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Journal Item

How to cite:

Lehsten, Veiko; Arneth, Almut; Spessa, Allan; Thonicke, Kirsten and Moustakas, Aristides (2015). The effect of fire on tree–grass coexistence in savannas: a simulation study. *International Journal of Wildland Fire*, 25(2) pp. 137–146.

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Version: Accepted Manuscript

Link(s) to article on publisher's website:
<http://dx.doi.org/doi:10.1071/WF14205>
<http://dx.doi.org/10.1071/WF14205>

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The effect of fire on tree-grass coexistence in savannas: a simulation study

Journal:	<i>International Journal of Wildland Fire</i>
Manuscript ID:	WF14205.R1
Manuscript Type:	Research Paper
Date Submitted by the Author:	n/a
Complete List of Authors:	Lehsten, Veiko; Lund University, Department of Physical Geography and Ecosystem Science Arneth, Almut; Karlsruhe Institute of Technology, Institute of Meteorology and Climate Research Spessa, Allan; The Open University, Department Environment, Earth & Ecosystems Thonicke, Kirsten; Potsdam Institute for Climate Impact Research (PIK), Telegrafenberg A62 Moustakas, Aristides; University of London, School of Biological and Chemical Sciences
Keyword:	Biodiversity, Ecosystems: savannah, Scale: local, Fire simulation modelling, Scale: continental

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ABSTRACT

The savanna biome has the highest amount of burned area globally. While the global distribution of most biomes can be predicted successfully from climatic variables, savannas are an exception. Attempts to dynamically model the distribution of savannas, including a realistically varying tree to grass ratio are fraught with difficulties. In a simulation study using the dynamic vegetation model LPJ-GUESS we investigate the effect of fire on the tree-grass ratios as well as the biome distribution on the African continent. We performed simulations at three spatial scales: locally, at four sites inside Kruger National Park (SA); regionally, along a precipitation gradient; and for the African continent. We evaluated the model using results of a fire experiment and found that the model underestimates the effect of fires on tree cover partially. On regional scale, high frequencies were able to prevent trees from out-competing grasses in mesic regions between ca. 700 to 900 mm MAP. Across the African continent incorporation of fire improved notably the simulated distribution of the savanna biome. Our model results confirm the role of fire in determining savanna distributions, a notion that has been challenged by competing theories of tree-grass coexistence.

Abstract for TOC (50 words for a more general audience)

A dynamic vegetation model is used to assess the effect of fire on tree to grass ratios and the African savanna biome distribution. High fire frequencies were found to maintain tree grass co-existence under mesic conditions (700 to 900 mm MAP) and the incorporation of fire substantially improved continental simulations of biomes.

INTRODUCTION

Savannas cover about one eighth of the global land surface (Scholes and Archer 1997) and have important functions for terrestrial carbon cycling (Grace *et al.* 2006), biodiversity, and food production (Hirota *et al.* 2011). On the African continent, 90 percent of the population are estimated to depend on rain-fed crop production and pastoralism within the savanna biome to meet its basic food supplies (Patt *et al.* 2007).

Given its importance for supply of numerous ecosystem services, the projection of the distribution of the savanna biome, as well as related properties such as standing biomass are of high interest (Scheiter and Higgins 2009), especially when considering that climate simulations for the next century project pronounced changes to the spatiotemporal distribution of precipitation across the African continent (Schreck and Semazzi 2004; Boko *et al.* 2007). Simulations of vegetation distribution and carbon stocks are done using dynamic vegetation models (DVMs) for both current as well as projected climate. However, most DVMs (Bonan *et al.* 2003; Hickler *et al.* 2006) are known to only poorly represent processes in tree-grass systems, including resource competition and interactions with fire (Scheiter and Higgins 2009). This leads to poor performance in simulating the contemporary distribution and structure of the savanna biome in some DVM studies, which casts doubts on the ability to accurately simulate the vegetation and carbon cycle response to future climate change in the tropics.

Savannas are characterized by the co-dominance of the two life forms trees and grasses, although large savanna regions are located within a climate space warm and wet enough to support closed forests (Bond 2008). While Bond and Keeley (2005) concluded that this mismatch between actual and (climatically) potential vegetation could be explained by fire, the co-existence of trees and grasses has also been hypothesised from a number of alternative mechanisms (for a review see: Sankaran *et al.* 2004; Murphy and Bowman 2012). These can be broadly separated into competition-based and demographic hypotheses. The first suite proposes a classic niche separation, resulting in co-existence by differences in resource acquisition. Niche separation can, for example, be achieved by differences in rooting depths (the so-called 'rooting niche model', Walter 1971) and according to this theory the co-existence of trees and grasses is maintained independent of disturbances. Here trees and grasses

77 compete for water in the first soil layer where grasses outcompete trees. Trees are able to persist in the
78 system because of exclusive access to deeper water (Sankaran *et al.* 2004; but see also February and
79 Higgins 2010 who found instances where grasses also accessed deeper water).

80 The second suite of hypotheses ('demographic bottleneck models') relies on recurring disturbance
81 events to prevent trees from dominating over grasses. Grasses are considered to be favoured by fires
82 since the fires occur in the dry season when the above ground biomass of the grasses is already
83 desiccated leading to minor damage only. Contrary to the grasses, tree susceptibility to these
84 disturbances is assumed to differ depending on life-history stages. Savannas can thus be viewed as
85 transitional 'disequilibrium' systems where frequent disturbance (i.e. fire or grazing) prevents
86 reaching the stable state of tree dominance (Sankaran *et al.* 2004).

87 Apart from analyses relating vegetation and fire to each other, many studies investigated properties of
88 savanna fires (see for example Hoffmann *et al.* 2003 for the effect of fires on above ground biomass
89 and Govender *et al.* 2006 for the effect of fuel on fire intensity).

90 Definitive testing of these explanatory models can only be conducted using large field manipulation
91 experiments. But such multi-factorial experiments, comparing the effects of different mechanisms, are
92 currently lacking, although experiments have been performed testing whether a single mechanism is
93 acting (e.g. for a review of root partitioning between woody and herbaceous species see Schenk and
94 Jackson 2002).

95 Despite the attempts to explain the co-occurrence of trees and grasses in the past by single
96 mechanisms, Murphy and Bowman (2012) concluded in a review that savannas are complex systems
97 in which forest and grassland dominated vegetation can be viewed as fire mediated alternative stable
98 states. They developed a conceptual model of savanna occurrence which included fire activity, water
99 and nutrient availability and suggested that the ability of dynamic vegetation models to accurately
100 reproduce vegetation pattern should be used to validate the underlying conceptual models.

101 In this study, we aim at providing improved understanding of savanna vegetation dynamics focussing
102 at the effects of wildfires. We use a dynamic vegetation model for the African continent to assess the
103 potential effect of wildfires on the tree to grass ratio. We also investigate under which environmental
104 conditions (i.e. mean annual precipitation) wildfires are able to maintain tree grass coexistence. We

simulate vegetation dynamically along a precipitation gradient, vary the relative extent of the investigated factor, using foliar cover as diagnostic parameter for competitive ability and evaluate the performance of the model with site data from burn plots of the Kruger National Park in South Africa. To see whether the incorporation of wildfires is of relevance for the biome distribution at a continental scale, we simulate African potential vegetation with and without and wildfires using fire fractions derived from the remotely sensed MODIS MCD45 (Roy *et al.* 2008) burned area dataset.

Methods

Simulation model

We used the dynamic vegetation model LPJ-GUESS (Smith *et al.* 2001; Sitch *et al.* 2003), coupled to an extended version of the fire model SPITFIRE (Thonicke *et al.* 2010) with the modifications described in Lehsten *et al.* (2009). LPJ-GUESS is applied as a gap-model (Smith *et al.* 2001), simulating the competition of different age cohorts of a number of plant functional types (PFTs) for light and water within a number of repeatedly simulated patches. Stomatal conductance which is linked to photosynthesis and availability of water and light is calculated separately for each age cohort. The age cohorts differ in growth characteristics as well as in their susceptibility to fire. This allows simulating size-specific fire effects on vegetation since the fire effect is estimated by the ratio between the flame height and the tree height, which can lead to a dynamic, fire-dependent age distribution of trees. Fire effects on vegetation also depend on the susceptibility of the plant type to fire and on the fireline intensity. Fireline intensity is calculated based on the equation developed by Byram (1959) which multiplies the caloric heat content (reduced depending on the fuel moisture), the weight of the fuel consumed and the rate of spread (which depends on the wind speed reduced by the roughness of the vegetation following the equations by Rothermel (1972)). These fire equations are in use in a large number of contemporary fire behavior models. Flame height is calculated following Peterson and Ryan (1986) as the product of a plant functional type parameter multiplied with the fireline intensity to the power of 0.667. Details on this calculation are given in Thonicke *et al.* (2010).

Fire properties are calculated depending on the fuel quality (type, moisture), fuel quantity (calculated by LPJ-GUESS-SPITFIRE) and the climate (which is read in). Trees can either be damaged by the fire, resulting in a loss of biomass (esp. leaves), or they can be killed. If a tree is killed by a fire, all biomass which has not been burned (above and below ground) is transferred to the litter carbon pool. All individuals establish from seeds, re-sprouting is not implemented in the model. For each simulated grid cell a number of replicate patches are simulated (see below) and the results are averaged to account for stochastic effects of senescence and establishment or fire events. Re-establishment of trees can occur once per year and depends only on the amount of light reaching the ground. For the simulation experiments performed in this study we additionally include a modified water uptake routine for trees which scales root water uptake exponentially with an exponent of 0.6 compared to the exponent of unity in the standard water uptake routine of LPJ-GUESS (Sitch *et al.* 2003). This increases water uptake under dry conditions, since initial runs (data not shown) have shown that the standard water uptake routine as in Sitch *et al.* (2003), and Gerten *et al.* (2004) underestimated tree biomass in seasonally dry areas. Grasses retain the original linear water uptake scheme. All parameter settings of the plant functional types in the simulations are similar to Lehsten *et al.* (2009), except for the additional plant functional type ‘shrub’. This PFT retains all plant specific parameters from the tropical broad leaved raingreen tree PFT (Sitch *et al.* 2003) but with changes in two allometric parameters: the linear factor in the height – diameter relationship (Sitch *et al.*, 2003) was set to one eighth of the value used for trees and the maximum crown diameter was set to 10 m² (compared to 27 m² used for trees; Sitch *et al.*, 2003). These settings result in a PFT with considerably lower total height and stem diameter compared to the PFT tropical broadleaved raingreen tree, but retains all other characteristics such as phenology or root distribution from this PFT. This plant type has a considerably higher chance of being killed by a fire, caused by its lower height, though moist fuels or low fuel loads can lead to flame heights below the height of the shrub and hence allow the shrub to survive a low intensity fire. Additionally to the changes mentioned above, phenology has been adapted to assure that the leaves are shed in the beginning of the dry season and not at the end of the calendar year as in the original LPJ-GUESS version (for details see Lehsten *et al.* 2009).

Climate data

All simulations were performed at a 1 degree grid scale applying daily values for temperature and precipitation from NCEP (Kalnay *et al.* 1996) for the period 1980 to 2007 with precipitation values corrected using precipitation data from TRMM (re-gridded to one degree resolution). The ratio between the annual precipitations recorded by TRMM and NCEP was calculated from the period in which the respective series overlapped, and this was used to correct the precipitation values from NCEP for the whole time span (for details on data generation see Weber *et al.*, 2009). Model spin up (i.e. simulation time to allow stabilising the carbon pools and vegetation) was performed for a period of 1000 years repeating the available 27 years of climate data, at a constant atmospheric CO₂ concentration of 341 ppm. Soil texture data were similar to the one used in Sitch *et al.* (2003), based on the FAO dataset (FAO 1991), atmospheric CO₂ concentration in the transient simulation increased up to 384 ppm according to the measurements at (www.esrl.noaa.gov/gmd/ccgg/trends/).

Patch scale general model setup

We simulated a number of replicates for each grid cell, accounting for the stochastic elements in some process-descriptions in LPJ-GUESS-SPITFIRE, especially in the simulation of growth dynamics and wildfires. At continental scale, 200 replicates were calculated for each simulated location (each replicate is equivalent to a size of approximately 1000 m² Smith *et al.*(2001)). The number of simulated patches was increased to 500 for the detailed study of changes in tree to grass ratio along the latitudinal and precipitation gradient. Since we aimed to elucidate the influence of fire frequency on the tree to grass ratio, the application region, chosen to follow the eastern 20 degree meridian from 5 to 15 degrees north, covered a transect with pronounced environmental differences. Along this transect, mean annual precipitation decreases approximately linearly. Fractional cover for trees and grasses was simulated in response to artificially prescribed fire return intervals.

Patch scale simulations

We artificially prescribed fire frequency along a precipitation gradient from 100 to 1400 mm annually (MAP), spaced over approximately 1100 km (Fig. 1). This allows assessing the main effects of fire on

vegetation, without it being confounded by other factors. We prescribed a burning probability corresponding to a fire return interval of 1, 2, 4, 8, 16 and ∞ years. While the average fire return interval of evergreen tropical forest was estimated to be around 500 years, the fire regime in African savannas may cover the full range from more than 1000 years (virtually no fire) to annual fire according to Scholes *et al.* (1996). For our simulation experiment, fire is simulated to occur on December 15, coinciding with the peak of the seasonal distribution of burned area in northern hemisphere sub-Saharan Africa (Fig. 2) identified from MODIS MCD45A1 data (Roy, *et al.* 2008; <http://modis-fire.umd.edu/MCD45A1.asp>).

Tree cover data from experimental plots

Data were collected in the Kruger National Park (KNP), South Africa between February and March 2010. The park is situated in the savannas of north-eastern South Africa, and covers an area of $\sim 19,633 \text{ km}^2$. The vegetation in the park is mainly characterized by dense savanna dominated by *Acacia* and *Combretum* species. Within the park there are long-term Experimental Burning Plots (EBPs) where fire is manipulated as a treatment since more than 50 years and thus KNP is an ideal environment for comparing fire effects on vegetation (Govender *et al.* 2006; Higgins *et al.* 2007). Each replicate plot consists of different experimental burning treatments as well as a control treatment (no fire) and each treatment is implemented in a 7-ha plot in a split-plot randomized design (see Fig. 2a in Moustakas 2015). The burning treatments include several experiments manipulating fire return interval (burning every 1, 2, 3, 4, and 6 year) as well as fire seasonality. We have used annual burning every August which is the dry season and the control treatment that excludes fire. We have decided against using the 3, 4, and 6 year burning treatments since we were not able to obtain tree cover estimates for the 4 year burning and our simulations did not contain burning every 3 or every 6 years. Tree cover data were collected in 2009 at the sites: Mopani (496 mm MAP), Satara (544 mm MAP), Skukuza (550 mm MAP) and Pretoriuskop (737mm MAP). The fractional tree cover was estimated using the Kendall-Moran algorithm (KM2P; Kendal and Moran 1963). The KM2P algorithm estimates tree cover based upon the distance to the second nearest neighbours of each tree. The KM2P was ranked amongst the best estimating methods of plant cover when sample size was around 25 focal

trees (White *et al.* 2008) which was the case in each plot. These data were not intended to be used as a quantitative model evaluation at site scale, but as a visualisation of how well the model performs compared to site data. The reasons why we did not perform a proper model evaluation are that this would have required site specific climate data over several decades to configure its spin-up and transient simulations which were not available.

Continental scale simulations

We simulated vegetation at the African continent in response to presence and absence of wildfires. In the first simulation, burnt area was prescribed from the MODIS burned area product MCD45A1 (Roy, *et al.* 2008), which lists the fire date using 500*500m pixels, while the fire effects on vegetation were dynamically calculated by LPJ-GUESS-SPITFIRE (depending on fuel load, dryness, and total height and fire susceptibility of the plant type). The proportion of burned area per one-degree grid cell was prescribed, using an average daily probability of burning derived from the MODIS data. This was done under the assumption that MODIS pixels that could not be classified, e.g. due to cloud cover, had a similar burning frequency as the remaining pixels within the one degree cell. Since the burned area is likely to be underestimated by current remote sensing products (Roy, *et al.* 2008) we chose quality level four which represent the highest detection rate, noting that this quality level also has highest rate of commission errors (i.e. rate of areas being erroneously detected as burned). The daily varying proportion of burned area was subsequently transformed into a daily varying burning probability for each simulated patch. Further details on the implementation and effects of fire on the vegetation are provided in Lehsten *et al.* (2009).

Vegetation data

We compared simulated vegetation distribution with and without wildfires to the map of potential vegetation by Ramankutty and Foley (1999) that was derived on the basis of the 1km global satellite based DISCover land cover dataset (Loveland and Belward 1997). In contrast to Ramankutty and Foley (1999) who differentiated between savannas and tropical deciduous forest, we combined these classes into a single class 'savanna' because both classes seem to have a similar relationship to

wildfires (i.e. do not differ in their typical fire frequency) which leads to a fine-scaled mixture of both biomes in the southern hemisphere of Africa (Ratnam *et al.* 2011). After re-gridding the potential vegetation map to a one degree scale, the distribution of savanna and tropical deciduous forest exert a more or less random rather than an environmentally determined pattern. We therefore differentiate only rainforest, savanna, open shrubland, dense shrubland, grassland and desert (Fig. 5). The simulated mixture of plant functional types per grid-cell was converted into biome types applying the classification scheme of Hickler *et al.* (2006), adopted to match the potential vegetation classes for the African continent (Tab. 1). Comparison between our simulated and the mapped potential vegetation of Ramankutty and Foley (1999) was performed using the Kappa statistic, developed especially for the purpose of comparing vegetation maps (Monserud and Leemans 1992). Kappa values range between zero and one. Values below 0.05 indicate no; 0.05 – 0.20 very poor; 0.2 – 0.4 poor; 0.4 – 0.55 fair; 0.55 – 0.7 good; and 0.7 – 0.85 very good agreement (Monserud and Leemans 1992). We calculated the Kappa statistic for each vegetation class as well as a global Kappa statistic combining all vegetation types.

Results

Effects of fire on tree to grass ratio

Prescribing fire along the precipitation gradient did not affect the dominance of trees at the wet, and grasses at the dry end (Fig. 3). However, in regions between MAP of around 600 to 900 mm, fire prevented trees and shrubs from out-competing grasses, but only when the prescribed fire return interval was around eight years, or less. In these ‘mid-mesic’ regions, trees and grasses co-dominated at variable ratios depending on fire return interval. When fire was excluded, grasses reached a maximum cover of 0.4; while at frequent fire return intervals (e.g. annual fires) the maximum grass cover simulated by LPJ-GUESS-SPITFIRE was up to 0.7 (Fig. 3).

Experimental tree cover data versus simulated tree cover data

To confront model outputs with observed data we plotted the tree cover percentage under annual burning, biennial burning and no burning aside the field data derived from the experimental burning plots from the Kruger National Park (Fig. 4). Results show that tree cover for the burned plots is underestimated by the model, while at unburned plots the simulated tree cover is in the range indicated by the experimental data. They also show that fire is having an clear effect on tree cover starting at ca 540 mm MAP (Mopani, Satara and Skukuza) while at Pretoriuskop the tree cover values are in a relatively small range (though the highest value is found in the unburned plot and the lowest in the annually burned plot in Pretoriuskop).

Vegetation-fire interactions on continental scale

Excluding fire in an African-continental scale simulation resulted in a notable expansion of the equatorial rainforest belt towards the northern and southern direction, emergence of tropical evergreen plant functional types along the continent's south-east coastal regions and across the island of Madagascar (Fig. 5), compared to simulations that had fire prescribed. While the expansion of tropical rainforest vegetation was at the expense of savannas, the extension and location of shrublands was unaffected by the presence of fire. The Kappa-statistic for the comparison of the potential vegetation of Ramankutty and Foley (1999) to our simulations (Table 2) improved notably for the 'fire present' case, both for the vegetation classes 'tropical evergreen forest' and 'deciduous forest / savanna', as well as for the overall total.

Discussion

The predominant factors controlling the co-existence of trees and grasses in savanna ecosystems have been of longstanding interest to ecological research (for a reiview see: Sankaran *et al.* 2004; Murphy and Bowman 2012). A number of hypotheses, including resources acquisition and demographic bottleneck models, have been put forward to explain observed vegetation patterns in savannas but as yet, no conclusive multi-factorial model that applies to all savanna environments has emerged. Our simulation study aims to contribute to efforts to develop such a general model, by investigating the role of wildfires in savanna vegetation dynamics.

A synthesis of tree cover for 854 savanna locations in Africa identified a strong effect of MAP on the tree to grass ratio (Sankaran *et al.* 2005). Soil physical properties that determine the water storage capacity are an additional key factor closely related to rainfall and that needs to be considered for a more process-based interpretation of a relationship between canopy structure and MAP (Sankaran *et al.* 2005). This data can be interpreted in terms of envelope functions that set an upper limit (*sensu* Sankaran *et al.*, 2005) or in terms of a sigmoidal function through the bulk of the data (Bucini and Hanan 2007). For both analyses it was argued that disturbance may play an important additional role to determine savanna vegetation structure atop the climatic effects, although Sankaran *et al.* (2005) could not detect a consistent response to herbivory. Regarding the role of soil and nutrients, in a meta-analysis of several datasets examining tree-grass interactions across precipitation gradients in savannas it was found that soil and plant nutrient ratios did not change along with precipitation (Dohn *et al.* 2013). Further, soil properties were not notably influential in determining tree-grass interactions at the Kruger National Park sites where our field data were collected in the absence of fire (Moustakas *et al.* 2013).

Based on extensive empirical data, Sankaran *et al.* (2004) predicted that a sigmoidal increasing woody cover with increasing MAP in the absence of fire or other disturbances should be transformed into a more linear (i.e. gradual) increase of woody cover with MAP if disturbances like fire are taken into account as per the ‘demographic bottleneck model’. Driving LPJ-GUESS-SPITFIRE with typically observed fire frequencies of between 3 to 8 years (Tansey *et al.* 2008), our simulations resulted in a fractional tree cover along the precipitation gradient that more closely resembles a linear relationship between tree cover and MAP, lending further support to the ‘demographic bottleneck model’.

The main assumption of the ‘demographic bottleneck model’ is that different species groups and age classes of trees differ in their susceptibility to disturbances such as fire. Fire mortality of mature trees in savannas and tropical forests is generally determined by bark thickness, which in turn is related to stem diameter and species groups (Hoffmann *et al.* 2012). The long history of fires in tropical savannas has led to a variety of adaptations to fire (Bond and Keeley 2005) resulting in high resistance against cambial damage of typical savanna trees, while evergreen trees are known to have a very low resistance against cambial damage, resulting in a strong disadvantage in fire prone sites. However,

top-kill still results in a high mortality regardless of the tree type. This determines the land use practice of frequent burns of at least every 2-3 years in national parks and tree plantations to minimize the risk of intensive fire by preventing fuel accumulation (Saarnak 2001).

Rainforest trees have comparatively thinner bark compared with savannah trees. Seedlings, having low stem height are most susceptible to fire damage since their crowns are located within the flame height. Older, tall tropical broad-leaved raingreen trees have low direct or post-fire mortality, which depends mainly on the amount of crown scorching. These fire effects are especially pronounced in the mid-mesic range. At sites with high precipitation, fire intensity is very low due to the wet conditions, and any effect of fires on established trees is compensated by rapid post-fire tree re-growth in our simulations. By contrast, at very dry sites, establishment of trees is prevented by soil water shortage, rather than by fire disturbance. At these sites, the effect of fire disturbance is already comparably low due to low grass productivity and thereby low fuel loads. Recently, several empirical-based studies have demonstrated that tree cover-fire feedbacks are critical for maintaining forest and savannah boundaries (Sankaran *et al.* 2004; Lehmann *et al.* 2011; Hoffmann *et al.* 2012; Murphy and Bowman 2012). In essence, the interaction between tree growth rates and fire frequency limits forest development. Hence, canopy closure will be favoured by any factor that increases growth (e.g. elevated availability of water or in some cases also nutrients), or decreases fire frequency.

In an analysis by Scheiter and Higgins (2009) the combination of a simplified DVM with a dynamic fire model that relied solely on fuel load, fuel moisture and wind speed yielded a much larger area influenced by fires compared to studies based on remote sensing data. While the knowledge and understanding of the drivers of fire is improving (Archibald *et al.* 2009, 2010) these drivers are complex and far from well understood. Saarnak (2001) estimates the number of natural ignitions to be currently below one percent. Several studies have linked fire occurrence and climatic variables (e.g. Lehsten *et al.* 2010; Lehmann *et al.* 2011) demonstrating that the human decision process leading to the fire application is driven at least partially by climatically determined factors. Regions differ in their culture of how to apply fires. To cover these variances, a complex model of human application of fires would be required which would introduce a considerable amount of additional uncertainty.

Hence we decided to prescribe remotely-sensed fire as an input to the LPJ-GUESS-SPITFIRE model in this study, which allowed us to focus on the influence of fire on recent vegetation without potentially confounding effects of simulated fire activity uncertainties.

When comparing the experimental data and the simulation results, local-scale heterogeneity (all plots cover around 7 ha) induced by local conditions such as soils and grazing will not be covered at DVM-scales. Based on the model results with annual fire frequency, Skukuza and Satara would be classified as grasslands, having a woody leaf area index of below 0.5. Vegetation at the third experimental site would be classified as savanna, since tropical broadleaf raingreen trees dominate in the simulations. Our simulations in which annual burning led to tree cover being too low compared to experimental data indicates that the post-fire survival rates of young trees is too low in the model where one year old trees are not above the flame escape height and hence are killed with a high probability. At higher precipitation levels, fires are less intense due to higher fuel moistures, thereby allowing more trees to survive due to less intense fires (which result in lower flame height). The experimental results suggest a possible improvement to the model, while for the purpose of classifying biomes at continental scale this seems not to be important because an annual fire frequency is rarely detected at a spatial resolution of one degree.

Though our simulation results were strongly improved by the incorporation of fire in the model, our results (notably at the patch scale) are contradicting the result of Staver *et al.* (2011) who show that fire only influences tree cover above a precipitation level of 1000mm MAP while in our simulation significant effects are starting at 400mm MAP. When plotting continental scale tree cover and MAP in burned and unburned conditions many other factors might be influencing the fire regime, for example grazing, differences in seasonality or soil conditions. This has potentially led to the large variability in the tree cover of the analysis of (Staver *et al.* 2011). Since the experimental data shows a significant effect even at the lowest MAP level of 550 mm this shows that more research is needed to identify how fires and vegetation are linked to other factors (e.g. grazing and soils). Another continental scale analysis (Lehmann *et al.* 2011) showed that savannas are present up to precipitations well above the precipitation level which prevents grasses from persisting even at high fire frequencies. The reason for the underestimation of the effect of fires at high precipitations in our simulation is that we

use a daily average burning probability and even slight differences in the timing of the seasons can lead to fires occurring at wet days which will have only limited effects on the vegetation. While climate data is currently available for a century, only slightly more than a decade of remotely sensed burned area has been recorded (at sufficiently high resolution). Since it is necessary to use the full time series of climate data to meaningfully run LPJ-GUESS-SPITFIRE we decided to transform the burned area data into a probability of burning only related to the day of the year to be able to prescribe fire over the whole simulation. Although not included here, effects similar to fire may also be caused by herbivory which also acts as size-selective population harvesting. In the Eastern Cape region (South Africa), Trollope (1974) showed experimentally that a combination of fire and grazing is required to keep the landscape open, since the burned bushes suffered a severe damage of the stems, but coppiced from the base of the system. Only light grazing by goats prevented a fast shrub encroachment in the area. Staver *et al.* (2012) also showed that grazing and fire and herbivory can form a single trait off axis. Acacia saplings showed a continuum of adaptations responding to herbivory and fire and the species occurrence depended upon both. Our study aimed to show that the simulation of biome distributions are markedly improved by incorporating wildfire which was achieved even without the incorporation of herbivory. The incorporation of additional processes such as re-sprouting and herbivory might improve the models ability to predict vegetation, especially if applied at a fine scale. Yet, it also requires the parameterisation of the additional processes and in the case of the incorporation of herbivory a reliable spatio-temporal dataset of grazing pressure including both wild animals as well as livestock. Such a dataset is, to the knowledge of the authors, currently not available for simulations at continental scale. Additional anecdotal evidence that fire is crucial to maintain an open landscape even in the presence of large densities of herbivores comes from most national parks in African savannas where artificially maintained burning regimes are necessary to prevent shrub encroachment and to support grass growth for livestock herbivory (Saarnak 2001). Browsing densities can be considered relatively high in these parks since the visibility of game for tourists is the economic basis of most parks, thus herbivory alone seems not sufficient to maintain the *status quo*.

All simulations performed in this study include differences in phenology between trees and grasses. Some models suggest that these differences alone can maintain co-existence of trees and grasses ('phenological niche separation model' *versus* Sala *et al.*, 1997). However, since the simulations without wildfires resulted in a poor agreement between simulated and observed biome distribution for the savanna biome, we have no indication that this is the case.

A strong sensitivity of African biome distribution in response to fire (similarly to our study) was also demonstrated by Bond *et al.* (2005) applying the Sheffield Dynamic Vegetation Model without fire and comparing it to satellite derived vegetation data.

Still, considerable differences remain between the simulated and mapped potential vegetation in case of open and dense shrublands and grasslands. These vegetation classes occur at a very narrow range of low MAP, limited to a thin band along the Mediterranean, the southern and northern edge of the Sahara desert, next to the Kalahari Desert, and at the horn of Africa. For these biomes, successful representation by vegetation models has to rely not only on the correct representation of growth processes but equally so on the availability of high resolution rainfall data and soil physical parameters to match the exact geographic location. Our simulations were based on adjusted NCEP reanalysis data (Kalnay *et al.*, 1996; for details see Weber *et al.*, 2009). Although this climate input data had a spatial resolution of one degree, it was generated in parts from coarser resolution raw data that requires spatial interpolation for the reanalysis. Visual inspection of the vegetation maps shown in Figure 4 indicates the presence of simulated shrublands and grasslands in regions close (but not identical) to those identified by Ramankutty and Foley (1999). This spatial mismatch may, at least in parts, result from imprecision in the precipitation input. The Kappa statistic only provides a measure of how many cells of similar vegetation type are exactly at the same position in different maps. Similar cells in close proximity are identified as mismatch, which leads to the low values for the simulated grasslands and shrublands.

Conclusion

Through incorporation of fire into a dynamic vegetation model the simulation of the distribution of biomes on the African continent was markedly improved. Our work supports data-based predictions that the tree to grass ratio in tropical savannas depends strongly on the fire frequency (following the

‘demographic bottleneck model’) especially in the mid-mesic climate space. Though there is abundant evidence that a multitude of disturbances including grazing and climatic variability influences vegetation structure, we have shown that the sole application of typical fire frequencies to drive vegetation simulations was sufficient to generate realistic vegetation pattern at a continental scale. Further improvement of simulation results will require higher resolved climate and soil data, especially for the precise simulation of locations of grassland and shrubland biomes, as well as accounting for landscape management, for example, grazing and agriculture.

Acknowledgements

This study was supported by the European Commission within the sixth Framework Program under the project CarboAfrica (contract nr: 037132). We would like to thank Ulrich Weber for providing parts of the climate data.

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595 Table 1. Classification scheme for the simulated maps of plant functional types, adopted from Hickler
 596 *et al.* (2006), all values are maximum annual LAI values.

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Biome	Classification	Dominant PFT
Tropical rain forest	Tree LAI >2.5	Tropical broadleaved raingreen
Savanna / trop. deciduous forest	0.5 < Tree LAI >2.5	Tropical broadleaved raingreen tree or shrub
Grassland / steppe	Tree LAI <0.5 and Grass LAI >0.2	
Dense shrubland	Shrub LAI > 1.5	Shrub
Open shrubland	Shrub LAI < 1.5	Shrub
Desert	Total LAI < 0.2	

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599 Table 2. Kappa statistic of agreement between the simulated biomes to the biomes mapped by
600 Ramankutty and Foley (1999).

Biome	Kappa	Kappa
	without fire	with fire
Tropical rain forest	0.49	0.67
Savanna / tropical deciduous forest	0.46	0.71
Grassland / Steppe	0.15	0.15
Dense Shrubland	0.23	0.23
Open Shrubland	0.12	0.11
Desert	0.86	0.86
Total	0.53	0.64

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Figure 1. Continental and latitudinal mean annual precipitation.
 Left panel: mean annual precipitation, derived from adjusted NCEP and locations of the simulated latitudinal gradient. Right panel: mean annual precipitation over the simulated latitudinal gradient.
 96x55mm (300 x 300 DPI)

Figure 2. Average monthly burned area over the years 2000–2007 of the African continent derived from the MODIS MCD45 remotely sensed data. The error bars indicate one standard deviation.
70x26mm (300 x 300 DPI)

Figure 3. Stand scale analysis: Cover ratio of grasses (panel a) and trees (panel b) along the 20° meridian from 5° to 15° north. The precipitation decreases along the gradient linearly from 1400 to 100 mm mean annual precipitation (see Fig. 1). Simulation results with varying fire return interval. The cover is shown as absolute ratio ranging from 0 to 1.

131x188mm (300 x 300 DPI)

Figure 4. Simulated experimental and tree cover
The circles are the experimental data collected at Kruger National Park (4 plots per site and fire frequency)
and the lines with error bars show the simulated results. The error bars indicate one standard deviation.
Different colours indicate different fire frequencies.
279x361mm (300 x 300 DPI)

Upper right panel: Annual ratio of burned area at a one degree spatial resolution as detected by MODIS MCD 45. Remaining panels: biome classification: Upper left: biome distribution according to Ramankutty and Foley (2006). The lower panels displays the biome distribution as simulated with LPJ-GUESS SPITFIRE, lower left panel with fire and lower right panel without fire.
185x173mm (300 x 300 DPI)