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Ecosystem management can mitigate vegetation shifts induced by climate change in West Africa

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ABSTRACT

The welfare of people in the tropics and sub-tropics strongly depends on goods and services that savanna ecosystems supply, such as food and livestock production, fuel wood, and climate regulation. Flows of these services are strongly influenced by climate, land use and their interactions. Savannas cover c. 20% of the Earth's land surface and changes in the structure and dynamics of savanna vegetation may strongly influence local people's living conditions, as well as the climate system and global biogeochemical cycles. In this study, we use a dynamic vegetation model, the aDGVM, to explore interactive effects of climate and land use on the vegetation structure and distribution of West African savannas under current and anticipated future environmental conditions. We parameterized the model for West African savannas and extended it by including sub-models to simulate fire management, grazing, and wood cutting. The model projects that under future climate without human land use impacts, large savanna areas would shift toward more wood dominated vegetation due to CO_2 fertilization effects, increased water use efficiency and decreased fire activity. However, land use activities could maintain desired vegetation states that ensure fluxes of important ecosystem services, even under anticipated future conditions. Ecosystem management can mitigate climate change impacts on vegetation and delay or avoid undesired vegetation shifts. The results highlight the effects of land use on the future distribution and dynamics of savannas. The identification of management strategies is essential to maintain important ecosystem services under future conditions in savannas worldwide.

1. Introduction

Tropical savannas provide ecosystem goods and ecosystem services (ESS), such as food production, livestock grazing, fuel wood production, climate stabilization and biodiversity (Costanza et al., 1997). Many ESS have a high socio-economic value (Costanza et al., 1997) and their sustained flow is essential for the survival and welfare of many people living in savanna regions. Savannas cover c. 20% of the Earth's land surface and contribute approximately 30% of global net primary productivity (Grace et al., 2006). Hence, changes in climatic conditions and land use in savannas may have significant impacts at both local and continental scales. At a local scale, climate and land use change modify vegetation dynamics and thereby the flow of ESS, which may directly affect the people who depend on savanna ecosystems. At the continental or global scale, climate change induced biome shifts may have strong feedback effects on the climate system via changes in biogeochemical fluxes and albedo (Bonan, 2008), thereby influencing the Earth system (Lenton et al., 2008).

In recent decades, an increasing human population density lead to the transformation of large savanna areas for livestock and crop production, thereby influencing ESS (Ramankutty et al., 2008). The Millennium Ecosystem Assessment (2005) reported that, of the 24 ecosystem services examined, only four have improved in the last 50 years while the others have remained unchanged or declined markedly. For example, food production has increased, however, the general picture includes significant declines in biodiversity, depletion of natural resources and ecosystem degradation (Sala et al., 2000; Hooper et al., 2012). In this context, West African savannas are one of the hotspots (Brito et al., 2014). Land use in these

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regions is intense and an assessment of land use impacts on vegetation and ESS is needed to develop management strategies that ensure the continuation of subsistence farming, timber production, livestock grazing, extraction of fuel wood and conservation of biodiversity (Bellefontaine et al., 2000; Savadogo et al., 2009; Bodart et al., 2013). Current management practices in West Africa often focus on woody vegetation and typically include fire, selective tree cutting and prohibition of grazing (Bellefontaine et al., 2000; Savadogo et al., 2009). Thus, Eva and Lambin (1998) estimated that 1% of the Sahel, 28.2% of the Sudan zone and 57.7% of the Guinea zone in West Africa burn annually. Most of these fires are anthropogenic dry season fires (Menaut et al., 1991; Savadogo et al., 2007a) to promote pasture growth and species richness (Savadogo et al., 2007b). However, the management strategies adopted in many savanna zones are not based on sound scientific evidence (Savadogo et al., 2007a) and underlying studies have focused on impacts of single management activities rather than on their interactive effects (Savadogo et al., 2007a, 2008). Thus, the suitability of current management strategies for savanna ecosystems is uncertain from both ecological and economic perspectives.

Management of savanna ecosystems is also complicated by the complexity of grass-tree dynamics (Higgins et al., 2000) and the interactions between vegetation and climate change. Savannas are typically characterized by a homogeneous layer of C_4 grasses and scattered trees (Ratnam et al., 2011). It has been argued that many savannas are bi-stable, that is, the environmental conditions are suitable to support forests, however, fire, herbivory and anthropogenic impacts maintain an open savanna state (Hirota et al., 2011; Staver et al., 2011; Higgins and Scheiter, 2012). Many savanna systems across Africa experience woody encroachment, suggesting that vegetation shifts from an open savanna state toward a tree dominated woodland or forest state are ongoing (Kgope et al., 2010; Buitenwerf et al., 2012; Donohue et al., 2013). In these studies, vegetation shifts have been attributed to factors associated with climatic and atmospheric changes, particularly CO_2 fertilization and the advantage of C_3 vegetation over C_4 vegetation at elevated CO_2 concentrations (Ehleringer et al., 1997), rather than changes in land use.

Field studies have explored the responses of the vegetation to variations in land-use at the site-scale. In West Africa, results from long-term field experiments in Burkina Faso highlight the importance of management impacts on vegetation dynamics, vegetation structure and biodiversity (Savadogo et al., 2008, 2009; Dayamba et al., 2011), suggesting that landscape-scale approaches are required to understand impacts of disturbances on savanna ecosystem dynamics. Models can serve as a tool to address questions related to complex interactions in savannas as they allow integration of knowledge about processes and parameters drawn from multi-disciplinary studies and the projection of results from short-term and small-scale studies to larger spatial and temporal scales (Lohmann, 2012). Sophisticated vegetation models are required in order to model interactions between vegetation, climate and anthropogenic impacts in complex ecosystems and to establish robust knowledge. Dynamic global vegetation models (DGVMs, Prentice et al., 2007) are appropriate tools; these models simulate vegetation dynamics based on ecophysiological processes at the leaf, plant and population level and they allow simulation of the impacts of climate change and land use at large temporal and spatial scales. Previous DGVM studies projected vegetation shifts in Africa under future climate conditions (e.g. Higgins and Scheiter, 2012; Sato and Ise, 2012). However, many DGVMs do not represent complex grass-tree dynamics in savannas adequately (Scheiter and Higgins, 2009) and model projections often focus on potential vegetation, while ignoring land use and management.

In this study we used the aDGVM (adaptive dynamic global vegetation model), an individual-based dynamic vegetation model developed and parameterized for African savannas (Scheiter and Higgins, 2009), to investigate the long-term impacts of fire, wood cutting and grazing on the future vegetation of West African savannas. We test the hypothesis that management can contribute to maintain vegetation in a desired ecosystem state, prevent woody encroachment and shifts toward tree-dominated biomes under anticipated future climate scenarios.

2. Methods

2.1. The aDGVM

We used the adaptive Dynamic Global Vegetation Model (aDGVM, Scheiter and Higgins, 2009), a dynamic vegetation model for tropical grass-tree systems. A detailed model description is provided by Scheiter and Higgins (2009), here we summarize important model features. The aDGVM integrates plant physiological processes generally used in dynamic global vegetation models (DGVMs, Prentice et al., 2007) and processes that allow plants to dynamically adjust leaf phenology and carbon allocation to environmental conditions. The aDGVM is individual-based, i.e., it simulates state variables such as biomass, height and photosynthetic rates of individual plants. This approach is necessary to adequately model the impacts of herbivores (Scheiter and Higgins, 2012) and fire (Scheiter and Higgins, 2009) on vegetation structure and demography because these impacts are influenced by the height of individual plants. Grasses are simulated by two super-individuals, representing grasses beneath and between tree canopies. The aDGVM only requires generally available environmental input data and typically simulates vegetation in 1 ha stands. The original version of the aDGVM as described by Scheiter and Higgins (2009) only simulates fire-resistant savanna trees and C_4 grasses. Here, we used an updated model version, with details provided in Scheiter et al. (2012). The updated version simulates both C_3 and C_4 grasses as well as fire-resistant savanna trees and fire-sensitive forest trees. The grass types mainly differ in leaf level physiology (C_3 or C_4 photosynthesis). Differences between tree types are mainly related to re-sprouting behavior after fire and to carbon allocation patterns (Bond, 2008; Ratnam et al., 2011).

Fire is an important driver of savanna vegetation dynamics and is simulated in the aDGVM. In the model, a fire starts when an ignition event occurs. The number of ignitions per year is linked to tree cover because grass biomass is the main fuel type and the tree cover influences how quickly the grass layer desiccates in the dry season. In the model, we assume that the ignition probability is low in vegetation stands with high tree cover and high in open vegetation stands. Days when ignition events occur are randomly generated. An ignition event does not necessarily imply fire spread; fire only spreads with a certain probability (p_{fire}) and when the fire intensity exceeds a threshold value of 300 kJ/m/s (Van Wilgen and Scholes, 1997). Fire intensity is a function of fuel loads, fuel moisture and wind speed (Higgins et al., 2008). This fire sub-model ensures that fire regimes are influenced by fuel biomass and climate. Fires are more likely in the dry season because grass biomass, the main fuel, cures rapidly in the dry season and high fire intensities are possible. Fire removes aboveground grass biomass while the response of trees to fire is a function of tree height and fire intensity (“topkill” effect, Higgins et al., 2000). Seedlings and juveniles in the flame zone are damaged by each fire while adult trees are more fire-resistant and are only damaged by intense fires. In the aDGVM, savanna trees have lower topkill probabilities than forest trees. Grasses and topkilled savanna trees can regrow from root reserves after fire (Bond and Midgley, 2001). After fire and the removal of leaf biomass, the carbon balance of a tree may be negative, which increases the probability of mortality in the aDGVM. By this process, fire influences tree mortality indirectly but does not directly kill trees.

2.2. Land use sub-models

The original version of aDGVM does not include model components to simulate land use and management (Scheiter and Higgins, 2009; Scheiter et al., 2012). We therefore extended the model to include sub-models that simulate fire management, wood cutting and grazing. These sub-models represent land use strategies that are widely applied in West African savannas and have been explored in long-term field studies in Burkina Faso (Savadogo et al., 2009).

We assumed that managed fires occurred in the early dry season, between the end of October and December (Savadogo et al., 2009). The specific day of fire ignition within this period was randomly selected and fires were forced to ensure that one fire spreads during the burning season. Fire intensity is calculated from fuel biomass, fuel moisture and wind speed and fire only spreads when fire intensity exceeds 300 kJ/m/s (Van Wilgen and Scholes, 1997, see Section 2.1). Hence, grasses influence fire intensity and whether a fire spreads while the fire return interval and burning season are prescribed. We did not consider situations where repeated fires are required until a certain proportion of vegetation is consumed or where fire management is adjusted to fuel loads. The fire return interval (in years) in the management scenario is a model parameter that can be prescribed for a simulation run. Impacts of management fires are similar to impacts of ‘natural’ fires simulated by the aDGVM, that is, fire removes aboveground grass biomass and, depending on tree height, aboveground tree biomass.

In our simulations, wood cutting removed trees with a stem diameter between 10 and 25 cm, until 50% of the original basal area was left. This sub-model is in accordance with practices in Burkina Faso (Savadogo et al., 2009). The return interval of wood cutting (in years) is a model parameter that can be prescribed for a simulation run. We model grazing by removing a pre-defined proportion G of standing aboveground grass biomass per day in the dry season. We do not account for the fact that in reality, grazers move through the landscape and do not feed on the same vegetation stand every day. Grazing influences live grass biomass whereas dead biomass is not affected. The parameter G was derived from fitting the model to field data (see Section 2.3).

2.3. Model parameterization and benchmarking

The aDGVM has been parameterized for African savanna systems and adequately simulates the broad vegetation patterns at the continental scale. Previous studies show that the aDGVM simulates the distribution of different vegetation types across Africa better than alternative models (Scheiter and Higgins, 2009; Scheiter et al., 2012) and that simulations at the site scale agree well with tree biomass observed in a fire exclusion experiment in Kruger National Park (Higgins et al., 2007a; Scheiter and Higgins, 2009). To improve the model for the study region, we fitted the model to tree basal area and grass biomass data from long-term experiments at Tiogo (12°27.3′ N, 3°27.8′ W, 813 mm MAP) and Laba (11°45′ N, 2°55.8′ W, 878 mm MAP), Burkina Faso. In these long-term experiments, interactive effects of grazing, fire and wood cutting on the vegetation were explored by tracking vegetation growth under various combinations of these management activities (eight treatments in total, Savadogo et al., 2009). Tree basal area data were collected in 1992, 1997, 2002 and 2007, and grass biomass data were collected annually between 1993 and 2005. To parameterize and benchmark the model, we imitated these treatments. Model fitting was conducted to derive model parameters which improve the agreement between data and model.

Model fitting was conducted using a genetic optimization algorithm (dynamic evolution optimization algorithm, DEoptim, Mullen et al., 2011). The model fitting procedure optimized tree demography parameters (mortality P_{carb}, P_{comp}, P_{frost}, and seed germination φ_{germ}, with notation of parameters as described by Scheiter and Higgins, 2009), light extinction in the canopy (γ_{tree} and γ_{grass}), light competition parameters (μ), growth respiration parameters (σ_{tree}, σ_{grass}), fire model parameters (p_{fire} and i_2) and grazing intensity (G). We used these parameters because they are difficult to measure in the field or they remain some of the greatest sources of uncertainty in the aDGVM. We defined minimum and maximum values for the parameters that ensure that fitted values are valid. Observed and simulated time series of basal area and grass biomass are provided in Fig. 1, original and fitted parameter values are provided in Table 1.

We constrained the optimization using the following assumptions. First, the simulated initial vegetation state in 1992 had to be within the range of basal area and grass biomass measurements in the different treatments of the field study. Second, the differences between observed and simulated trends and absolute values of grass biomass and basal area were minimized. We only used scenarios with and without fire and grazing for the model fitting because wood cutting impacts were well defined by the field experiments. We conducted five replicate simulations for each scenario to account for stochastic effects in the aDGVM such as plant demography and fire. Simulations were conducted in the presence of natural fire regimes up to the year 1992. Following this period, management scenarios were applied. Model fitting modified the demographic rates of trees (Table 1) with lower seed germination and mortality rates (except mortality due to frost, which has only minor impact in the study region), light competition both between different vegetation types and within vegetation types, as well as respiration rates. The model fitting improved data-model agreement compared to the original parameter values. Differences between data and model (Fig. 1) can be explained by small-scale heterogeneity of soil conditions in different treatments and replicates of the field experiment, that are not considered in the model, by different initial grass-tree ratios and biomass at the start of the field experiment in 1992 and by differences between meteorological data at the study sites and environmental forcing data used for simulations. Model behavior is defined by the underlying assumptions and processes and it is, to a certain degree, predictable. As a consequence, the model projects, for example, higher tree basal area and lower grass biomass in the presence of grazing due to reduced grass biomass and changes in grass-tree competition. This pattern is not consistently observed in the field experiments (Fig. 1).

2.4. Simulation experiments

As a baseline scenario, we simulated the potential vegetation until 2100 using the SRES (special report on emission scenarios) A1B scenario from the 4th assessment report of the intergovernmental panel on climate change (IPCC, 2007). We used simulation runs of the Max Planck Institute for Meteorology in Hamburg (ECHAM model, Roeckner, 2005). This scenario projects an increase in atmospheric CO_2 concentration to approximately 700 ppm and a temperature increase of approximately 4 °C by 2100. We first ran a 100-year model spin-up using climate conditions for the reference period between 1960 and 1990 (New et al., 2002) to ensure that the model was in equilibrium with the environment. After the spin-up, the model was forced with temperature, precipitation and CO_2 trends from the SRES A1B scenario. In the baseline scenario we simulated natural fire regimes using the standard aDGVM fire model (see Section 2.1) whereas fire management, wood cutting and grazing were not simulated. Simulations were conducted for West Africa, more specifically for the region 2° N to 24° N and 17° E to 16° W at a 1° grid resolution. Simulated vegetation was classified into biome types (desert, grassland, savanna, woodland,

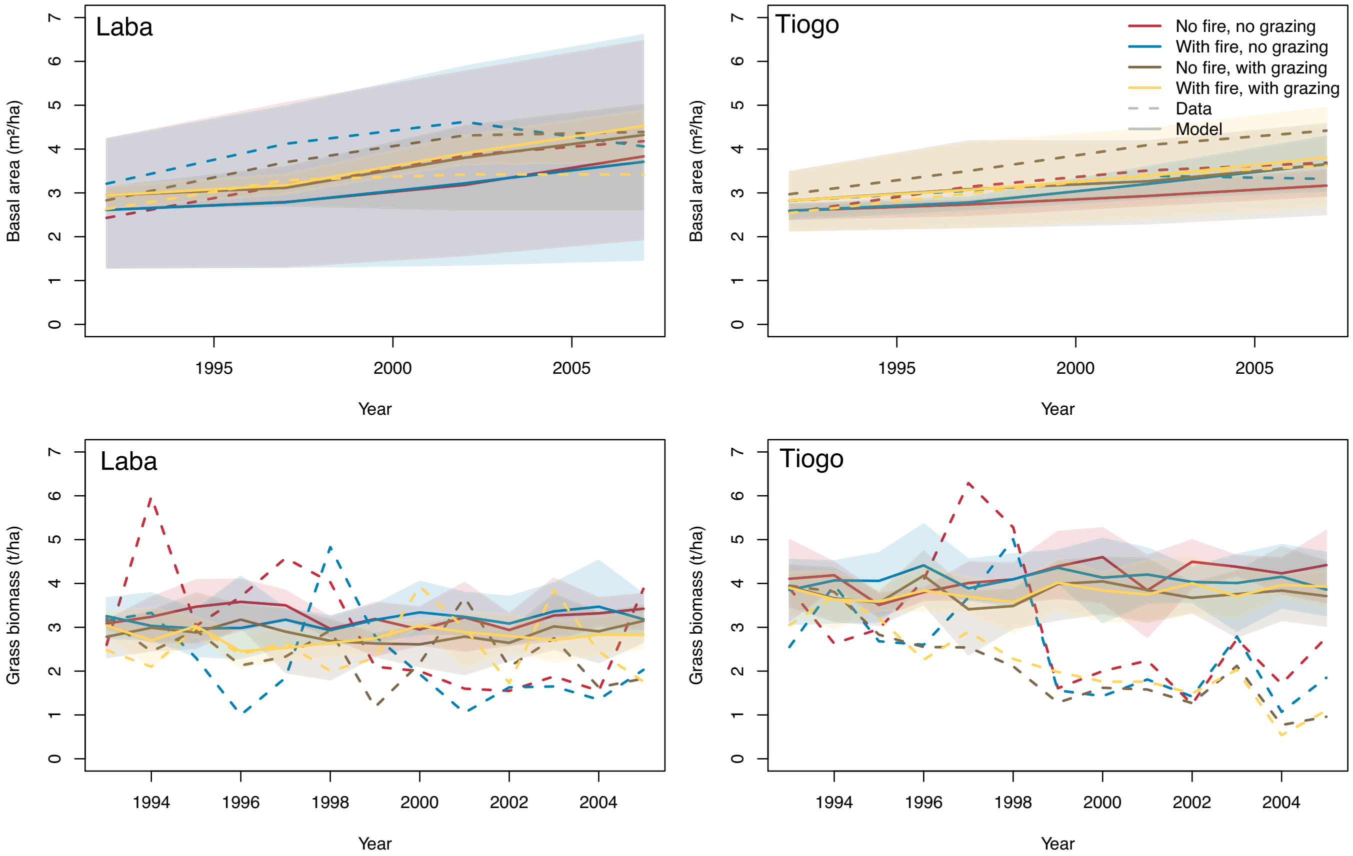

Fig. 1. Time series of simulated and observed tree basal area and grass biomass for the Laba and Tiogo study sites. Data were collected in the long-term savanna-woodland disturbance ecology monitoring experiment and were provided by P. Savadogo. Shaded areas represent minimum and maximum biomasses of five replicate simulation runs for each scenario.

forest) based on tree cover and grass biomass (Fig. S1 in supplementary information; Scheiter et al., 2012).

We then projected vegetation until 2100 under different land use scenarios. Simulations were conducted analogously to the simulations for potential vegetation (see previous paragraph). Yet, we applied land use scenarios after 1992 as the field experiments we used for model parameterization began in that year. In reality the land use practices in the study region began earlier, but this was implicitly considered by fitting the model to the vegetation state in 1992. We then simulated all 24 combinations of the following management scenarios: early dry season management with fire every 1, 2 and 5 years and fire suppression after 1992 (four scenarios), wood cutting every 10 and 20 years and no wood cutting after 1992 (three scenarios), no grazing and removal of G% of the grass biomass per day in the dry season (two scenarios).

Table 1

Original parameter values for African savannas (Scheiter and Higgins, 2009) and fitted parameter values for west African savannas as used in this study. Columns ‘Min’ and ‘Max’ provide the parameter ranges used for the model fitting. Variable names and original values were taken from the model description provided by Scheiter and Higgins (2009) and from Scheiter et al. (2012).

Name	Description	Original	Fitted	Min	Max
p_{fire}	Fire ignition probability	0.01	0.003	0.001	0.9
i_2	Parameter for fire ignition sequence	0.1	0.86	0.001	0.9
γ_{tree}	Light extinction in tree canopy	0.5	0.465	0.3	0.5
γ_{grass}	Light extinction in grass canopy	0.5	0.436	0.3	0.5
σ_{tree}	Tree growth respiration	0.35	0.57	0.2	0.6
σ_{grass}	Grass growth respiration	0.35	0.51	0.2	0.6
φ_{germ}	Seed germination probability	0.25	0.14	0.01	0.5
P_{frost}	Tree mortality: frost	0.001	0.098	0.0001	0.1
P_{carbon}	Tree mortality: carbon deficiency	0.001	0.0001	0.0001	0.1
P_{comp}	Tree mortality: competition	0.001	0.0001	0.0001	0.1
G	Grazing intensity (%)	0	1.2	0	100
μ_{ss}	Light competition: savanna trees → savanna trees	0.5	1	0	1
μ_{s4}	Light competition: savanna trees → C_4 grasses	0.5	0	0	1
μ_{s3}	Light competition: savanna trees → C_3 grasses	0.15	0	0	1
μ_{4s}	Light competition: C_4 grasses → savanna trees	0.5	0.337	0	1
μ_{44}	Light competition: C_4 grasses → C_4 grasses	0.5	0.471	0	1
μ_{43}	Light competition: C_4 grasses → C_3 grasses	0.15	1	0	1
μ_{3s}	Light competition: C_3 grasses → savanna trees	0.5	0.498	0	1
μ_{34}	Light competition: C_3 grasses → C_4 grasses	0.5	0.346	0	1
μ_{33}	Light competition: C_3 grasses → C_3 grasses	0.15	0.215	0	1

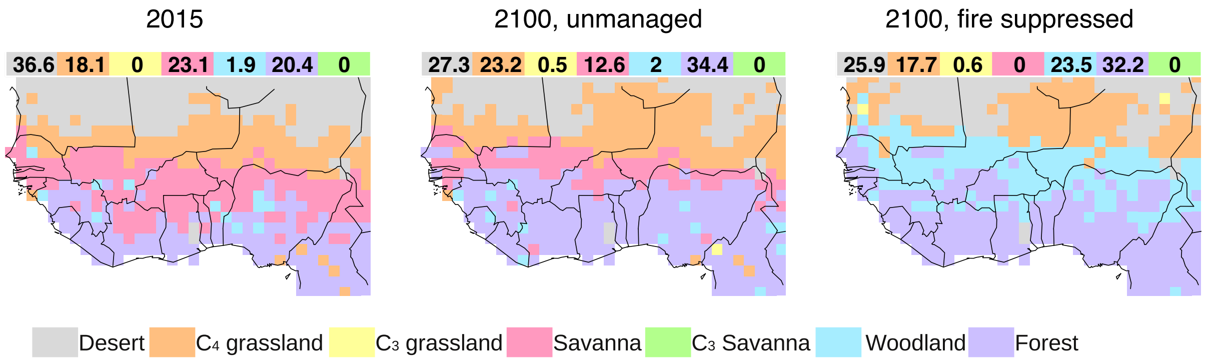

Fig. 2. Potential biome distributions in 2015 and 2100. Simulations were conducted both with natural fire regimes as projected by the aDGVM fire model and in the absence of fire. Wood cutting, grazing and fire management were not applied. Numbers in the panels indicate the percentages of cells covered by different biome types. See Supplementary Fig. S1 for biome classification scheme.

For the Tiogo and the Laba study sites in Burkina Faso, we analyzed in more detail how management influences the vegetation state. We conducted simulations analogously to the simulations for the West Africa study region, however, we investigated more management scenarios after 1992. We simulated vegetation for combinations of early dry season fire every 1, 2, . . ., 10 years, for wood cutting every 5, 10, 20 and 30 years and in the presence and absence of grazing (80 simulation runs in total). We conducted forward projections until 2100 using the IPCC (2007) A1B scenario. For each site and each scenario, we conducted 100 replicate simulations to account for stochastic processes in the aDGVM such as demography or fire. Using these model results, we plotted (1) tree biomass in the different management scenarios in 2015 and 2100 and (2) the probability of C_3-dominated vegetation states (forests or woodlands) and C_4-dominated vegetation (savannas or C_4 grasslands), as a function of time and the applied management strategy.

3. Results

The aDGVM projects that under current conditions without land use impacts, 41% of the study area would be covered by savannas and grasslands while 22% would be covered by forests and woodlands (Fig. 2). Under future conditions without land use activities, the area covered by savannas and grasslands decreases to 36% while the area covered by forests and woodlands increases to 36%. The area covered by deserts decreases by 9% as grasslands invade into these areas owing to increases in water use efficiency under elevated CO_2 concentrations. Fire has a strong impact on future biome patterns. When fire is suppressed between 1992 and 2100, the aDGVM projects that most areas covered by grasslands and savannas in the presence of fire are replaced by forests and woodlands (Fig. 2). Under future conditions and in the absence of fire, the area covered by savannas and grasslands is reduced to

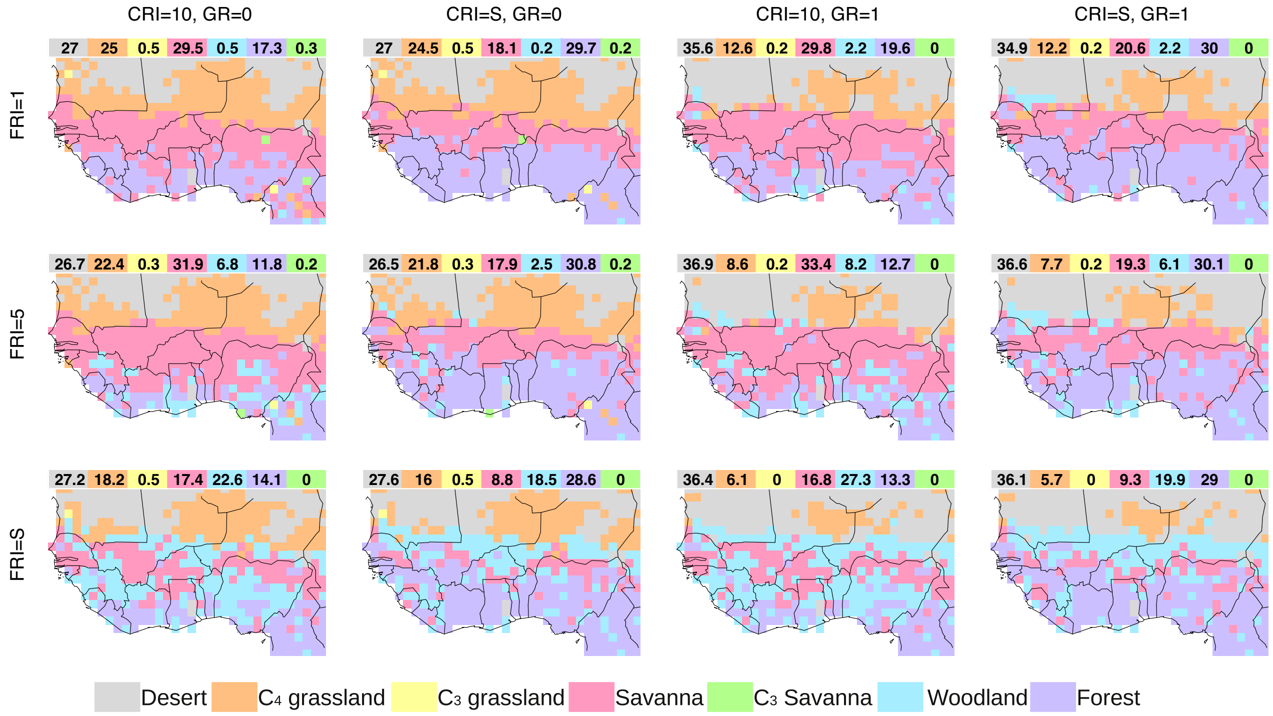

Fig. 3. Management impacts on biome distributions in 2100. Simulations were conducted with different wood cutting return intervals (CRI, years), different fire return intervals (FRI, years) and in the presence (GR = 1) and absence (GR = 0) of grazing. Management fires occur in the early dry season. 'S' indicates a scenario where fire or wood cutting were suppressed and not applied between 1992 and 2100. Numbers in the panels indicate percentages of cells covered by different biome types. Supplementary Figs. S2 and S3 show the results for all simulation scenarios described in Section 2.

only 18% whereas woodlands and forests cover 56% of the study region.

As expected, land use activities strongly affect the future vegetation patterns in West Africa (Fig. 3 and Figs. S2 and S3) and have the potential to maintain vegetation in a savanna or grassland state. Both fire and wood cutting open the landscape, promoting grasses and fire intensity and thereby savannas. For instance, in the absence of grazing, the area covered by grasslands and savannas is between 54.5% (annual fire, wood cutting every 10 years) and 46.4% (fire every 5 years, wood cutting every 20 years). In these scenarios, the area covered by woodlands and forests is 18.7% and 25.4%, respectively.

Grazing reduces grass biomass and as a result fuel biomass and fire intensity. This implies shifts in the competitive interactions between grasses and trees as well as changes in fire regimes. Both factors promote tree dominance and vegetation shifts toward more tree-dominated systems. When averaged for all fire and wood cutting scenarios considered in this study, grazing increases the area covered by forests and woodlands in 2100 by c. 10% compared to simulations without grazing, while the area covered by

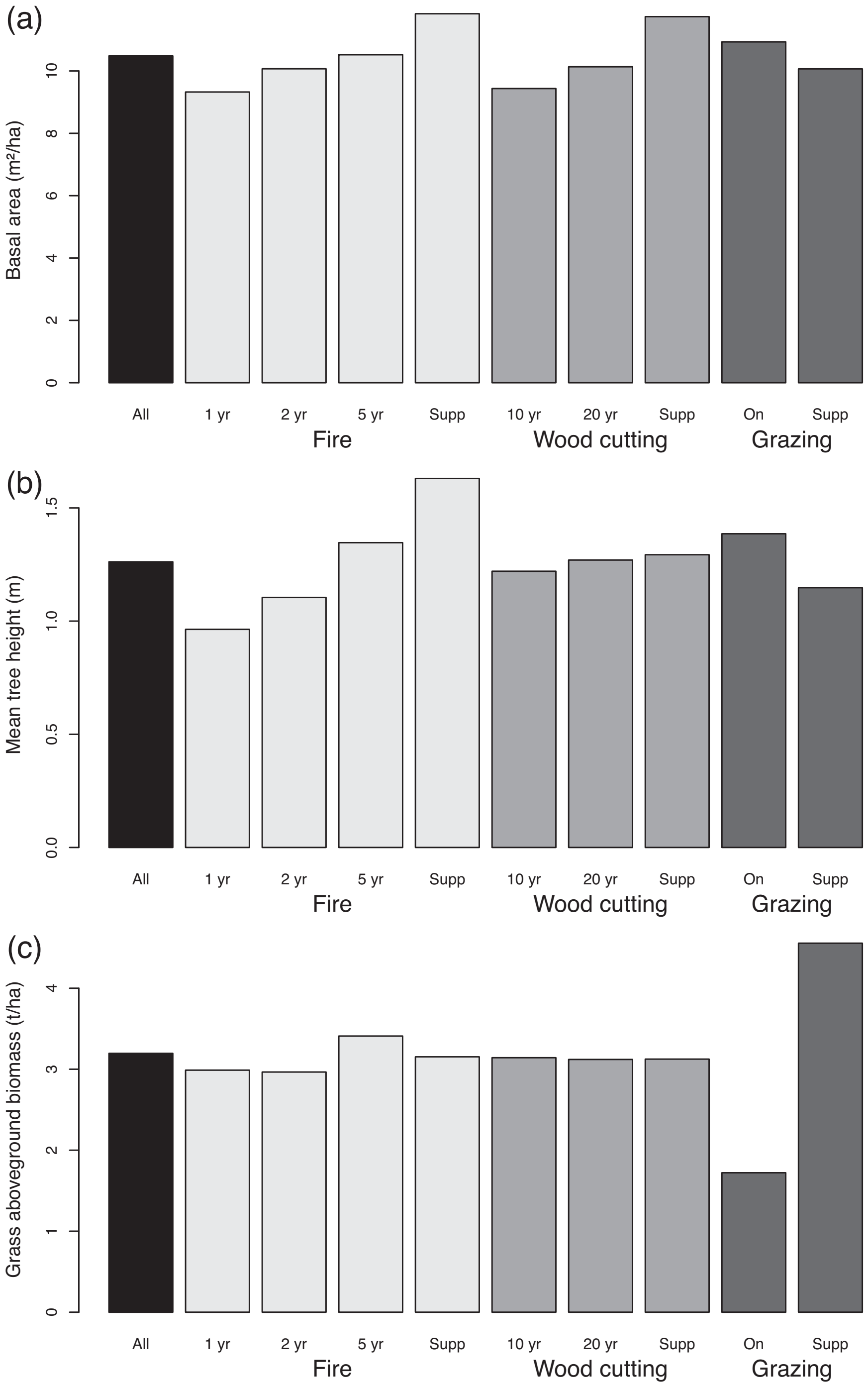

Fig. 4. Management impacts on vegetation structure in 2100. Bars show mean values of tree basal area, tree height and grass biomass for the entire study region in different treatments. Simulations were conducted with different wood cutting return intervals (CRI), different fire return intervals (FRI) and in the presence and absence of grazing. Management fires occur in the early dry season.

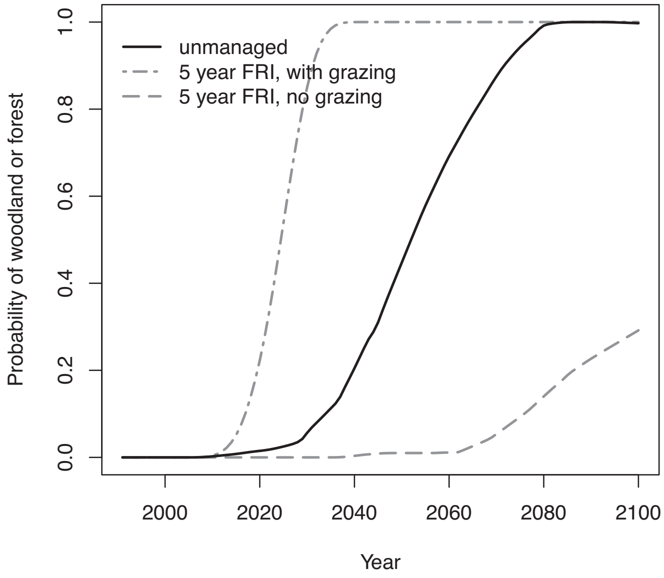

Fig. 5. Probability of woodland or forest occurrence in response to management at the Laba study site. For both simulations with and without grazing, we assumed a fire return interval of 5 years and no wood cutting. For the unmanaged scenario we assumed natural fire regimes as simulated by the aDGVM. Lines represent smoothed averages of 100 replicate simulations. See Supplementary Fig. S4 for results at the Tiogo study site.

savannas and grasslands decreases by c. 23%. Large grassland areas are degraded and transformed into bare ground by grazing.

The application of management activities not only modifies biome patterns but it also influences characteristics of vegetation structure such as basal area, mean tree height and grass biomass (Fig. 4). Basal area and mean tree height increase as the return intervals of fire and wood cutting increase. Owing to increased tree height, grass biomass is slightly reduced due to grass-tree competition. In contrast, grazing strongly reduces grass biomass and thereby promotes trees.

Managing vegetation by wood cutting, fire and grazing has a strong potential to promote (by grazing), delay or mitigate (by wood cutting and fire) anticipated shifts toward closed canopy, tree-dominated systems simulated in situations without disturbances (Fig. 5). Thus, at the Laba site, the aDGVM projects that in a situation without management, a 100% probability for forest dominance is reached in 2080 while with a five-year fire return interval and in the presence of grazers, it is reached in 2034. In a situation with a five-year fire return interval but without grazing, a 100% probability of forest dominance is not reached during the study period. The extent to which management activity influences vegetation shifts is site-specific. Vegetation dynamics at the site level are driven by the specific climate and soil conditions and these drivers influence the relative impact of management on vegetation (compare Fig. 5 and Fig. S4).

Fig. 6 shows in more detail how different management regimes modify aboveground tree biomass in 2015 and 2100 at the stand level. The aDGVM projects that in 2015 fire would lower the average biomass at the Tiogo site to between approximately 3 t/ha and 8 t/ha, depending on the fire return interval. However, the impacts of wood cutting are negligible under ambient conditions. Under future conditions, both long-term fire management and wood cutting have strong impacts on biomass, potentially reducing it to 5 t/ha. Frequent fires and frequent wood cutting reduce biomass most, maintaining it close to current levels. However, the relative effects of different management strategies and the degree to which management can influence vegetation are site-specific due to different climate or soil conditions (Fig. 5 and Fig. S4).

4. Discussion

The aDGVM projects shifts from grasslands and savannas toward woodlands and forests in the study region if vegetation is not managed by fire, wood cutting or grazing. The increase of forests and woodlands can be explained by the CO_2 fertilization effect on trees and increasing water use efficiency which, in the aDGVM, promote tree growth and thereby suppress grasses (Scheiter and Higgins, 2009; Scheiter et al., 2015). These feedback effects imply a shift toward higher tree cover. Similar vegetation shifts have been reported in previous simulations with both the aDGVM (Scheiter and Higgins, 2009; Higgins and Scheiter, 2012; Scheiter et al., 2015) and other modeling approaches (Heubes et al., 2011; Sato and Ise, 2012). Shifts toward more tree-dominated vegetation have also been observed in empirical studies and often been attributed to

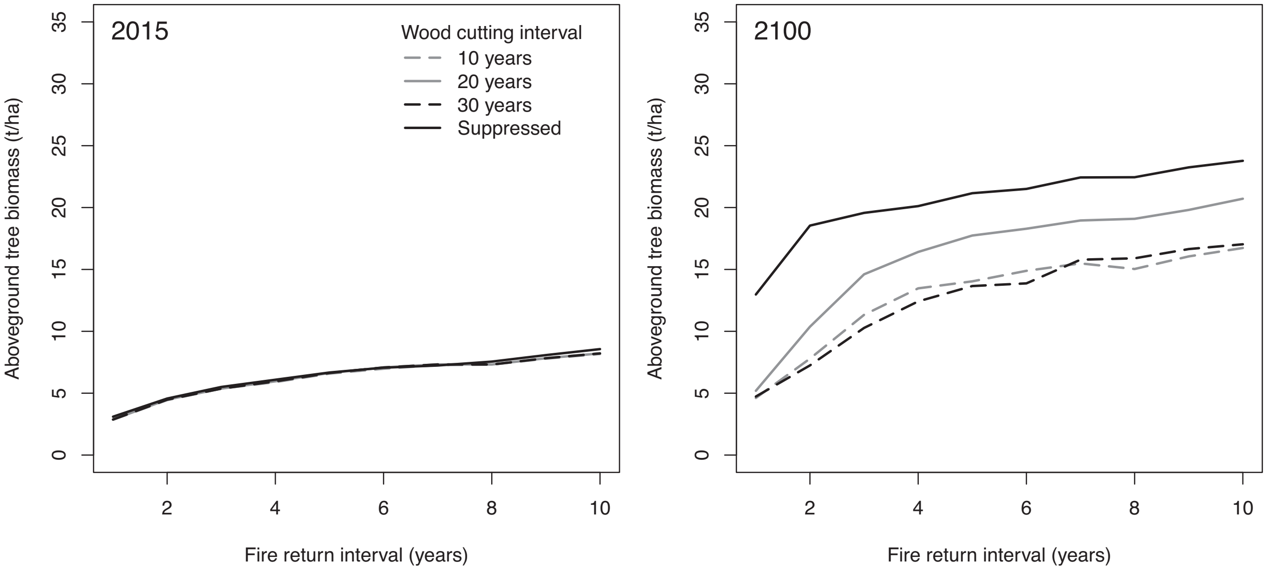

Fig. 6. Management impacts on woody biomass in 2015 and 2100 at the Tiogo study site. Lines represent the averages of 100 replicate simulations per management scenario. See Supplementary Fig. S5 for results at the Laba study site.

increasing CO_2 concentrations and CO_2 fertilization effects that favor woody vegetation over C_4 grasses (Wigley et al., 2009; Buitenwerf et al., 2012; O'Connor et al., 2014). Notably, Donohue et al. (2013) attributed a 5–10% increase in foliage cover in warm and arid environments between 1982 and 2010 to a 14% increase in atmospheric CO_2 during this period.

Our simulations indicate that land use activities can have significant impacts on vegetation patterns and need to be considered in projections of the future vegetation state (Heubes et al., 2011). By utilizing fire, wood cutting and grazing over longer periods, vegetation patterns and structure can be kept in, or transformed into, a desired state and climate change impacts on vegetation can potentially be mitigated. In the model, land use may even allow the preservation of vegetation patterns similar to those observed under ambient conditions and delay or avoid vegetation shifts toward more tree-dominated states. Management policies currently used in West Africa focus on trees and the maintenance of essential ecosystem services such as livestock production, wood production, fuel wood extraction and biodiversity (Bodart et al., 2013). The model suggests that flows of these ecosystem services can be maintained during the next decades by frequent early dry season burning, frequent wood cutting and low levels or cessation of grazing. Intentionally lighting fires early in the dry season is also beneficial as it minimizes risks of more destructive fires later in the season.

In this study, we considered static management practices over large spatial scales and showed the potentially significant impacts on vegetation. Management did not change over time and was not dynamically adjusted to the vegetation state or environmental conditions. However, in reality, adaptive management paradigms have been adopted in which actions are applied when ecological indicators exceed critical thresholds (e.g. Van Wilgen and Biggs, 2011). Management is also driven by costs and economic return of products (Börner et al., 2007). Further studies should focus on management options of single stakeholders and simulate sustainable management strategies at the local scale. To achieve this goal, DGVMs should be coupled with more complex management and optimization models that include dynamic adjustments of management strategies and technological developments (Higgins et al., 2007b; Heubes et al., 2011). Such a modeling framework could be used for more detailed and in-depth studies of management impacts under future climate conditions and inform stakeholders of the potential impacts of applying a specific management strategy.

A limitation of this study is, that it focuses on biome patterns, biomass and vegetation structure, whereas functional diversity is not represented adequately. Dynamic vegetation models typically adopt a plant functional type (PFT) approach, where species with similar form and function are aggregated (Prentice et al., 2007). Thus, aDGVM only simulates PFTs that represent savanna and forest trees as well as C_3 and C_4 grasses. However, in the context of management it might be necessary to extend DGVMs by keystone species that provide important ecosystem functions and ecosystem services (Hooper et al., 2005). Under future climate conditions, some of these species may not be able to adapt and may be outcompeted. This has severe implications as important ESS linked to these keystone species may be lost (Nano et al., 2012; Helm and Witkowski, 2012). Further, wood cutting is often selective and different species are harvested at different intensities (for example *Detarium microcarpum* Guill. & Perr., *Combretum nigricans* Lepr. ex Guill. & Perr., *Entada africana* Guill. & Perr., *Anogeissus leiocarpa* (DC.) Guill. & Perr. are commonly cut, Sawadogo et al., 2010). The aDGVM has the potential to include more PFTs or even species, and future studies could condition management on species or different PFTs and investigate how management influences ESS linked to specific keystone species. Alternatively, more complex vegetation models that include variability of traits could be used (aDGVM2, Scheiter et al., 2013; LPJmL-FIT, Sakschewski et al., 2015). These models can simulate changes in (functional) diversity and community assembly induced by changes in climate and land use. Such changes are already observed (Sala et al., 2000; Savadogo et al., 2008, 2009).

In this study, we present a framework for assessing long-term impacts of management on vegetation structure in West African savannas. In contrast to many alternative DGVMs, the aDGVM is individual-based, which allows us to link the impacts of different management activities to individual plant height. Fire, grazing and human exploitation are drivers affecting savanna ecosystems in addition to the impacts of climate variability on vegetation. Management of these disturbances has the potential to modify vegetation, maintain vegetation in a desired state and avoid shifts of vegetation toward tree-dominated or degraded systems. This result highlights, that the identification of management goals and strategies is essential for the maintenance of important ecosystem services under future climate conditions such as grass biomass for livestock or fuel wood. The model used in this study is based on common ecophysiological principles and management activities such that our approach is applicable for grass-tree systems worldwide.

Authors' contributions

SS and PS designed the study. SS conducted model simulations, analyzed the data and lead the writing. PS provided field data.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.03.022.

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