Reply to editor decision "minor review" for manuscript Baudena at al., BGD, 2014

The text from the editor's comment file is reported in black (Editor words are in bold), the authors' reply follows (in red).

-1-
Reviewer comment: 9. p9489, l19W20: ". . . at high precipitation, the fuel does not dry out sufficiently to promote fire spread. This may be caused partly be the average fire probability used in this version of SPITFIRE. . .". I do not see the connection of the former sentence (related to drying out to promote fire spread) with the average fire probability, which is related to the representation of fire triggering. Better explanation of what you meant. Besides, has LPJWGUESS been benchmarked for Africa? The authors mentioned DGVMs are not parameterized for tropical ecosystems, but could not find any commentary on a specific usage of this model for Africa.
YOUR REPLY: To connect the two parts better, we rephrased the sentence in the following way:
"This may be partly due to the fact that this version of SPITFIRE uses a probability of fire spread which depends on average fuel conditions, and thus it is not fully coupled to the drought periods.
It is necessary to better explain the text here. This sentence is not understandable and the reader cannot follow the argumentation. Please refer to the specific SPITFIRE equation as published in Thonicke et al. 2010 and if applicable how this has been modified for your version. Then you need to explain how this relates to the drying of dead fuel.

R1- We completely rewrote that part. It now reads:
"At the same time, this issue is also likely to be connected to fire intensity depending on fuel moisture. In this model, fire occurrence in a patch is calculated probabilistically from the proportion of burned area as determined from the remote sensing product. If fire occurs in a period of high fuel moisture, the intensity will be limited, thus having little effect on vegetation. This probabilistic approach is necessary because the temporal extent of the remote sensed data (now only ca. 10 years), used to generate the probability of burned area for each pixel, is much shorter than the extent of the climate data for which the model was run (ca. 100 years).".

We also added a further detail in the explanation in paragraph § 2.2 about model setup: "If the fire is supposed to start but the fuel moisture is high, the fire starts instead on the driest day within a 10-day period."
We hope that this clears now the issue.

-2-
However, this assumption is necessary because the temporal extent of remotely sensed data for burned area (now ca. 10 years) is well below the temporal extent of the available climate data (50 years)."
I do not understand the logic of this argumentation. Ten years of burnt area detection are already a considerable data set for model evaluation which can be used to evaluate the fire module. Please clarify and improve the manuscript text accordingly.

R2-
Please see the text above. We now explain in more detail that we had to use the burned area probability as a seasonal dataset, which was applied to each of the years for which we had climate data.
We did not use the MODIS data to evaluate the fire module, it was an input to be able to drive the model with the most precise burned area available.

-3-
About benchmarking, LPJ-GUESS simulations of vegetation distribution have been compared to potential

natural vegetation at global scale (including Africa) in Sitch et al. (2003). So, far only aDGVM has been applied specifically to Africa.

I disagree with this argumentation. The Sitch et al. 2003 is not a suitable reference as this is the LPJ original paper, while you are using LPJ-GUESS (Smith et al. 2001 and follow-up publications). Why don't you cite, e.g. Lehsten et al. 2009 or Hickler et al. 2005, 2009? This needs to be improved in the text!

R3- We agree that the mentioned sentences can be read as if LPJ-GUESS has been applied specifically to Africa, which is indeed not the case as the editor correctly points out. So far no comparison specifically of African vegetation types simulated by LPJ-GUESS with independent data has been published. Furthermore, the editor is correct in mentioning that Sitch et al. 2003 is not using LPJ-GUESS but LPJ. However, Smith et al. 2001 has shown that the differences between the vegetation types simulated by the two models are marginal, although we shall notice that Smith et al. 2001 only use Europe as an investigation area. Hence, whether this holds true for the African continent as well is to be seen. We can here add that a manuscript in which the comparison between African modelled and remotely-sensed vegetation types is performed is currently in review, using LPJ-GUESS SPITFIRE and looking especially at the effect of fires (Lehsten et al.).This work shows that the distribution of African biomes is well covered by LPJ-GUESS if fires are included in the simulation.

We now revised the sentence in the introduction about model application to Africa, to include the references mentioned:
"In the following, we will focus on the African continent, where savannas occupy large areas, and where all of the three models have been applied (Brovkin et al., 2009; Hickler et al., 2009; Higgins and Scheiter, 2012; Lehsten et al., 2009; Scheiter and Higgins, 2009)".

-4-
Reviewer comment: It is interesting to see the evaluation on how elevated CO2 can affect the dynamics of forest-savanna transition zones. But remember nutrient dynamics have shown to play a key role in elevated CO2 responses of forests (e.g. Norby et al. 2010). Many tropical forests and savannas are nutrient limited(especially P-limited). However it seems like the role of nutrient dynamics is poorly explored here. I understand that none of the employed models have nutrient cycling (even though I was curious because JSBACH was one of the first DGVMs to implement N and P cycle, but the authors probably used an earlier model version), but the topic could be further explored. Otherwise the scientific utility of the elevated-CO2 exercise (which in fact is not properly explained in the method section) is reduced.
YOUR REPLY:
We agree with the reviewer that nutrient cycles are fundamental for many tropical savannas and forests and it is very important for CO2-enriched experiment. However, within the ecological literature, nutrient limitations are currently not considered as one of the main reason behind savanna existence. Moreover, for the conceptual CO2-experiment, including a nutrient cycling would not have dramatic impacts (as nutrient limitations would mainly reduce, or eventually stop, the CO2-fertilization effect). Because we only discuss the direction of change within our conceptual experiment, this would not change our interpretation. About the description of the CO2 experiment, please see also above the reply to point #2 of this reviewer. The JSBACH version used was indeed the CMIP5 version of the model without N and P cycles.
This is an important point which must be added to the manuscript text. So please add the role of nutrient limitation to your thought-experiment in the text and check recent literature on FACE experiments, e.g. Zaehle et al. 2014. Also clarify in the method description that the JSBACH version that you used was not the one with N and P cycles. Please add how this model version could have helped in your analysis.

R4- We did not include a study of the role of nutrients in savannas because, in most ecological literature, the role of nutrients in determining savanna/forest transitions is considered secondary to

the mechanisms illustrated here. To underline this better in connection to the DGVMs, we now rephrased a sentence in §3.4: "Secondly, although it has been observed that savannas can be associated with nutrient poor soils (Lloyd et al., 2008), it is generally accepted that nutrient limitation does not explain the savanna-forest transition (Bond, 2010; Favier et al., 2012; Murphy and Bowman, 2012). For these reasons, and to avoid inconsistencies while evaluating different models, we only used DGVMs that did not include nutrient cycling."

Thus, we cannot really comment on if and how the nutrient cycling could have helped in the analyses or influenced the conceptual experiments. However, while evidence from studies at elevated CO2 (to which we would like to refer to Smith et al. 2014 instead of Zaehle et al. 2014, since the FACE experiments concern temperate forests only), suggest impacts on productivity, evidence on impacts of nutrients in interaction with elevated CO2 on the savanna/forest transitions is scant.

About JSBACH, we note here that we already included a sentence about the fact that none of the DGVMs we consider includes nutrient cycling in §2.1: "The models used in this study have their intrinsic limitations, for example they all neglect nutrient cycling". For this reason we do not have a specific sentence about this in the paragraph about JSBACH.

References cited

Smith, B., Wärlind, D., Arneth, a., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S. (2014). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences*, *11*, 2027–2054. doi:10.5194/bg-11-2027-2014

Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hickler, T., … Norby, R. J. (2014). Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO2 Enrichment studies. *New Phytologist*, *202*, 803–822. doi:10.1111/nph.12697

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

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Abstract

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. 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 compared 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 forest trees, and fire-resistant and shade-intolerant savanna 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.

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

1 vegetation), and grasses (i.e. grasses and herbs). In most of the savanna ecosystems, we

2 observe highly shade intolerant and fire tolerant C_4 grasses and C_3 trees. This savanna

3 definition is generally valid, with the exception of a few regions (e.g. the Neotropical

4 cerrado where C_3 grasses dominate, see Lloyd et al., 2008, Ratnam et al. 2011). For a

5 long time ecologists have been fascinated by savannas, because trees and grasses

6 coexist, while competing mainly for the same resource, namely water, which is the main

7 limiting factor (Sankaran et al., 2004; Scholes and Archer, 1997; Walter, 1971).

8 Classical ecological theory, such as the competitive exclusion principle, predicts that

9 only one vegetation type can survive in these conditions (Hutchinson, 1961; Tilman,

10 1982). To solve this conundrum, numerous experimental and modeling studies explored

11 the nature of tree-grass competition and coexistence (e.g. Higgins et al., 2000; House et

12 al., 2003; Sankaran et al., 2004; Scholes and Walker, 1993; Walker and Noy-Meir,

13 1982). Grasses can outcompete trees in the driest environments, where tree growth is

14 water-limited (Higgins et al., 2012), and they have a particularly strong competitive

15 effect on tree seedlings, as grasses and tree seedlings compete for water in the same

16 surface layer (Baudena et al., 2010; Bond, 2008; February et al., 2013; Sankaran et al.,

17 2004; Wakeling et al., 2011; Yin et al., 2014b). In less arid conditions, however, adult

18 trees can potentially grow deeper roots and reach deeper water than grasses (Kulmatiski

19 and Beard, 2013; Walter, 1971; Ward et al., 2013), although overlap between grass and

20 tree roots can be high in some savannas (e.g. February and Higgins, 2010; Higgins et

21 al., 2000; House et al., 2003).

22 In addition to water availability, fire is an important driver of tree-grass dynamics. C_4

23 grass biomass enhances fire spread in open ecosystems, due to its high flammability. At

24 the same time, grasses benefit from fire because they recover faster than trees, and

25 profit of the open spaces after fire, thus originating a positive feedback mechanism that

26 enhances savanna formation and presence (as shown by e.g. long term fire-exclusion

27 experiments, Higgins et al., 2007, or model studies, e.g. Higgins et al., 2008; van

28 Langevelde et al., 2003; see also Hoffmann et al., 2012). Fires may also limit tree

29 seedling recruitment and growth, thus reducing tree dominance further (e.g. Hanan et

30 al., 2008; Higgins et al., 2000). This grass-fire feedback is characteristic of tropical

31 savannas and grasslands, while in most of the other biomes woody species produce

32 most fuel for fires (e.g. boreal forests, Bonan and Shugart, 1989). Fire is essential to

33 savanna persistence in wetter areas, which would be forested otherwise. The grass-fire

1 feedback is reinforced by the differences between savanna and forest trees. In contrast

2 to savanna trees and grasses, forest trees are fire prone and shade tolerant, adapted to

3 persist in conditions of low light availability and in absence of fire (Ratnam et al., 2011;

4 Rossatto et al., 2009). Thus, when fires are absent and water supply is sufficient, forest

5 trees outcompete grasses and savanna trees because of light limitation, while if fires are

6 active, savanna trees persist but fires and shade intolerance limit their cover, keeping

7 savannas open (Hoffmann et al., 2012). This feedback, which we define as "vegetation-

8 fire feedback", and which is an extended description of the abovementioned grass-fire

9 feedback, possibly leads to bistability of forest and savanna in mesic regions (e.g. van

10 Nes et al., 2014; Staver and Levin, 2012).

11 Savannas are expected to undergo major changes in the future due to increasing

12 temperature and CO_2 concentration, modified rainfall patterns, and subsequently

13 changed variability in fire regimes (Intergovernmental Panel on Climate Change -

14 IPCC, 2007). In recent years, an increase in woody cover has been observed in savannas

15 all over the world (e.g. Bowman et al., 2010; Buitenwerf et al., 2012; Donohue et al.,

16 2013; Ward, 2009; Wigley et al., 2010). Several studies tried to explain wood expansion

17 by overgrazing or decreasing fire frequency, which would enhance grass mortality and

18 thus favor woody vegetation (Scholes and Archer, 1997). However, CO_2 increase is

19 probably one of the main causes of woody encroachment, leading to savanna

20 expansions (e.g. at the expense of grasslands). As water use efficiency increases with

21 CO_2 (e.g. de Boer et al., 2011), thus decreasing the water need for grow, increased CO_2

22 concentration leads to a shift in tree-grass competition for water, possibly favoring C_3

23 trees over C_4 grasses (Bond and Midgley, 2000; Bowman et al., 2010; Kgope et al.,

24 2010; Polley et al., 1994; Wigley et al., 2010). In African savannas, paleo-ecological

25 evidence of the last glacial period, as well as observations of the last 50-100 years,

26 suggests that increasing CO_2 coincides with an increase in savanna woody plant growth

27 (Bond et al., 2003; Scheiter and Higgins, 2009). These transformations could have

28 larger effects on global biogeochemical cycles and precipitation than for any other

29 biome, due to the large extent and productivity of savannas (IPCC, 2007; Snyder et al.,

30 2004).

31 Dynamic Global Vegetation Models are an important tool to understand large scale

32 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. For example, they represent the enormous plant trait diversity of tropical regions through distinguishing only one or two plant functional types (PFTs). 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; Hely 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 on the representation of what in the following we call the "ecological interactions" between grasses and trees, i.e. the most important tree-grass competition mechanisms, and the feedbacks with their environment. 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

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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 applied (Brovkin et al., 2009; Hickler et al., 2009; Higgins and Scheiter, 2012; Lehsten et al., 2009; Scheiter and Higgins, 2009). 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.

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, C_3 and C_4 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 C_4

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1 grassland, while forests have mostly tropical, broadleaved, evergreen trees ("forest
2 trees" here after).

3 DGVMs in general have a quite standard set of assumptions to represent plant
4 physiology, including photosynthesis and biomass production. Most of them calculate
5 Gross Primary Production (GPP) by a coupled photosynthesis-transpiration scheme and
6 estimate autotrophic respiration as a function of temperature. Net Primary Production
7 (NPP) is dependent on the climate and CO_2, and scaled up to the plant or PFT level by
8 building up below and above ground carbon and leaf area (e.g., Sitch et al., 2003).
9 Processes affecting PFT composition, such as competition for resources, mortality, and
10 demography (i.e. what we call here the ecological interactions) are included into
11 DGVMs as separate modules that interact with the physiological and phenological
12 modules.

13 For the purpose of this paper, we will focus on the description of how the ecological
14 processes relevant for tropical vegetation dynamics are included in the three selected
15 DGVMs (JSBACH, LPJ-GUESS-SPITFIRE and aDGVM). Only the physiological
16 aspects relevant for the difference in PFT composition in grasslands, savannas and
17 forests will be described. JSBACH is part of an ESM, and was designed to represent the
18 interactive role of vegetation and land surface in the climate system. While LPJ-GUESS
19 has been included in an ESM in several studies, LPJ-GUESS-SPITFIRE has never been
20 used in such contest, and the same holds for aDGVM. Both models are so far used only
21 "offline", i.e. they are driven by external forcing, such as climate and CO_2 changes,
22 without being coupled to a general circulation model, and thus without feeding back to
23 the climate. The models used in this study have their intrinsic limitations, for example
24 they all neglect nutrient cycling. A summary of the ecological interactions important in
25 the tropical areas and included into the models is presented in Table 1.

26 **2.1.1 JSBACH (DYNVEG)**

27 DYNVEG (Brovkin et al., 2009; Reick et al., 2013) is the submodel for vegetation
28 dynamics implemented in the land surface component JSBACH (Raddatz et al., 2007)
29 of the Max Planck Institute - Earth System Model (MPI-ESM, (Giorgetta et al., 2013).
30 DYNVEG groups its various PFTs into a grass class (C_3 and C_4 grasses), and a woody
31 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 CO_2 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 (C_4) 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

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1   tolerant. In LPJ-GUESS, trees and grasses use common water in a superficial soil layer

2   (0.5 m deep), but trees have part of their roots in a deeper soil layer (1 m). At high water

3   availability, trees outcompete grasses by limiting light availability.

4   The fire module SPITFIRE (SPread and InTensity of FIRE, Lehsten et al., 2009;

5   Thonicke et al., 2010) was coupled to LPJ-GUESS to include the role of vegetation

6   fires. The effect of fire, simulated by SPITFIRE, varies for the different demographic

7   stages (or height classes). For each fire, fuel load, wind speed and a proxy for fuel

8   moisture are used to calculate the rate of spread of a potential fire. The fuel load

9   depends on NPP and decomposition rates, which are both related to climate. Grassy

10   fuels are more flammable (due to their lower fuel bulk density), but trees can

11   accumulate more fuel over years without fire, since they decompose more slowly.

12   Hence if burned at high to medium fire frequency, grasslands provide more fuel than

13   forests, while if forests are allowed to accumulate fuel over longer time periods, they

14   result in higher fuel loads than grasslands. All fires remove the above ground biomass

15   of all grasses. Low intensity fires can cause high mortality of all young trees, while the

16   effects on tall trees are limited for savanna trees, and more pronounced for forest trees.

17   In general, damage to trees may be underestimated by SPITFIRE in the current

18   parameterization. In fact, frequent fires lead to high mortality of young (small) age

19   cohorts, while the direct effects on old age cohorts are very limited, and only large fires

20   can cause a high mortality even for highly resistant savanna trees. Further details on the

21   implementation of fire effects on vegetation can be found in Lehsten et al. (2009).

22   2.1.3 aDGVM

23   The aDGVM (Scheiter and Higgins 2009) is explicitly designed to study tree-grass

24   dynamics in savannas. While the original version of the model only simulates savanna

25   trees and C_4 grasses (Scheiter and Higgins, 2009), an updated version, used for the

26   current paper, simulates C_4 grasses, C_3 grasses, fire-resistant, shade intolerant, savanna

27   trees and fire-sensitive, shade tolerant forest trees (Scheiter et al., 2012). The model

28   uses an individual-based structure to represent trees. Tree recruitment occurs from seed,

29   and tree seedlings compete with grasses more directly than adult trees.

30   Plants compete mostly for water and light. Light competition is modeled by considering

31   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 photosynthesis 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 drought tolerance (i.e. the ability to withstand a low soil water content) 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).

10

2.2   The model experiment setups

To simulate current conditions, transient simulations were performed where CO_2 increased to 390 ppm. The JSBACH run used here was a pre-existing CMIP5 historical simulation under transient forcing from 1850 to 2005, with horizontal resolution of 1.9x1.9^o (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 temperature 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, with resolution of 1x1^o. 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 1° cells, and each patch had a probability to burn related to the proportion of burned area calculated from the MODIS burned area product. If the fire is supposed to start but the fuel moisture is high, the fire starts instead on the driest day within a 10-day period. Fires spread only if their potential rate of spread was above a certain threshold. Since the patch sizes of each of the replicates were 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), and model resolution was 1x1^o. 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 neighbouring trees that shade (and hide) the tree itself. Tree cover in aDGVM could reach 100% because of the individual canopy overlaps.

2.3   Observational datasets

For the comparison between data and models, we used 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

11

1 Hirota et al., 2011; Staver et al., 2011b). In both cases, we selected only the data points

2 between 35° S and 15° N (following Hirota et al., 2011).

3 The dataset from Sankaran et al. (2005) includes data from 854 field sites across Africa.

4 They gathered data from several sources, with no recent human influence, not situated

5 in riparian or seasonally flooded areas, and where vegetation was sampled on a

6 sufficiently large area (> 0.25 ha for plot measurements and > 100m for transect

7 sampling). Here, we used projected woody cover and mean annual precipitation. The

8 latter included estimates from field measurements and regional rainfall maps, and from

9 fitted climatic grids (see Sankaran et al., 2005 for details). See Fig. 1A for a

10 visualization of the tree cover as a function of mean annual rainfall.

11 The tree cover dataset, derived from remote sensing data, was the result of two

12 combined databases. Tree cover data were obtained from the MODIS woody cover

13 product (MOD44B), developed by Hansen et al. (2003). This product used MODIS

14 images between Oct 2000 and Dec 2001 to calculate the fraction of tree cover, with a

15 spatial resolution of 500m. To exclude areas highly influenced by humans, we

16 combined this data with the global land cover map (GlobCover 2009) with a high

17 spatial resolution (300m). We excluded land cover types that were classified as "Post-

18 flooding or irrigated croplands", "Rainfed croplands", "Mosaic Cropland (50-70%) /

19 Vegetation (grassland, shrubland, forest) (20-50%)", "Mosaic Vegetation (grassland,

20 shrubland, forest) (50-70%) / Cropland (20-50%)", "Artificial surfaces and associated

21 area (urban areas > 50%)", "Water Bodies" and "Permanent snow and ice". The mean

22 annual precipitation was obtained by averaging 42-year (1961-2002) precipitation

23 record from the CRU project (CRU TS 2.1) with 0.5° resolution. See Fig. 1B for an

24 illustration of the resulting natural woody cover as a function of mean annual

25 precipitation. We must note here that despite its wide use, this dataset for tree cover has

26 received some criticism, since: maximum tree cover never reaches 100%, even for

27 tropical forests, shrub and small woody plants are under-detected (Bucini and Hanan,

28 2007), and the observed bimodality between forest and savanna in certain precipitation

29 ranges (Hirota et al., 2011; Staver et al., 2011) might possibly be induced by the

30 algorithm used for vegetation classification (Hanan et al., 2014).

12

1 **2.4 Model comparison to observations**

2 As for the data, for the three models we analyzed the simulated tree cover output (i.e. all
3 woody vegetation) as a function of the corresponding mean annual rainfall conditions,
4 and we select only the points in the African continent between 35° S and 15° N. We
5 masked land use, and we used both vegetation and precipitation averaged over thirty
6 years. To evaluate the effect of rainfall on the upper limit of tree cover, following e.g.
7 Sankaran et al. (2005), we used nonlinear quantile regression (Koenker and Park, 1996),
8 as implemented in the 'quantreg' library of the R program. We used 0.90 to 0.99
9 quantiles and we chose the following nonlinear function:

10
$$y = a\frac{x^2}{b+x^2},$$
(1)

11 where x is the mean annual rainfall, y the estimated quantile regression for percent tree
12 cover, a the maximum tree cover (setting a=100%, while b was estimated by the
13 regression).

14 In the models, the precipitation ranges where grasslands, savannas and forests were
15 simulated resulted not only from the different representations of vegetation dynamics,
16 but also from the way climate was included. aDGVM and LPJ-GUESS-SPITFIRE were
17 forced with (different) climate data, while JSBACH was coupled to an atmospheric
18 model. Both the rainfall (NCEP, CRU and TRMM) datasets and the simulated climate
19 have inevitable biases, and are hard to compare with each other. Therefore, precipitation
20 estimations were not totally comparable, and for this reason, we will compare the
21 models in the parameter space (i.e., vegetation cover versus mean annual rainfall) and
22 not in the geographical space. Also, we will not discuss the exact mean annual rainfall
23 values at which forest, savanna and grassland are observed, but we mostly refer to
24 ranges of low, medium or high mean annual rainfall. For these ranges, we will perform
25 a qualitative comparison of the modeled and observed data in the parameter space (i.e.
26 maximum values, spread, distribution).

27 In addition to mean annual rainfall, other factors such as temperature (Higgins and
28 Scheiter, 2012), or temporal distribution of rainfall, are known to be important for
29 tropical grasslands, savannas and forests too. Rainfall heterogeneity, intermittency, and
30 seasonality affect water availability (D'Onofrio et al., 2014) and fire return times, and

13

are very important predictors of savanna/forest distribution (Lehmann et al., 2011), with rainfall seasonality reducing growth rates (e.g. limiting water availability, Sarmiento, 1984), influencing root-shoot biomass ratio and local cover (Yin et al., 2014a) and increasing fire frequency (Archibald et al., 2009). 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 future climatic changes 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 y^{-1} (Sankaran et al., 2005, see also Fig. 1A) and 1000 mm y^{-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).

1   At a first glance, the relation between tree cover and mean annual rainfall simulated by

2   the models (Fig. 2) is similar to that observed in the data (Fig. 1). In JSBACH output,

3   the maximum tree cover increases between zero and 800 mm y^{-1} approximately, where

4   it reaches its largest cover (see 90th quantile regression curve in Fig. 2A; similar results

5   are obtained with the 99th quantile regression lines, not shown). This increase is mostly

6   due to the fact that all the PFTs can colonize only a part of the space, which is

7   calculated dynamically and increased with water availability (although indirectly, via

8   NPP). In addition, fire related mortality increases with decreasing air humidity, thus

9   representing another source of water-related limitation in drier areas. At the same time,

10   the limitation to tree maximum cover is not likely to be the result of competition with

11   grasses, since trees are assumed to outcompete grasses, and they are affected by some

12   sort of grass competition at low water availability only temporarily after e.g. a fire (see

13   also Fig. 3B). JSBACH has a tendency to overestimate maximum tree cover at very low

14   values of mean annual rainfall (<100 mm y^{-1}), as this model is known to overestimate

15   GPP and NPP (Brovkin et al., 2013).

16   In the LPJ-GUESS-SPITFIRE model output (Fig. 2B), almost no tree cover is observed

17   until mean annual rainfall is about 300 mm y^{-1}. In this precipitation range, modeled

18   trees are water limited and outcompeted by grasses. Compared to the observations, this

19   model seems to limit tree cover in this precipitation range too strongly. Between about

20   300 and 900 mm y^{-1} annual rainfall, the maximum vegetation cover in LPJ-GUESS-

21   SPITFIRE increases until it reaches a maximum value (about 90% tree cover, see 90th

22   quantile regression line in Fig. 2B), partly due to water limitation that allows tree-grass

23   coexistence (between about 350 and 650 mm y^{-1}, Arneth et al., 2010), and partly due to

24   fires, which further limit tree cover.

25   In the aDGVM output, the tree cover displays a maximum value that grows with

26   precipitation between zero and about 500 mm y^{-1} (Fig 2C). In this range, modeled trees

27   are water limited, while grasses are better competitors in these drier conditions, thus

28   further reducing the tree cover, which would be higher if the model were run without

29   grasses (not shown). The aDGVM and LPJ-GUESS-SPITFIRE include differential

30   rooting depths for individuals, depending on their root biomass, and therefore both

31   models also represent water competition between grasses and tree seedlings. This

32   competition is known to be important for tree-grass coexistence (Hanan et al., 2008;

15

1 Sankaran et al., 2004), while adult trees have deeper roots that make them better
2 competitors in more humid environments (see Fig 3A and 3C respectively).

3 **3.2 Humid savannas and forests: the role of fire**

4 In more humid conditions, bimodality of vegetation cover below and above 60% is
5 observed in the MODIS data for precipitation in a range between around 1000 and 2000
6 mm y^{-1} (e.g. Hirota et al., 2011; Staver et al., 2011b, see also Fig 1B), i.e. clusters with
7 low and high tree cover values are observed, corresponding to a bimodality of savanna
8 and forest cover. Although the validity of this result still needs further investigation
9 (Hanan et al., 2014), this bimodality has been related to the vegetation-fire feedback,
10 possibly leading to bistability of savanna and forest in this range, as shown using simple
11 models (e.g. van Nes et al., 2014; Staver and Levin, 2012). In brief, grass, particularly
12 abundant in these wet areas, becomes an extremely good fuel in the dry season, which
13 promotes fire occurrence (i.e. the grass-fire feedback, Higgins et al., 2008; Trollope,
14 1984). When fire occurs, above ground biomass of all plants is removed. Established
15 savanna trees and grasses can resprout after fire, but tree seedlings are subject to high
16 mortality rates and many forest tree species cannot resprout. Together with grasses,
17 which regrow quickly in the open space after fires, savanna trees benefit from removal
18 of forest tree competitors, (Ratnam et al., 2011; Hoffmann et al., 2012) leading to a
19 stable savanna biome at intermediate rainfall values. Yet, environmental conditions
20 would allow forests in the absence of fire (e.g. Staver and Levin, 2012). Fig. 3A
21 provides a schematic diagram of this feedback. At the highest end of the rainfall range,
22 fires are totally suppressed and only forests are observed, since grass growth is inhibited
23 by tree shade.

24 The role of fire in maintaining savannas in humid environments is included in all of the
25 models, although in different ways. At high precipitation, JSBACH tree cover output
26 displays a constant maximum value (above about 800 mm y^{-1}), but the data display
27 considerable scattering below full tree cover (Fig 2A). In other words, the model
28 predicts savannas and forests in this range, but the data do not display bimodality of
29 high and low tree cover values (see Supplementary material, Appendix 1). This is a
30 consequence of the fact that in this model fire is triggered more by trees than by grasses,
31 since trees produce larger amounts of litter and thus of fuel. Fire favors grasses because

16

1 it opens the landscape by reducing the tree cover and generates space for them. Thus,

2 fire creates a negative feedback because fewer fires occur when tree cover is lower (Fig.

3 3B), thus preventing hysteresis and bistability in this model.

4 LPJ-GUESS-SPITFIRE simulation results do not show any low tree cover value (e.g.

5 below 50% cover) for rainfall higher than about 900 mm y^{-1}(Fig. 2B). Therefore, quite

6 surprisingly, this model does not predict any savanna in mesic environments. In the

7 model, though fire frequency is prescribed from the satellite data, fire spread depends

8 on fuel load (Fig. 3C) and fuel moisture, and thus unfavorable conditions might still

9 prevent fires. Both grass and tree presence increases fire intensity, opening up space,

10 and thus favoring grasses. This is not strictly a positive grass-fire feedback, because also

11 grass-free areas can burn. Thus, as grasses are not fostered by a positive feedback with

12 fire, they are always outcompeted by trees in LPJ-GUESS-SPITFIRE when water

13 availability is high, and they do not survive above approximately 900 mm y^{-1}. At the

14 same time, this issue is also likely to be connected to fire intensity depending on fuel

15 moisture. In this model, fire occurrence in a patch is calculated probabilistically from

16 the proportion of burned area as determined from the remote sensing product. If fire

17 occurs in a period of high fuel moisture, the intensity will be limited, thus having little

18 effect on vegetation. This probabilistic approach is necessary because the temporal

19 extent of the remote sensed data (now only ca. 10 years), used to generate the

20 probability of burned area for each pixel, is much shorter than the extent of the climate

21 data for which the model was run (ca. 100 years).

22 In aDGVM, maximum tree cover values can reach full cover above about 500 mm y^{-1},

23 but the points are still very scattered, and display some clustering at cover around 30-

24 60% for intermediate rainfall values (Fig. 2C). If we only select points in such rainfall

25 range (e.g. between 800 mm and 1200 mm y^{-1}), we observe that the tree cover

26 distribution is bimodal (see Appendix 1; note that this conclusion is robust to different

27 choices for the limits of the rainfall range). aDGVM includes explicitly the grass-fire

28 feedback, which is reinforced by the difference between fire tolerant savanna trees and

29 fire sensitive forest trees (Fig 3 A). When the forest trees suppress the savanna trees and

30 the grasses through light competition, the result is a forest biome with low fire

31 frequency or even fire suppression, primarily due to scarcity of (grass) fuel. At sites

32 with regular fire, forest trees cannot persist, resulting in low forest tree cover and

1   intermediate savanna tree cover, with grasses colonizing the open spaces and fostering

2   fire occurrence. This vegetation state represents a savanna biome. In a certain range of

3   environmental (e.g. rainfall) conditions, a system initialized as a forest will not shift to a

4   savanna, unless fire ignition probability is high, while a system initialized as a savanna

5   will persist in the same state unless fire ignition probability is very low. As a

6   consequence of including this positive feedback, experiments with the aDGVM show

7   that fire suppression can lead to transitions and hysteresis between savanna and forest

8   states (Higgins and Scheiter, 2012; Moncrieff et al., 2013).

9   Finally, we note that at extremely high rainfall values, when water is not limiting and

10   tree canopies close into a forest, both in LPJ-GUESS-SPITFIRE and in aDGVM trees

11   exclude grasses through light competition (Fig. 2B-C). This mechanism is included only

12   implicitly in JSBACH, and it acts along the whole precipitation gradient giving

13   competitive advantage to trees in general.

14   ### 3.3   Effects of future climatic changes

15   Hereafter we discuss results from two simple conceptual experiments (namely,

16   increasing CO2 concentrations, and decreasing precipitation) to illustrate how the

17   different representations of the ecological interactions in the three DGVMs could lead

18   to different predictions of the state of the grassland-savanna-forest transition under

19   future climatic changes.

20   Expected increase in CO_2 concentration in the future is likely to affect the outcome of

21   tree-grass competition, mediating both important mechanisms we discussed so far, i.e.

22   competition for water, and fires. Fire is expected to decrease under increased CO_2 level

23   because of the decrease in grass fuel load, given that C_3 woody plants are favored over

24   C_4 grasses under elevated CO_2 levels (Ehleringer et al., 1997). In JSBACH, higher CO_2

25   leads to higher productivity of grasses and trees, which in turn increases fire spread and

26   hence introduces a negative feedback, dampening the increase of tree biomass. In

27   aDGVM, CO_2 fertilization promotes tree growth, and thus tree establishment in

28   grasslands, transforming them into savannas or woodlands (with or without fire,

29   respectively). So in contrast to JSBACH, aDGVM includes a positive feedback, leading

30   to tree canopy closure in savannas, which, suppressing grass growth, reduces also fire

31   activity, transforming them into woodlands and forests (Scheiter and Higgins 2009).

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1   Due to this positive feedback, CO_2 concentration can induce hysteresis effects on the
2   vegetation states (Higgins and Scheiter 2012). LPJ-GUESS-SPITFIRE has an
3   intermediate behavior between the other two models, because grass and woody
4   vegetation contribute similarly to fuel formation. Also, since in this model fire
5   frequency is prescribed from remotely sensed data, any effect of changes of CO_2 levels
6   on fire occurrence would be very limited, though there might be pronounced effects on
7   resulting vegetation composition.

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

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

27   ## 3.4   Other mechanisms influencing tropical savannas, grasslands and
28   forests

29   Up to now we considered water limitation and fires as the main drivers of grassland,
30   savanna and forest distribution. Several additional factors can be important for
31   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, although it has been observed that savannas can be associated with nutrient poor soils (Lloyd et al., 2008), it is generally accepted that nutrient limitation does not explain the savanna-forest transition (Bond, 2010; Favier et al., 2012; Murphy and Bowman, 2012). For these reasons, and to avoid inconsistencies while evaluating different models, we only used DGVMs that did not include nutrient cycling. 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, 2013; 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 (Ratnam et al., 2011). Changes in land use have therefore strong influences on the current and future outcomes of tree-grass competition. Also, 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. This grass-fire feedback is reinforced by the higher flammability of forest trees with respect to savanna trees. 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 the main features of 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 vegetation-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 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

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1 overestimation. At the same time, in this model, fire is fostered disproportionately by
2 woody vegetation as compared to grasses, resulting in a negative feedback. This is
3 responsible for observing savannas in larger parts of the rainfall gradients, and no
4 savannas would be simulated without them. Although the three models display
5 comparable outcomes under the current climate, the presence of a negative fire-
6 vegetation feedback in JSBACH, a positive feedback in aDGVM, and an intermediate
7 behavior in LPJ-GUESS-SPITFIRE, leads to different predictions of fire frequency and
8 effects under climate change scenarios between the three models. In JSBACH, the
9 initial increase in woody vegetation, due to higher CO_2 concentrations, would get
10 dampened by the consequent increase in fire spread. Interesting in this perspective is
11 that the sensitivity to shifts between forests and savannas is low for JSBACH, as
12 negative feedbacks are more important, while in aDGVM the positive grass-fire
13 feedback mechanism results in a large sensitivity to shifts of the different tree-grass
14 systems. LPJ-GUESS-SPITFIRE has an intermediate behavior between the other two
15 models, since grass and woody vegetation foster fire in a similar way. Also, in this
16 model fires seem to be suppressed too easily by high humidity conditions, which cause
17 savannas to be absent at medium-high annual rainfall values.

18 Tree seedlings are the bottleneck stage of tree life in the forest-savanna-grassland
19 transition (Salazar et al., 2012; Sankaran et al., 2004), and the two most important
20 mechanisms we identified here, i.e. water competition and limitation, and fires, tend to
21 affect tree seedlings particularly strongly. Thus, including tree demography as in LPJ-
22 GUESS and the aDGVM, improves the representation of ecological interactions in the
23 models. Also, representing forest and savanna trees with different flammability and
24 shade tolerances (as in LPJ-GUESS and aDGVM) is beneficial, and they reinforce the
25 positive grass-fire feedback, if included (as in aDGVM).

26 Having in mind that DGVMs need to be kept as simple as possible, we conclude that the
27 most important mechanisms to better represent the forest-savanna-grassland transition
28 are i) how water limits tree growth and regulates tree-grass competition, and ii) the
29 grass-fire feedback. Distinguishing between tree life stages and representing the
30 different responses of forest and savanna trees, are less important features for the
31 models, although they can considerably ameliorate the representation of the two main
32 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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31

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)	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	No	LAI, PFT fractions, carbon in vegetation pools	No	No	Uncolonized space, hospitable land (water, indirectly via NPP)	Dominant woody (tree, shrub) PFTs	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	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.	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	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	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

1 **Figure captions**

2 Figure 1

3 Tree cover as a function of mean annual rainfall (mm y^{-1}). A) Savanna field data, reprinted

4 from Sankaran et al. (2005); B) tree cover obtained from MODIS woody cover product (as

5 e.g. Hirota et al., 2011), where anthropogenic land use is masked as described in the text. For

6 clarity of representation, we selected only 0.05% of the data. For both databases, we selected

7 only the data points between 35° S and 15° N in Africa. The dots are data; the continuous

8 lines are the 90th quantile nonlinear regression (99th quantile not shown; see values of b

9 coefficients in Tab. B1 in the Supplement). Notice that the field data (A) correspond only to

10 savanna sites, and thus encompass a smaller rainfall range than the satellite data (B).

11

12 Figure 2

13 Model outputs for tree cover as a function of mean annual rainfall (mm y^{-1}) in Africa

14 between 35° S and 15° N: A) JSBACH; B) LPJ-GUESS-SPITFIRE; C) aDGVM. The dots are

15 data, the continuous lines are the 90th quantile nonlinear regression (99th quantile not shown;

16 see value of b coefficients in Table B1 in the Supplement).

17

18 Figure 3

19 Schematic diagram of the main ecological interactions that determine the forest-savanna-

20 grassland transition, according to: A) Ecological theory, and the aDGVM; B) JSBACH; C)

21 LPJ-GUESS-SPITFIRE. Light blue arrows represent positive effects, dark blue arrows

22 negative effects. The aDGVM (A) was designed to include the key ecological mechanisms

23 known from theory, namely: grasses increasing fire spread (positive feedback), distinction

24 between forest and savanna trees (with fires damaging forest tree mostly, shade intolerant

25 savanna seedlings and shade tolerant forest seedlings), separate resource competition between

26 trees and grasses depending on their size (grasses and tree seedlings compete for the same

33

1   water, while adult trees outcompete grasses for both water and light). JSBACH (B) includes

2   fires as mainly fostered by tree litter, which are also mainly damaged by fire (negative

3   feedback). Trees competitively exclude grasses, although temporarily after disturbances

4   grasses also compete with them for the same water. LPJ-GUESS-SPITFIRE (C) is on one

5   hand similar to the aDGVM, since it distinguishes tree life stages and it separate between

6   savanna and forest trees, with analogous representation of water and light tree-grass

7   competition. On the other hand, it includes a similar effect of tree and grass biomass in

8   fostering fires.

A

grass as fuel **+** → 🔥

damage to trees **−**

Savanna Trees   Forest Trees

trees as fuel **+**

water competition grass-tree seedlings **−**

competition tree-grass (light and water) **−**

Light competition **−** **−** **−**

Grass

Ecological theory & aDGVM

B

grass as fuel **+** → 🔥

damage to trees **−**

Trees

trees as fuel **+**

water use by grass (only transitory) **−**

Competitive exclusion of trees on grass (light) **−**

Grass

JSBACH

C

grass as fuel **+** → 🔥

damage to tree seedlings **−**

Savanna Trees   Forest Trees

trees as fuel **+**

water competition grass-tree seedlings **−**

competition tree-grass (light and water) **−**

Light competition **−** **−** **−**

Grass

LPJ-GUESS-SPITFIRE