

**Forests, savannas
and grasslands:
bridging the gap
between ecology and
DGVMs**

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Forests, savannas and grasslands: bridging the knowledge gap between ecology and Dynamic Global Vegetation Models

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The forest, savanna, and grassland biomes, and the transitions between them, are expected to undergo major changes in the future, due to global climate change. Dynamic Global Vegetation Models (DGVMs) are very useful to understand vegetation dynamics under present climate, and to predict its changes under future conditions. However, several DGVMs display high uncertainty in predicting vegetation in tropical areas. Here we perform a comparative analysis of three different DGVMs (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM) with regard to their representation of the ecological mechanisms and feedbacks that determine the forest, savanna and grassland biomes, in an attempt to bridge the knowledge gap between ecology and global modelling. Model outcomes, obtained including different mechanisms, are compared to observed tree cover along a mean annual precipitation gradient in Africa. Through these comparisons, and by drawing on the large number of recent studies that have delivered new insights into the ecology of tropical ecosystems in general, and of savannas in particular, we identify two main mechanisms that need an improved representation in the DGVMs. The first mechanism includes water limitation to tree growth, and tree-grass competition for water, which are key factors in determining savanna presence in arid and semi-arid areas. The second is a grass-fire feedback, which maintains both forest and savanna occurrences in mesic areas. Grasses constitute the majority of the fuel load, and at the same time benefit from the openness of the landscape after fires, since they recover faster than trees. Additionally, these two mechanisms are better represented when the models also include tree life stages (adults and seedlings), and distinguish between fire-prone and shade-tolerant savanna trees, and fire-resistant and shade-intolerant forest trees. Including these basic elements could improve the predictive ability of the DGVMs, not only under current climate conditions but also and especially under future scenarios.

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1 Introduction

Savannas cover about a fifth of the Earth land surface, and have wide socioeconomic importance regarding land use and biodiversity (Scholes, 2003). Savannas are the central biome in the transition between grasslands and forests, and they are characterized by the coexistence of two types of vegetation: trees (i.e. woody vegetation), and grasses (i.e. grasses and herbs). In most of the savanna ecosystems, we observe highly shade intolerant and fire tolerant C_4 grasses and C_3 trees. This savanna definition is generally valid, with the exception of a few regions (e.g. the Neotropical cerrado where C_3 grasses dominate, see Lloyd et al., 2008; Ratnam et al., 2011). For a long time ecologists have been fascinated by savannas, because trees and grasses coexist, while competing mainly for the same resource, namely water, which is the main limiting factor (Sankaran et al., 2004; Scholes and Archer, 1997; Walter, 1971). Classical ecological theory, such as the competitive exclusion principle, predicts that only one vegetation type can survive in these conditions (Hutchinson, 1961; Tilman, 1982). To solve this conundrum, numerous experimental and modeling studies explored the nature of tree-grass competition and coexistence (e.g. Higgins et al., 2000; House et al., 2003; Sankaran et al., 2004; Scholes and Walker, 1993; Walker and Noy-Meir, 1982). Grasses can outcompete trees in the driest environments, where tree growth is water-limited (Higgins et al., 2012), and they have a particularly strong competitive effect on tree seedlings, as grasses and tree seedlings compete for water in the same surface layer (Baudena et al., 2010; Bond, 2008; February et al., 2013; Sankaran et al., 2004; Wakeling et al., 2011; Yin et al., 2014b). In less arid conditions, however, adult trees can potentially grow deeper roots and reach deeper water than grasses (Kulmatiski and Beard, 2013; Walter, 1971; Ward et al., 2013), although overlap between grass and tree roots can be high in some savannas (e.g. February and Higgins, 2010; Higgins et al., 2000; House et al., 2003).

In addition to water availability, fire is an important driver of tree-grass dynamics. C_4 grass biomass enhances fire spread in open ecosystems, due to its high flammability.

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At the same time, grasses benefit from fire because they recover faster than trees, and profit of the open spaces after fire, thus originating a positive feedback mechanism that enhances savanna presence (as shown by e.g. long term fire-exclusion experiments, Higgins et al., 2007, or model studies, e.g. Higgins et al., 2008; van Langevelde et al., 2003; see also Hoffmann et al., 2012). Fires may also limit tree seedling recruitment and growth, thus reducing tree dominance further (e.g. Hanan et al., 2008; Higgins et al., 2000). This grass-fire feedback is characteristic of tropical savannas and grasslands, while in most of the other biomes woody species produce most fuel for fires (e.g. boreal forests, Bonan and Shugart, 1989). Fire is essential to savanna persistence in wetter areas, which would be forested otherwise. In contrast to savanna trees and grasses, forest trees are fire prone and shade tolerant, adapted to persist in conditions of low light availability and in absence of fire (Ratnam et al., 2011; Rossatto et al., 2009). Thus, when fires are absent and water supply is sufficient, forest trees outcompete grasses and savanna trees because of light limitation, while if fires are active, savanna trees persist but fires limit their cover, keeping savannas open (Hoffmann et al., 2012), thus possibly leading to bistability of forest and savanna in mesic regions (e.g. van Nes et al., 2014; Staver and Levin, 2012).

Savannas are expected to undergo major changes in the future due to increasing temperature and CO₂ concentration, modified rainfall patterns, and subsequently changed variability in fire regimes (IPCC, 2007). In recent years, an increase in woody cover has been observed in savannas all over the world (e.g. Bowman et al., 2010; Buitenwerf et al., 2012; Donohue et al., 2013; Ward, 2009; Wigley et al., 2010). Several studies tried to explain wood expansion by overgrazing or decreasing fire frequency, which would enhance grass mortality and thus favor woody vegetation (Scholes and Archer, 1997). However, CO₂ increase is probably one of the main causes of woody encroachment, leading to savanna expansions. As water use efficiency increases with CO₂ (e.g. de Boer et al., 2011), thus decreasing the water need for grow, increased CO₂ concentration leads to a shift in tree-grass competition for water, possibly favoring C₃ trees over C₄ grasses (Bond and Midgley, 2000; Bowman et al., 2010; Kgope et al.,

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2010; Polley et al., 1994; Wigley et al., 2010). In African savannas, paleo-ecological evidence of the last glacial period, as well as observations of the last 50–100 years, suggests that increasing CO₂ coincides with an increase in savanna woody plant growth (Bond et al., 2003; Scheiter and Higgins, 2009). These transformations could have larger effects on global biogeochemical cycles and precipitation than for any other biome, due to the large extent and productivity of savannas (Intergovernmental Panel on Climate Change, 2007; Snyder et al., 2004).

Dynamic Global Vegetation Models are an important tool to understand large scale vegetation dynamics, and they are considered important also to study the forest, savanna, and grassland biomes, and their interactions within past, current and future climates (Higgins and Scheiter, 2012; Murphy and Bowman, 2012). Some DGVMs are part of Earth System Models (ESMs), where they describe the interactive role of the Earth land surface in the climate system. Given their global application, DGVMs necessarily keep the descriptions of vegetation dynamics simple. Nevertheless, they realistically reproduce the distribution of the majority of the world biomes (Fisher et al., 2010; Sitch et al., 2003). However, projections of vegetation distribution by DGVMs are often uncertain, especially for the forest, savanna, and grassland biomes (Bonan et al., 2003; Cramer et al., 2001; Hély et al., 2006; Hickler et al., 2006; Sato et al., 2007; Sitch et al., 2008). This is probably a consequence of the fact that most DGVMs were not specifically designed for these tropical systems (House et al., 2003), and thus they do not include the specific internal feedbacks typical of these biomes (Moncrieff et al., 2013). Improving the DGVM representation of ecological processes under present climatic conditions is essential for projecting biome boundary shifts and climate change impacts into the future (Beerling and Osborne, 2006; Murphy and Bowman, 2012; Sitch et al., 2008).

To evaluate why DGVMs may have difficulties predicting the distribution and dynamics of savannas, we will analyze three DGVMs, with a particular emphasis to the representation of the interactions between grasses and trees, including the most important tree-grass competition mechanisms, and the feedbacks with their environment, which

we will call “ecological interactions” in the following. While physiological processes are often included in detail into DGVMs, the ecological interactions are not represented with the same accuracy in many models, despite their potentially large influence on the DGVM outcomes (e.g. Fisher et al., 2010; Scheiter et al., 2013). Reflecting on the current ecological understandings about savannas, we will describe whether and how the key mechanisms are included in current DGVMs. We chose to analyze three different DGVMs: JSBACH (Brovkin et al., 2009; Raddatz et al., 2007; Reick et al., 2013), LPJ-GUESS-SPITFIRE (Smith et al., 2001; Thonicke et al., 2010) and aDGVM (Scheiter and Higgins, 2009). JSBACH represents a DGVM as typically used in ESMs (and representative for most models included in the current IPCC coupled model inter-comparison project, CMIP5). LPJ-GUESS additionally includes the demography of plant functional types (PFTs), which is likely to affect competition dynamics, and it includes SPITFIRE, i.e. a new specific module to represent fire dynamics. Finally, aDGVM represents a new class of DGVMs, including functional variation within PFTs (e.g., phenology, allocation and physiology adapt to changing environmental conditions). The aDGVM was specifically designed for African vegetation and savannas. In the following, we will focus on the African continent, where savannas occupy large areas, and where all of the three models have been benchmarked. Focusing on one continent has also the advantage that the mechanisms driving the dynamics are more likely to be similar (Lehmann et al., 2014). We will compare the model outputs with observations from field and remote sensing data (Hirota et al., 2011; Sankaran et al., 2005; Staver et al., 2011). We attempt to bridge the knowledge gap between our ecological understanding and the representations of vegetation in global vegetation models. Our aim is to determine which mechanisms need to be included or improved in the representation of ecological interactions of existing DGVMs in the forest, savanna, and grassland biomes, to ameliorate the current vegetation model predictions, as well as their projections under future (e.g. climate change) scenarios.

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2 Methods

2.1 Model descriptions

DGVMs were developed to quantify transient responses of terrestrial ecosystems to past, present and future climates, and this required an inclusion of modeling vegetation dynamics in addition to biogeochemical processes (Cramer et al., 2001; Pitman, 2003; Prentice et al., 2007). To account for processes at subgrid-scale, DGVMs often assume fractional vegetation cover within the model grid cell (tiling, or mosaic approach). Vegetation description is based on PFTs, which aggregate and represent species with similar functions. Biomes are then represented by a mixture of PFTs, such as evergreen and deciduous, broadleaved and needleleaved trees, shrubs, C₃ and C₄ grasslands, which dominate in a particular climate. Savannas are typically simulated as a mixture of tropical, broadleaved, deciduous trees (“savanna trees” here after), and mostly C₄ grassland, while forests have mostly tropical, broadleaved, evergreen trees (“forest trees” here after).

DGVMs in general have a quite standard set of assumptions to represent plant physiology, including photosynthesis and biomass production. Most of them calculate Gross Primary Production (GPP) by a coupled photosynthesis-transpiration scheme and estimate autotrophic respiration as a function of temperature. Net Primary Production (NPP) is dependent on the climate and CO₂, and scaled up to the plant or PFT level by building up below and above ground carbon and leaf area (e.g., Sitch et al., 2003). Processes affecting PFT composition, such as competition for resources, mortality, and demography (i.e. what we call here the ecological interactions) are included into DGVMs as separate modules that interact with the physiological and phenological modules.

For the purpose of this paper, we will focus on the description of how the ecological processes relevant for tropical vegetation dynamics are included in the three selected DGVMs (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Only the physiological aspects relevant for the difference in PFT composition in grasslands, savannas and forests will be described. JSBACH is part of an ESM, and was designed to represent

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the interactive role of vegetation and land surface in the climate system. While LPJ-GUESS has been included in an ESM in several studies, LPJ-GUESS-SPITFIRE has never been used in such contest, and the same holds for aDGVM. Both models are so far used only “offline”, i.e. they are driven by external forcing, such as climate and CO₂ changes, without being coupled to a general circulation model, and thus without feeding back to the climate. The models used in this study have their intrinsic limitations, for example they all neglect nutrient cycling. A summary of the ecological interactions important in the tropical areas and included into the models is presented in Table 1.

2.1.1 JSBACH (DYNVEG)

DYNVEG (Brovkin et al., 2009; Reick et al., 2013) is the submodel for vegetation dynamics implemented in the land surface component JSBACH (Raddatz et al., 2007) of the MPI Earth system model (MPI-ESM, Giorgetta et al., 2013). DYNVEG groups its various PFTs into a grass class (C₃ and C₄ grasses), and a woody class (trees and shrubs). Within the woody class, DYNVEG distinguishes between two PFTs for tropical trees, with different photosynthetic abilities, which nonetheless do not have different fire or shade tolerances, so they do not correspond to what we call savanna and forest tree in this paper. DYNVEG assumes dominance of the woody over the grass class, i.e., trees have competitive advantage and typically outcompete grasses. Within a class, the competition among PFTs is indirect via NPP: a PFT with higher NPP outcompetes PFTs with lower NPP. All PFTs share the same soil water bucket, and there is no separation of root zones between woody and grass classes. Woody and grass classes compete for newly available habitable space, with woody types outcompeting grasses in the absence of disturbances. The space available for colonization can be only part of the total area, i.e. some parts of the habitat are considered inhospitable. This fraction constitutes a sort of resource limitation to tree development, since it is calculated as a function of the average NPP over the last years of simulations, which in turn depends on water (and other resource) availability (Reick et al., 2013). JSBACH overestimates GPP and NPP in water-stressed conditions (Dalmonech and Zaehle, 2013),

which partly explains an overestimation of tree cover fraction in drylands (Brovkin et al., 2013). Elevated CO₂ concentration increases water use efficiency of all PFTs.

DYNVEG includes a simple representation of fire disturbance. The fraction of burned area increases with higher amount of litter (i.e. fuel), mostly produced by woody vegetation, and decreasing air humidity (a substitute of litter moisture). As a result, savannas in North Africa with relatively low air humidity and high productivity are frequently burned. After the fire, the burned area is quickly occupied by grasses, while woody cover is recovering slowly. Thus, in these transient dynamics, grasses are indirectly slowing down tree growth. Fire disturbance is the main process that keeps a mixture of trees and grasses in drylands.

2.1.2 LPJ-GUESS-SPITFIRE

LPJ-GUESS (Smith et al., 2001) was developed to incorporate forest age structure into LPJ (Sitch et al., 2003), thus simulating gap model behavior and including the competition of different age cohorts for light and water. For each grid cell, LPJ-GUESS simulates a number of replicate patches. For the tropical regions, LPJ-GUESS results in one type of (C₄) grasses, and two types of tree PFTs, savanna and forest trees, where the former are fire tolerant and shade intolerant, and the latter are fire intolerant and shade tolerant. In LPJ-GUESS, trees and grasses use common water in a superficial soil layer (0.5 m deep), but trees have part of their roots in a deeper soil layer (1 m). At high water availability, trees outcompete grasses by limiting light availability.

The fire module SPITFIRE (SPread and InTensity of FIRE, Lehsten et al., 2009; Thonicke et al., 2010) was coupled to LPJ-GUESS to include the role of vegetation fires. The effect of fire, simulated by SPITFIRE, varies for the different demographic stages (or height classes). For each fire, fuel load, wind speed and a proxy for fuel moisture are used to calculate the rate of spread of a potential fire. The fuel load depends on NPP and decomposition rates, which are both related to climate. Grassy fuels are more flammable (due to their lower fuel bulk density), but trees can cumulate more fuel over years without fire, since they decompose more slowly. Hence if burned

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at high to medium fire frequency, grasslands provide more fuel than forests, while if forests are allowed to accumulate fuel over longer time periods, they result in higher fuel loads than grasslands. All fires remove the above ground biomass of all grasses. Low intensity fires can cause high mortality of all young trees, while the effects on tall trees are limited for savanna trees, and more pronounced for forest trees. In general, damage to trees may be underestimated by SPITFIRE in the current parameterization. In fact, frequent fires lead to high mortality of young (small) age cohorts, while the direct effects on old age cohorts are very limited, and only large fires can cause a high mortality even for highly resistant savanna trees. Further details on the implementation of fire effects on vegetation can be found in Lehsten et al. (2009).

2.1.3 aDGVM

The aDGVM (Scheiter and Higgins, 2009) is explicitly designed to study tree-grass dynamics in savannas. The original version of the model only simulates savanna trees and C₄ grasses (Scheiter and Higgins, 2009), whereas an updated version, used for the current paper, simulates C₄ grasses, C₃ grasses, fire-resistant, shade intolerant, savanna trees and fire-sensitive, shade tolerant forest trees (Scheiter et al., 2012). The model uses an individual-based structure to represent trees. Tree recruitment occurs from seed, and tree seedlings compete with grasses more directly than adult trees.

Plants compete mostly for water and light. Light competition is modeled by considering the light available to grasses below and between canopies. Hence, once a vegetation stand attains a high tree LAI, grass-growth is light-limited. In addition, seedlings and small trees are shaded by grasses and by adult trees. Savanna trees suffer more from light limitation than forest trees, which are more shade tolerant. Plants extract water from different soil layers, depending on their rooting depth, which increases with the individual root biomass, until reaching maximum value, typically parameterized as being deeper for trees than for grasses. This allows trees to have exclusive access to water in deep soil layers. A simple bucket scheme is used to simulate water extraction and percolation into deeper soil layers. The extent to which soil moisture limits photo-



synthesis is calculated as a function of soil moisture in the layers in which the plant has roots. Hence, rooting depth, the amount of water transpired, and the capacity to tolerate low moisture availability determine the outcome of competition for soil moisture.

Fire intensity in the aDGVM is a function of the grass fuel load, its moisture content and wind-speed (following Higgins et al., 2008). Fire spreads when the fire intensity exceeds a minimum intensity, when a fire ignition event (for example lightning strike) occurs, and when ignition probability is exceeded. Days when ignitions occur are random, the number of ignition events per year is linked to tree cover. Fire is assumed to consume a large proportion of above ground grass biomass. Aboveground grass biomass burns as a function of the fire intensity. The aDGVM models the probability of stem biomass combustion of individual trees (so-called “topkilled” trees, which remain alive after fire and can resprout from their roots) as being a logistic function of stem height and fire intensity (following Higgins et al., 2000). This function varies with tree type. Topkill rates are higher for forest than for savanna trees, and savanna trees have higher re-sprouting rates than forest trees, which can be killed by a sequence of fires. Fire affects tree mortality only indirectly, by influencing the carbon balance of topkilled trees. The fire sub-model and the topkill model together determine whether trees remain trapped in a cycle of topkill and resprouting, or whether they can attain larger, fire-resistant sizes. Scheiter and Higgins (2009) illustrated that the aDGVM simulates the current distribution of African biomes well, and that it can simulate biomass observed in a longterm fire manipulation experiment in the Kruger National Park, South Africa (Higgins et al., 2007).

2.2 The model experiment setups

To simulate current conditions, transient simulations were performed where CO₂ increased to 390 ppm. The JSBACH run used here was a pre-existing CMIP5 historical simulation under transient forcing from 1850 to 2005 (Giorgetta et al., 2013). LPJ-GUESS-SPITFIRE was driven by a combination of TRMM (Tropical Rainforest Measuring Mission) data for precipitation and NCEP data (Kalnay et al., 1996) for temper-

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ature and radiation (for details see Weber et al., 2009). The simulation was run with a spin up of 1000 years, and afterwards the simulation was performed from 1960 to 2007. Fire frequency was prescribed at each simulated cell using the MODIS MCD45A burned area product MCD 45 (Roy et al., 2005). LPJ-GUESS-SPITFIRE simulated 100 replicate patches for each of the 0.5 degree cells, and each patch had a probability to burn related to the proportion of burned area calculated from the MODIS burned area product. Fires spread only if their potential rate of spread was above a certain threshold. Since the patch sizes of each of the replicates are below the average fire size, we simulated the burning of the whole replicate (see Lehsten et al., 2009, for further details). All 100 replicates of the patch were finally averaged to get a representative value for the fractional tree cover. The aDGVM used monthly mean climate data from the CRU database (Climatic Research Unit, New et al., 2000). A 100 year model spin-up was conducted first, to ensure that the model was in equilibrium with the environmental conditions, then vegetation was simulated until 2010. Tree cover was calculated as the sum of the canopy areas of all trees higher than 0.5 m, without a competitor tree that can potentially shade (and hide) the target tree. Tree cover in aDGVM can reach 100 % because of the individual canopy overlaps.

2.3 Observational datasets

For the comparison between data and models, we use two different types of tree cover observational datasets that have been recently used to study savanna dynamics. One dataset is a collection of tree cover data from savanna field sites from Africa (Sankaran et al., 2005), while the other is derived from remote sensing (MODIS, as used e.g. in Hirota et al., 2011; Staver et al., 2011b). In both cases, we selected only the data points between 35° S and 15° N (following Hirota et al., 2011).

The dataset from Sankaran et al. (2005) includes data from 854 field sites across Africa. They gathered data from several sources, with no recent human influence, not situated in riparian or seasonally flooded areas, and where vegetation was sampled on a sufficiently large area (> 0.25 ha for plot measurements and > 100 m for transect

sampling). Here, we use projected woody cover and mean annual precipitation. The latter included estimates from field measurements and regional rainfall maps, and from fitted climatic grids (see Sankaran et al., 2005 for details). See Fig. 1a for a visualization of the tree cover as a function of mean annual rainfall.

The tree cover dataset, derived from remote sensing data, is the result of two combined databases. Tree cover data were obtained from the MODIS woody cover product (MOD44B), developed by Hansen et al. (2003). This product used MODIS images between October 2000 and December 2001 to calculate the fraction of tree cover, with a spatial resolution of 500 m. To exclude areas highly influenced by humans, we combined this data with the global land cover map (GlobCover, 2009) with a high spatial resolution (300 m). We excluded land cover types that were classified as “post-flooding or irrigated croplands”, “rainfed croplands”, “mosaic cropland (50–70 %)/vegetation (grassland, shrubland, forest) (20–50 %)”, “mosaic vegetation (grassland, shrubland, forest) (50–70 %)/cropland (20–50 %)”, “artificial surfaces and associated area (urban areas > 50 %)”, “water bodies” and “permanent snow and ice”. The mean annual precipitation was obtained by averaging 42 year (1961–2002) precipitation record from the CRU project (CRU TS 2.1) with 0.5° resolution. See Fig. 1b for an illustration of the resulting natural woody cover as a function of mean annual precipitation. We must note here that despite its wide use, this dataset for tree cover has received some criticism, since: maximum tree cover never reaches 100 %, even for tropical forests, shrub and small woody plants are under-detected (Bucini and Hanan, 2007), and the observed bimodality between forest and savanna in certain precipitation ranges (Hirota et al., 2011; Staver et al., 2011) might possibly be induced by the algorithm used for vegetation classification (Hanan et al., 2014).

2.4 Model comparison to observations

As for the data, for the three models we analyzed the simulated tree cover output as a function of the corresponding mean annual rainfall conditions, and we select only the points in the African continent between 35° S and 15° N. We masked land use, and

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Nevertheless, these factors have not yet been thoroughly examined in many ecological studies, possibly also because of lack of accurate rainfall datasets in these areas. Therefore, in the following, we will focus only on mean annual rainfall, whose importance has extensively been studied. We separately evaluate arid and semi-arid savannas (Sect. 3.1) and humid savannas and forests (Sect. 3.2), analyzing also whether and how the ecological interactions are included in the different models. Finally, we discuss the effect of expected increased CO₂ concentration level on the outcome of tree-grass competition in the three models (Sect. 3.3).

3 Results and discussion

3.1 Arid and semi-arid savannas and grasslands: the role of water limitation

In the drier African savanna regions, i.e. with mean annual precipitation lower than a value estimated between 650 mm yr⁻¹ (Sankaran et al., 2005, see also Fig. 1a) and 1000 mm yr⁻¹ (Staver et al., 2011, see Fig. 1b), observed tree cover displays a maximum value that is lower than full cover. In this range, for a given annual rainfall, multiple values of tree cover are observed, representing either grasslands or more or less closed savannas, but full cover is never reached. The maximum tree cover increases with mean annual rainfall (see 90th quantile regression lines in Fig. 1; similar results are obtained with the 99th quantile regression lines, not shown), i.e. it depends on water availability. Indeed, the main mechanisms governing the ecological interactions include: (i) water limitation on tree growth (Higgins et al., 2012); (ii) tree competition with grasses, which have an especially strong competitive impact on tree seedlings (February et al., 2013; Salazar et al., 2012); (iii) fires further reducing woody cover, although savannas are observed anyway, even if fires were excluded, as shown e.g. with fire exclusion experiments (Higgins et al., 2007).

The relation between tree cover and mean annual rainfall simulated by the models (Fig. 2) is similar to that observed in the data (Fig. 1). In JSBACH output, the maximum

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tree cover increases between zero and 800 mm yr^{-1} approximately, where it reaches its largest cover (see 90th quantile regression curve in Fig. 2a; similar results are obtained with the 99th quantile regression lines, not shown). This increase is mostly due to the fact that all the PFTs can colonize only a part of the space, which is calculated dynamically and increased with water availability (although indirectly, via NPP). In addition, fire related mortality increases with decreasing air humidity, thus representing another source of water-related limitation in drier areas. At the same time, the limitation to tree maximum cover is not likely to be the result of competition with grasses, since trees are assumed to outcompete grasses, and they are affected by some sort of grass competition at low water availability only temporarily after e.g. a fire (see also Fig. 3b). JSBACH has a tendency to overestimate maximum tree cover at very low values of mean annual rainfall ($< 100 \text{ mm yr}^{-1}$), as this model is known to overestimate GPP and NPP (Brovkin et al., 2013).

In the LPJ-GUESS-SPITFIRE model output (Fig. 2b), almost no tree cover is observed until mean annual rainfall is about 300 mm yr^{-1} . In this precipitation range, modeled trees are water limited and outcompeted by grasses. Compared to the observations, this model seems to limit tree cover in this precipitation range too strongly. Between about 300 and 900 mm yr^{-1} annual rainfall, the maximum vegetation cover in LPJ-GUESS-SPITFIRE increases until it reaches a maximum value (about 90 % tree cover, see 90 % quantile regression line in Fig. 2b), partly due to water limitation that allows tree-grass coexistence (between about 350 and 650 mm yr^{-1} , Arneeth et al., 2010), and partly due to fires, which further limit tree cover.

In the aDGVM output, the tree cover displays a maximum value that grows with precipitation between zero and about 500 mm yr^{-1} (Fig. 2c). In this range, modeled trees are water limited, while grasses are better competitors in these drier conditions, thus further reducing the tree cover, which would be higher if the model were run without grasses (not shown). The aDGVM and LPJ-GUESS-SPITFIRE include differential rooting depths for individuals, depending on their root biomass, and therefore both models also represent water competition between grasses and tree seedlings. This competi-

tion is known to be important for tree-grass coexistence (Hanan et al., 2008; Sankaran et al., 2004), while adult trees have deeper roots that make them better competitors in more humid environments (see Fig. 3a and c respectively).

3.2 Humid savannas and forests: the role of fire

5 In more humid conditions, bimodality of vegetation cover below and above 60% is observed in the MODIS data for precipitation in a range between around 1000 and 2000 mm yr⁻¹ (e.g. Hirota et al., 2011; Staver et al., 2011b, see also Fig. 1b), i.e. clusters with low and high tree cover are observed, corresponding to a bimodality of savanna and forest cover. Although the validity of this result still needs further investigation (Hanan et al., 2014), this bimodality has been related to the grass-fire feedback, possibly leading to bistability of savanna and forest in this range, as shown using simple models (e.g. van Nes et al., 2014; Staver and Levin, 2012). In brief, grass, particularly abundant in these wet areas, becomes an extremely good fuel in the dry season, which promotes fire occurrence (Higgins et al., 2008; Trollope, 1984). When fire occurs, above ground biomass of all plants is removed. Established savanna trees and grasses can resprout after fire, but tree seedlings are subject to high mortality rates and many forest tree species cannot resprout. Together with grasses, which regrow quickly in the open space after fires, savanna trees benefit from removal of forest tree competitors, resulting in a vegetation-fire feedback that leads to a stable savanna biome at intermediate rainfall values. Yet, environmental conditions would allow forests in the absence of fire (e.g. Staver and Levin, 2012). Figure 3a provides a schematic diagram of this feedback. At the highest end of the rainfall range, fires are totally suppressed and only forests are observed, since grass growth is inhibited by tree shade.

25 The role of fire in maintaining savannas in humid environments is included in all of the models, although in different ways. At high precipitation, JSBACH tree cover output displays a constant maximum value (above about 800 mm yr⁻¹), but the data display considerable scattering below full tree cover (Fig. 2a). In other words, the model predicts savannas and forests in this range, but the data do not display bimodality of

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also fire activity, transforming them into woodlands and forests (Scheiter and Higgins, 2009). Due to this positive feedback, CO₂ concentration can induce hysteresis effects on the vegetation states (Higgins and Scheiter, 2012). LPJ-GUESS-SPITFIRE has an intermediate behavior between the other two models, because grass and woody vegetation contribute similarly to fuel formation. Also, since in this model fire frequency is prescribed from remotely sensed data, any effect of changes of CO₂ levels on fire occurrence would be very limited, though there might be pronounced effects on resulting vegetation composition.

Another consequence of climate change is a possible decrease in precipitation. This scenario also leads to different model behavior. In JSBACH and LPJ-GUESS-SPITFIRE, drier conditions would lead to lower (woody) biomass productivity, but the impact on fire spread differs among the models. JSBACH predicts no major effect on fire, as drier conditions would lead to higher fuel flammability, thus compensating for the impacts of the woody biomass decrease. In LPJ-GUESS-SPITFIRE the decrease in productivity is dominant and hence a strong decrease of fire frequency is expected (Lehsten et al., 2010). In aDGVM the strong positive feedback would lead to a magnification of the woody vegetation decrease, as lower precipitation leads to increased grass productivity (because of less competition with woody vegetation) and lower humidity, increasing the likelihood of fire occurrence.

In summary, we expect that in JSBACH, LPJ-GUESS-SPITFIRE and aDGVM, savanna systems have quite different sensitivities to climate change, and their predictions on the effect of climate change on fire occurrence diverge substantially. Given the importance of fires for estimating the global carbon budget (Le Quéré et al., 2013), this is remarkable, and it illustrates clearly how representing the ecological interactions more or less accurately can lead in some cases to similar results under present conditions (where the models have been tuned), but their predictions can diverge substantially when the models are used for future scenarios.

3.4 Other mechanisms influencing tropical savannas, grasslands and forests

Up to now we considered water limitation and fires as the main drivers of grassland, savanna and forest distribution. Several additional factors can be important for vegetation dynamics, especially at the local scale. The first factor is herbivory. Browsing (particularly by mega-herbivores in Africa) is known to have an important limiting effect on tree cover, similar to the effect of fire (e.g. Scheiter and Higgins, 2012; Staver et al., 2012), while grazing can favor trees because it limits grass expansion (e.g. Sankaran et al., 2008). However, large herbivores seem not to be critical in determining forest and savanna distributions (Murphy and Bowman, 2012). Secondly, savannas tend to be associated with nutrient poor soils (Lloyd et al., 2008), although edaphic conditions seem to be less important than other factors such as climate (Favier et al., 2012; Murphy and Bowman, 2012). Thirdly, vegetation tends to have local spatial dynamics and to feed back to the environment at much smaller spatial scales than the DGVMs resolution. These local spatial water-vegetation interactions are strictly connected to vegetation resilience in arid and semiarid ecosystems (e.g. Rietkerk et al., 2004), and they can also influence the coexistence of trees and grasses in the most arid savannas (Baudena and Rietkerk, 2012; Nathan et al., 2013). Although the local scale is partly taken into account in some DGVMs by including individual based dynamics or tiling schemes (that represent different vegetation types and bare soil next to each other within the same cell), these assume a common use of soil and hydrological resources within the grid cell, thus not allowing to represent local, sub-grid mechanisms, which are not at all trivial to up-scale (Rietkerk et al., 2011). Finally, on the African continent the vast majority of fires is ignited by humans (Archibald et al., 2009; Saarnak, 2001), although their decisions on when to burn an area, as well as the fire spread and intensity, are still related to fuel composition (Govender et al., 2006). Humans maintain the grass-fire feedback, since they aim at keeping the land free from woody vegetation, and also because fire spread is favored by grass presence. Changes in land use have therefore strong influences on the current and future outcomes of tree-grass competition. Also,

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humans are expected to change their application of fire as a land use tool, as a consequence of changed environmental conditions. These elements are partly taken into account in some DGVMs (e.g. in LPJ-GUESS-SPITFIRE), but we do not consider them here for the purpose of this paper.

4 Concluding remarks

Current ecological understanding identifies water limitation and grass-fire feedback as dominant mechanisms driving the forest–savanna–grassland transition in Africa. In arid and semiarid savannas, trees are water-limited, and the water competition with grasses is the key factor determining savanna existence. In these conditions, grasses compete especially fiercely with tree seedlings. In wetter areas along the climatic gradient, savannas are maintained by the presence of a grass-fire positive feedback. Fire spread is increased by grasses, which provide fuel load. Grasses re-grow faster than trees after fires, while tree recruitment is limited. Thus, trees do not close their canopies, leaving more free space for grasses. On the other hand, when trees manage to close their canopies, grasses are outcompeted because of light limitations, and because fire is suppressed. Both water limitations and fires act differently on tree adults and seedlings, which compete more directly with grasses and are the most sensitive stage in tree life.

These mechanisms are to varying extent included in the three DGVMs we analyzed (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Indeed, the three models predict reasonably well the current tree cover along the mean annual rainfall gradient in Africa, as derived from ground and satellite observations. aDGVM output matches the observations better than the other two models. This is perhaps to be expected since this model is specifically designed for African vegetation and it includes more detailed representations of ecological interactions, especially the grass-fire feedback. For the other two models, the main differences between observations and model outputs are: (i) JSBACH overestimates tree cover in dry areas (see also Brovkin et al., 2013); (ii) LPJ-GUESS-SPITFIRE does not show any savanna at medium to high annual rainfall rates; (iii) both

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these DGVMs do not show bimodality of savannas and forests in humid areas. This latter point might feed the debate about whether bimodality between savanna and forest cover actually exists (see e.g. Hanan et al., 2014). Despite their reasonably good performances, not all the mechanisms included in JSBACH and LPJ-GUESS-SPITFIRE are fully appropriate to represent vegetation in the tropics and the subtropics. In JSBACH, competition between trees and grasses favors the former irrespectively of water availability, which is one of the reasons behind JSBACH tree cover overestimation. At the same time, in this model, fire is fostered disproportionately by woody vegetation as compared to grasses, resulting in a negative feedback. This is responsible for observing savannas in larger parts of the rainfall gradients, and no savannas would be simulated without them. Although the three models display comparable outcomes under the current climate, the presence of a negative fire-vegetation feedback in JSBACH, a positive feedback in aDGVM, and an intermediate behavior in LPJ-GUESS-SPITFIRE, leads to different predictions of fire frequency and effects under climate change scenarios between the three models. In JSBACH, the initial increase in woody vegetation, due to higher CO₂ concentrations, would get dampened by the consequent increase in fire frequency. Interesting in this perspective is that the sensitivity of shifts between forests and savannas is low for JSBACH, as negative feedbacks are more important, while in aDGVM the positive grass-fire feedback mechanism results in a large sensitivity to shifts of the different tree-grass systems. LPJ-GUESS-SPITFIRE has an intermediate behavior between the other two models, since grass and woody vegetation foster fire in a similar way. Also, in this model fires seem to be suppressed too easily by high humidity conditions, which cause savannas to be absent at medium-high annual rainfall values.

Tree seedlings are the bottleneck stage of tree life in the forest–savanna–grassland transition (Salazar et al., 2012; Sankaran et al., 2004), and the two most important mechanisms we identified here, i.e. water competition and limitation, and fires, tend to affect tree seedlings particularly strongly. Thus, including tree demography as in LPJ-GUESS and the aDGVM, improves the representation of ecological interactions in

the models. Also, representing forest and savanna trees with different flammability and shade tolerances (as in LPJ-GUESS and aDGVM) is beneficial, and they reinforce the positive grass-fire feedback, if included (as in aDGVM).

Having in mind that DGVMs need to be kept as simple as possible, we conclude that the most important mechanisms to better represent the forest–savanna–grassland transition are (i) how water limits tree growth and regulates tree-grass competition, and (ii) the grass-fire feedback. Distinguishing between tree life stages and representing the different responses of forest and savanna trees, are less important features for the models, although they can considerably ameliorate the representation of the two main mechanisms. As parts of these mechanisms are already included in most DGVMs, extensions should be relatively simple, but they would substantially improve the predictions of vegetation dynamics and carbon balance under future climate change scenarios.

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Table 1. Models and their specifics concerning the tree-grass transition.

Model	Specific for tropical vegetation	Variables representing vegetation	Distinction between savanna and forest trees	Tree age structure	Limiting resources for vegetation	Stable state(s) (in absence of fires)
JSBACH/DYNVEG	No	LAI, PFT fractions, carbon in vegetation pools	No	No	Uncolonized space, hospitable land (water, indirectly via NPP)	Dominant woody (tree, shrub) PFTs
LPJ-GUESS-SPITFIRE	No	Individual based model. LAI, PFT fractions, carbon in vegetation pools	Yes	Yes	Water and light	Depending on climate (mainly precipitation), either forest or grassland is the stable state. Savanna is observed in a relatively small precipitation range.
aDGVM	Yes	Individual based model. Plant level: LAI, height, basal area, canopy area, biomass in different pools Stand level: LAI, PFT fractions, carbon in vegetation pools of different PFTs, basal area, tree cover	Yes	Yes	Water, light, (space, via light competition)	Depending on climate (mostly defined by precipitation): desert, grassland, savanna, forest

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Table 1. Continued.

Model	How is fire represented?	Mechanisms driving savanna	Mechanisms driving forests/grasslands occurrence	Would a CO ₂ increase modify the tree-grass transition and how?	Reference
JSBACH/DYNVEG	Fire is a function of air humidity and litter. Fires are mainly fostered by trees, which are also damaged by fire (negative feedback)	Fires	Forests occur in absence of fires (at any climate), while grasslands appear at high frequency of fire occurrence, i.e. at very intense dryness	Only indirectly (by changing litter availability for wildfires)	Brovkin et al. (2009); Reick et al. (2013)
LPJ-GUESS-SPITFIRE	Fire is prescribed from remote sensing but its effects on vegetation depend on fuel availability and environmental conditions. Fires are fostered by both woody and grass biomass	Fires, water competition	Forests occur given sufficient precipitation, while grasslands appear at high frequency of fire occurrence, or low precipitation.	Higher CO ₂ would benefit C ₃ vegetation (trees) as compared to C ₄ grasses. At the same time though, grasses and trees would produce more litter, which would increase fire intensity and hence might have negative effects on trees.	Smith et al. (2001); Thonicke et al. (2010)
aDGVM	Fire intensity is defined by fuel moisture and fuel biomass; fire ignition probability is a constant; fire removes aboveground grass biomass and, depending on height, aboveground tree biomass (topkill); vegetation can re-sprout. Grasses foster fire spread and profit from recurrent fires (positive feedback).	Competition for water, fires	Forests occur at high rainfall levels (where fire is not possible) and at mesic conditions when fire is absent; grasslands occur at more arid conditions when precipitation does not allow tree growth, and at more mesic conditions in the presence of fire.	CO ₂ fertilization promotes tree growth and: (1) grasslands are transformed into savannas (2) tree canopy closure in savannas suppresses grass growth and fire activity, such that savannas are transformed into forests	Scheiter and Higgins (2009); Scheiter et al. (2012)



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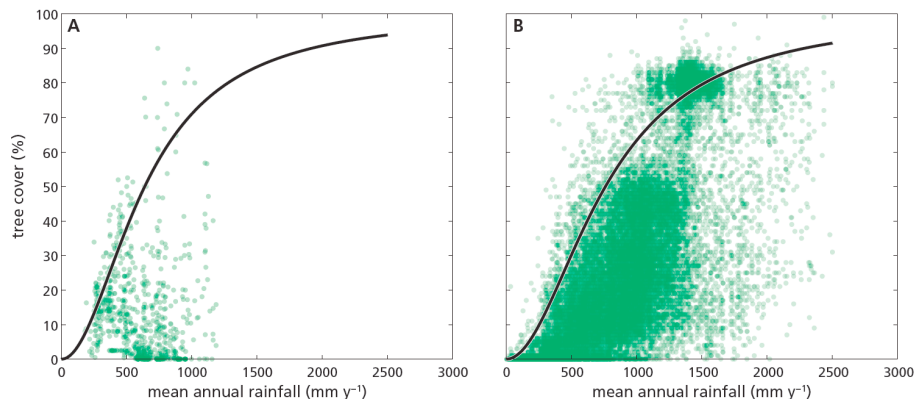


Figure 1. Tree cover as a function of mean annual rainfall (mm yr^{-1}). **(A)** Savanna field data, reprinted from Sankaran et al. (2005); **(B)** tree cover obtained from MODIS woody cover product (as e.g. Hirota et al., 2011), where anthropogenic land use is masked as described in the text. For clarity of representation, we selected only 0.05% of the data. For both databases, we selected only the data points between 35° S and 15° N in Africa. The dots are data; the continuous lines are the 90th quantile nonlinear regression (99th quantile not shown; see values of b coefficients in Supplement Table B1). Notice that the field data **(A)** correspond only to savanna sites, and thus encompass a smaller rainfall range than the satellite data **(B)**.

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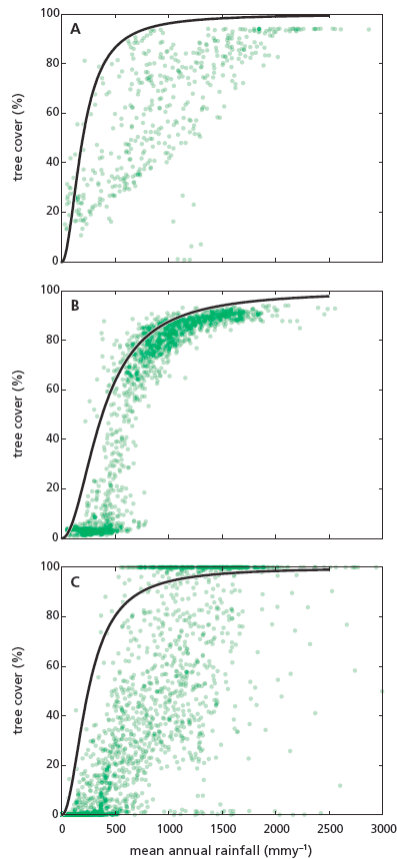


Figure 2. Model outputs for tree cover as a function of mean annual rainfall (mm yr^{-1}) in Africa between 35° S and 15° N: **(A)** JSBACH; **(B)** LPJ-GUESS-SPITFIRE; **(C)** aDGVM. The dots are data, the continuous lines are the 90th quantile nonlinear regression (99th quantile not shown; see value of b coefficients in Supplement Table B1).

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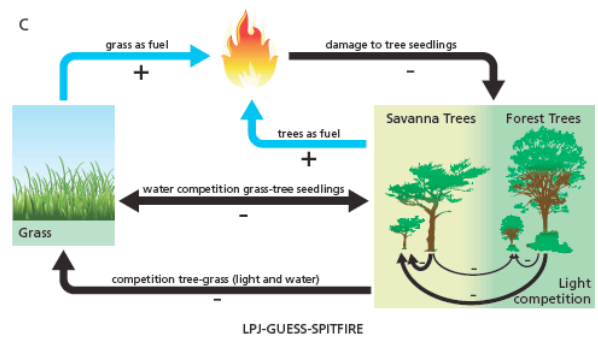
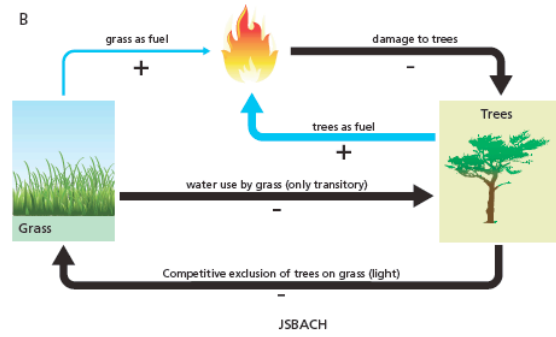
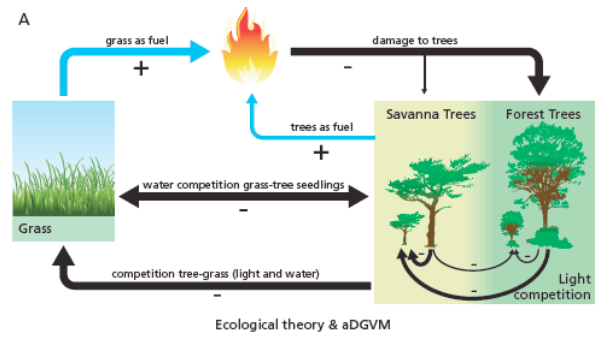


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Figure 3. Schematic diagram of the main ecological interactions that determine the forest–savanna–grassland transition, according to: **(A)** Ecological theory, and the aDGVM; **(B)** JSBACH; **(C)** LPJ-GUESS-SPITFIRE. Light blue arrows represent positive effects, dark blue arrows negative effects. The aDGVM **(A)** was designed to include the key ecological mechanisms known from theory, namely: grasses increasing fire spread (positive feedback), distinction between forest and savanna trees (with fires damaging forest tree mostly, shade intolerant savanna seedlings and shade tolerant forest seedlings), separate resource competition between trees and grasses depending on their size (grasses and tree seedlings compete for the same water, while adult trees outcompete grasses for both water and light). JSBACH **(B)** includes fires as mainly fostered by tree litter, which are also mainly damaged by fire (negative feedback). Trees competitively exclude grasses, although temporarily after disturbances grasses also compete with them for the same water. LPJ-GUESS-SPITFIRE **(C)** is on one hand similar to the aDGVM, since it distinguishes tree life stages and it separate between savanna and forest trees, with analogous representation of water and light tree-grass competition. On the other hand, it includes a similar effect of tree and grass biomass in fostering fires.

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