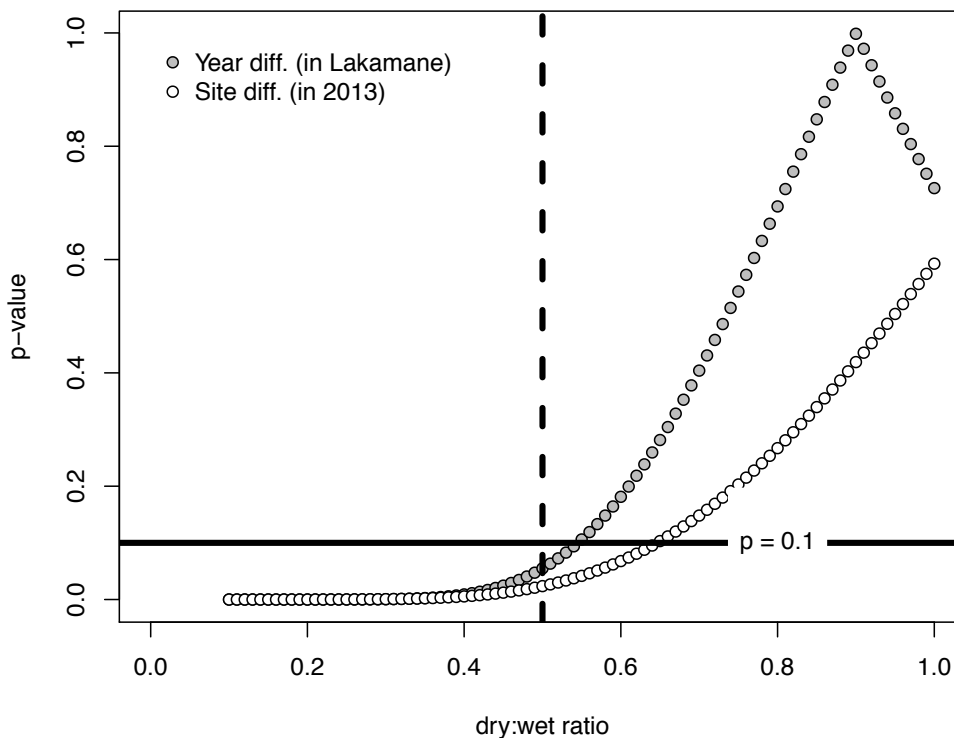
Figure S1. Results of our simulation test for bias induced by the wet:dry weight ratio. The open circles show the simulation results for the difference between sites in 2013. The grey filled circles show the simulation results for the difference between years in Lakamané. The solid black line shows a p-value of 0.1, and the dashed vertical line shows the dry:wet ratio of 0.5 that we used for the analyses presented in the main text.

Supplemental Information 2: Converting diameter measurements to biomass using allometric models

We measured the growth of non-harvested trees within our fully protected plots (*fh*; fire and large herbivores excluded) using dendrometer bands. Each measurement year (2011 and 2013) we recorded the change in diameter from the initial diameter measured in 2010. To compare these growth rates to those of the harvested trees, we converted diameter measurements to biomass estimated using a simple allometric model. We used data collected in 2010 from harvested trees to estimate the parameters in a log-log allometric regression:

$$\log(y) = a + b\log(D) \quad \text{[Eq. S1]}$$

where *y* is tree wood biomass, *a* is a normalizing constant, *b* is the scaling parameter, and *D* is tree diameter (see Tredennick et al. 2013 for more details on allometric models in savannas and the data used here).

We fit two competing models to the data: (1) a mixed-effects model with a random effect of species on the slope and (2) an interspecific model with no random effects. AICc (AIC for corrected for small datasets) among the two models were roughly equivalent (46.93 for (1) and 47.99 for (2)). So, we decided to use the interspecific model with the following parameters: $a = 3.26$ and $b = 2.78$ ($P < 0.0001$, $R^2 = 0.92$; Figure S2). We used this equation to estimate biomass of non-harvested trees in 2010, 2011, and 2013. Then, using those estimates, we were able to estimated the relative biomass growth rate ($rgr_{year} = [B_{year}/B_{2010}]/year-2010$) of non-harvested trees and compare those growth rates to the relative biomass regrowth rates of the harvested trees in each measurement year.

Below are the details of the log-log allometric model fit in R. *Y2* is wood biomass for each tree and *x* is the diameter of each tree.

```
Call:
lm(formula = log(Y2) ~ log(x))

Residuals:
     Min       1Q   Median       3Q      Max
-0.94569 -0.22800 -0.04236  0.17408  1.09724

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   3.2568     0.2990   10.89 6.03e-13 ***
log(x)        2.7763     0.1399   19.85  < 2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.3974 on 36 degrees of freedom
Multiple R-squared:  0.9163,	Adjusted R-squared:  0.914
F-statistic:   394 on 1 and 36 DF,  p-value: < 2.2e-16
```
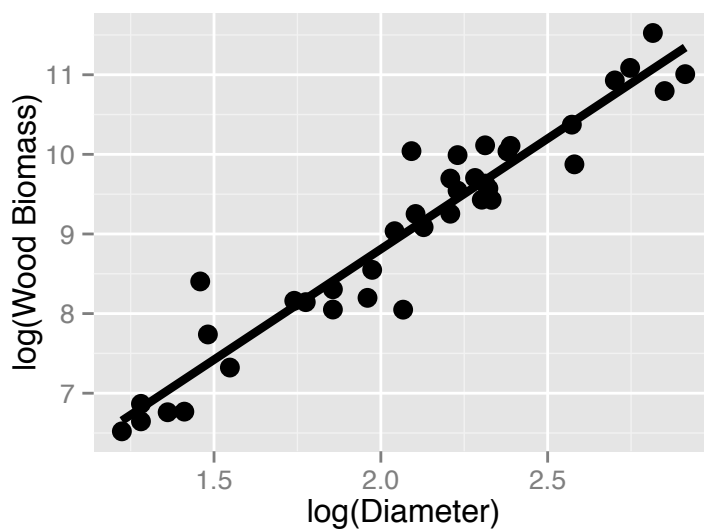
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Figure S2. Fitted regression of log(Biomass) ~ log(Diameter). The fitted line is the mean prediction from the log-log regression described above.

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Tredennick, A.T., Bentley, L.P., and Hanan, N.P. (2013) Allometric Convergence in Savanna Trees and Implications for the Use of Plant Scaling Models in Variable Ecosystems. PLoS One 8(3): e58241. doi:10.1371/journal.pone.0058241

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