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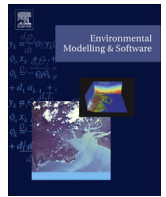
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Simulating the impacts of reduced rainfall on carbon stocks and net ecosystem exchange in a tropical forest

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ABSTRACT

Forest models can be useful tools to improve our understanding of forest dynamics and to evaluate potential impacts of climate change. There is an ongoing debate how drought events influence the dynamics of tropical forests. In this study, we explored the role of changes in precipitation on tropical forests in Madagascar. Therefore, we derived a new parameterization of the process-based forest model FORMIND using local forest inventory measurements. This model was extended by a drought sensitivity module based on a water use efficiency concept.

The objective of this study is to evaluate how different levels of water availability modify forest productivity, and net ecosystem exchange as a function of mean annual precipitation. Our simulation results indicate that a moderate precipitation decline (0%–30% of current precipitation conditions) has only minor impact on forest carbon stocks and exchange. A rainfall decline below 30% of current precipitation conditions would change forest structure considerably.

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1. Introduction

Tropical forests play a key role in the global carbon cycle. Approximately half of the aboveground carbon contained in the global vegetation (558 Pg C), is stored in tropical forests (Blanc et al., 2009; Houghton, 2005; Houghton et al., 2009). In this context, it is discussed that climatic changes, such as shifts in precipitation patterns, are expected to change the carbon pools and carbon cycle of tropical ecosystems (Grace, 2004; Hannah et al., 2011; Houghton et al., 2009; Malhi et al., 1999). In the extreme case, tropical forests might even switch from a carbon sink to a carbon source under severe climate change (Phillips et al., 2009). Accordingly, understanding and predicting tropical forest dynamics under climatic changes has become a highly relevant issue in ecological research (Lewis et al., 2004).

Tropical forest dynamics are determined by multiple and potentially interacting drivers, e.g. precipitation, temperature, CO₂ concentration and land use (Bonan, 2008). However, in order to predict forest dynamics it is crucial to understand the consequences of specific drivers on the performance of trees

independently. In field studies it is often challenging to disentangle the influences of several confounded drivers. Process-based forest models offer a promising tool for assessing tropical forest's responses to specific ecological drivers. In this study, we apply a process-based model to a rainforest on Madagascar and investigate in detail the potential consequences of varying precipitation, which is expected to be a key driver of forest dynamics and thus of aboveground carbon pools under climate change.

Large areas of tropical forests have been already affected by drought events, e.g. the Amazon in 2010 (Lewis et al., 2011). The IPCC predicts for several tropical regions a significant change in precipitation. For Madagascar a rainfall decline of approximately 20% up to the year 2100 has been estimated (Pachauri and Reisinger, 2008). During irregularly occurring El Nino events, the high mean annual rainfall in Madagascar (approximately 3000 mm) might be even reduced by up to 60% (Hannah et al., 2008; Pachauri and Reisinger, 2008). Because of these expected shifts in precipitation patterns in South-East Africa, this region is of high interest and priority for investigating the impact of precipitation on tropical forest dynamics and carbon pools (Malhi and Wright, 2004). However, to our knowledge, the impact of reduced precipitation on forest structure and productivity in this region has not been investigated yet.

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On a regional scale, the impact of climate on forest dynamics and carbon stocks has been assessed with dynamic global vegetation models (Cramer et al., 2001; Gerten et al., 2005; Hely et al., 2006; Huntingford et al., 2008). These models are using simplified approaches for modelling the vegetation dynamics and competition between trees, whereas local scale forest models include a more detailed description of these processes (Bugmann, 2001; Shugart, 2003). However, the impact of droughts has been scarcely explored so far using detailed local forest models.

The objective of this study is to investigate potential effects of reduced precipitation on tropical forests in Madagascar using a local forest model (stand-level model). The FORMIX3 model (Huth and Ditzer, 2000; Huth et al., 1998), which is applied in this study, combines the forest gap model approach with the calculation of tree growth based on a carbon balance approach. In this study, the individual-based forest model has been extended by incorporating a water cycle module, which is a precondition to analyse the effect of reduced precipitation on forest structure in a mechanistic manner. We especially focus on the question how reduced annual rainfall and soil water deficit affect aboveground biomass, primary production, carbon pools and net ecosystem exchange (NEE) in a tropical forest in Madagascar. In this way, we want to evaluate the robustness of forest dynamics and carbon cycling against changes in precipitation.

2. Methods

2.1. Study site

The tropical forests of Madagascar are known as hot-spots of biodiversity (Brummitt and Lughadha, 2003). Nevertheless, over the last century up to 90% of the forest area on the island has been destroyed (Green and Sussman, 1990; Sussman et al., 1994).

The study site is the tropical lowland forest of the Reserve Naturelle Integrale (RNI) de Betampona (Betampona Nature Reserve) in Madagascar. The protected area of RNI Betampona comprises 2228 ha and is located at 17°15'–17°55' S; 49°12'–49°15' E near the town of Toamasina, Madagascar. Approximately 50% of RNI Betampona is primary forest. The annual precipitation is about 3000 mm and the mean temperature is approximately 27 °C. The rainfall and temperature vary seasonally, with a hot, rainy season from November to April and a cooler, dry season from May to October.

To parameterize the FORMIX3 model for Madagascar's lowland forests, we utilized data from one hundred 10 m-diameter circular survey plots including all trees with a diameter at breast height (DBH) above 5 cm and scaled up these data to 1 ha. We found between 16 and 53 trees in a circular plot. The field surveys were completed in 2004 at random locations in the primary forest. For all trees, the following data were collected: species identity, DBH, tree height and the presence of qualitative health characteristics (Armstrong et al., 2011). In 2004, 2847 trees (DBH ≥ 5 cm) belonging to 244 tree species were measured. The DBHs were re-measured in 2005 to assess annual DBH growth.

2.2. The FORMIX3 forest model

2.2.1. Model overview

Individual-based gap models are often used to investigate forest dynamics and structure (Botkin, 1993; Bugmann, 2001; Shugart, 2003), but only a few forest models have been adapted to tropical forests. The FORMIX3 forest model (Huth and Ditzer, 2000; Huth et al., 1998) has been extensively tested and applied to tropical forests in Malaysia, French Guyana, Venezuela, Mexico, Brazil and Paraguay (Gutiérrez and Huth, 2012; Huth and Ditzer, 2000, 2001; Kammesheidt et al., 2001; Köhler et al., 2003; Köhler and Huth, 2004, 2007; Rüger et al., 2007, 2008). The FORMIX3 model is a spatially explicit, process-based and individual-based forest gap model. Forests up to several hectares in size (1 ha in this study) can be simulated. The forest stand area is divided into patches that represent the typical size of tree fall gaps (20 m × 20 m). These patches have an explicit spatial position, while trees within patches are not simulated in a spatially explicit way. FORMIX3 uses the gap model approach: simulating the formation and recovery of canopy gaps or patches across a forest over time. Patches are formed by falling canopy trees, which increases light availability and thus growth of sub-canopy trees and recruits. As main processes, the model includes tree growth (increment of tree biomass), competition for light and space, regeneration, and mortality. The vertical leaf distribution and light availability are calculated within each gap at the tree level. The biomass growth, also calculated at the tree level, is described on the basis of a carbon balance by modelling ecophysiological processes including: photosynthesis, respiration, biomass allocation and litter fall. Photosynthetic production is calculated as a

function of the local light availability (using light response curves). Other resource limitation factors like soil water deficit have not been included in previous versions of FORMIX3, but were incorporated for the purpose of this study (see below).

The model was simulated with a monthly time step for 600 years (see simulation experiments section). A detailed model description as well as more information on the parameterization process can be found in Appendix A and in Huth and Ditzer (2000).

2.2.2. Species grouping

Grouping species into plant functional types or groups with similar trait expressions is useful for analysing species rich forests (Smith and Shugart, 1997) – especially when the focus is not on analysing the species richness as in our study. Therefore, the 244 tree species recorded in the investigated forest were grouped into twelve plant functional types (see Table 1, species list see Appendix C) according to their maximum attainable height and their light requirements (Köhler et al., 2000). The classes of light requirements were shade-tolerant (climax species), intermediate shade-tolerant and shade-intolerant (pioneer species). Information on light requirement was collected from the literature (Schatz, 2001) as well as from local experts.

2.3. The soil water module

The biomass increase of a single tree in the FORMIX3 model depends on tree size, light, and space availability. For this study, a new module for the dependence of tree growth on soil water availability has been added. Water limitation has not been considered explicitly in previous model versions of FORMIX3. This extension was accomplished by introducing a drought-related reduction factor for photosynthesis. This reduction factor indirectly influences diameter growth and height growth.

The reduction factor due to water deficit (RW in %) lowers the photosynthesis rate of a single tree (P_B in $\text{Mg}_{\text{odm}} \text{ha}^{-1} \text{yr}^{-1}$, see Appendix A; Mg_{odm} = mega gram organic dry matter) and depends on soil water content, (θ in Vol%, Fig. 1) as follows:

$$P_B = P_B^{\text{pot}} \cdot \text{RW}(\theta), \quad (1)$$

where P_B^{pot} is the potential photosynthesis rate of a single tree (P_B in $\text{Mg}_{\text{odm}} \text{ha}^{-1} \text{yr}^{-1}$) without water stress.

Specifically, when the soil water content is lower than the permanent wilting point (PWP in Vol%), biomass growth ceases. The PWP value depends on soil type and was taken from the literature (soil type sandy loam; Maidment, 1993). When soil water content is above a certain level – the minimum soil water content for unstressed photosynthesis (MSW in Vol%) – tree growth occurs without limitation. Soil water content values between these two endpoints result in a linear constraint on photosynthesis rate based on the approach of Granier (Granier et al., 1999; Hanson et al., 2001; see Fig. 1). The critical soil water content MSW (in Vol%) is determined using Granier's approach (Granier et al., 1999):

$$\text{MSW} = \text{PWP} + \frac{1}{3}(F_C - \text{PWP}), \quad (2)$$

where F_C is the field capacity of the soil and PWP is the permanent wilting point. It is important to note that this water stress approach included three simplifications: (1) no distinction was made between individual tree species, (2) every tree was

Table 1

Species grouping for the RNI Betampona. The classification includes five size classes and three light demand classes. The light class indicates shade tolerance. Shade-intolerant trees correspond to pioneer trees. The shade-tolerant trees are the climax species. The size class depends on the maximum height of the tree species. The height range is given in the 'Height Range (m)' column.

PFT	Name	Size class	Max. height (m)	Light class
1	Late successional emergent trees	Emergent	>33	Shade tolerant
2	Mid successional emergent trees	Emergent	>33	Intermediate
3	Late successional canopy trees	Canopy	24–33	Shade tolerant
4	Mid successional canopy trees	Canopy	24–33	Intermediate
5	Late successional large trees	Large	16–24	Shade tolerant
6	Mid successional large trees	Large	16–24	Intermediate
7	Early successional large trees	Large	16–24	Shade intolerant
8	Late successional small trees	Small	10–16	Shade tolerant
9	Mid successional small trees	Small	10–16	Intermediate
10	Early successional small trees	Small	10–16	Shade intolerant
11	Late successional understory trees	Understory	<10	Shade tolerant
12	Mid successional understory trees	Understory	<10	Intermediate

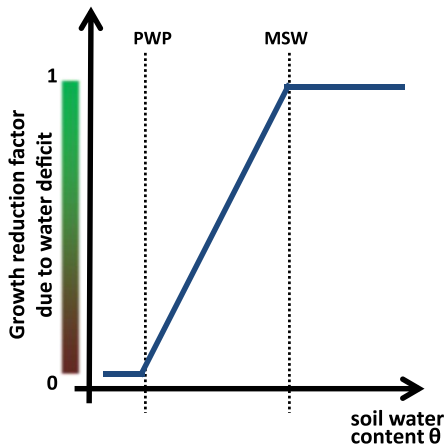


Fig. 1. Reduction of tree photosynthesis due to water deficit. The reduction factor depends on the actual soil water content. If the soil water content drops below the MSW threshold, tree growth will be reduced. PWP = Permanent wilting point; MSW = Minimum soil water content for potential photosynthesis.

assumed to have the same rooting depth, and (3) only one soil layer was built into our model (soil depth 2.5 m). This approach is comparable with aggregation techniques done in the process-based forest model SIERRA (Mouillot et al., 2001) and in dynamic global vegetation models like LPJ (Sitch et al., 2003) and LPJ-GUESS (Hickler et al., 2006, 2004). Also the forest carbon allocation model 3-GP uses an aggregated approach, but with nonlinear soil water response (Landsberg and Waring, 1997). Due to our mortality approach, the decrease in tree growth caused by a water deficit also increases tree mortality (Eqs. (A.8) and (A.9) in Appendix A).

2.3.1. Soil water content

The soil water content (θ in Vol%) is computed with a daily time step using a differential equation (Eq. (3)), which quantifies temporal changes in the soil water (Kumagai et al., 2004) depending on precipitation (P), interception (IN), run-off (RO), and transpiration (TR).

$$\frac{d\theta}{dt} = P(t) - IN(t) - RO(t) - TR(t) \quad (3)$$

2.3.2. Interception

The main input to soil water is daily precipitation (P in mm). A fraction of rainfall is captured in the crowns of trees and evaporates before reaching the ground. This capture is defined as the interception process (IN in mm). Here, daily interception is assumed to be directly proportional to the leaf area index (LAI) of a forest patch area with the size of 20 m × 20 m (Liang et al., 1994):

$$IN(t) = \min(K_L \cdot LAI, P(t)), \quad (4)$$

where K_L is the interception constant (for value see Table A.3 in Appendix A). The daily interception cannot be greater than the precipitation on that day.

2.3.3. Surface/subsurface run-off

Calculating the run-off, we computed the remainder of the rainfall that reaches the surface of the ground either as stem flow or as throughfall. We consider two different forms of run-off (RO in mm): surface run-off and subsurface run-off. Surface run-off (RO_1 in mm) is defined in the following way:

$$RO_1 = \max(0, \theta(t) + P(t) - IN(t) - Por), \quad (5)$$

where Por (in Vol%) is the soil porosity, defined as the maximum water intake of the soil. The surface run-off increases when the soil is fully saturated with water. Because of the high porosity of the soils in tropical forests, surface run-off occurs only rarely (Bonnell and Balek, 1993).

The second form of flow is subsurface run-off (RO_2 in mm) due to gravitation. We used the Brooks–Corey relationship to estimate this flow (Liang et al., 1994):

$$RO_2 = K_s \left(\frac{\theta(t) - \theta_r}{Por - \theta_r} \right)^{\frac{2}{\lambda} + 3}, \quad (6)$$

where K_s is the fully saturated conductivity, θ_r the residual water content, and λ the pore size distribution index.

2.3.4. Transpiration

Daily transpiration (TR in mm) is the loss of water vapour from plants due to photosynthesis. Here, it is calculated based on the water use efficiency concept (Lambers et al., 2008) as follows:

$$TR(t) = \frac{P_B(t)}{WUE}, \quad (7)$$

where WUE (in $\text{Mg}_{\text{odm}} \text{kgH}_2\text{O}^{-1}$) is the water use efficiency and P_B (in $\text{Mg}_{\text{odm}} \text{ha}^{-1} \text{yr}^{-1}$) is the photosynthesis rate of the trees. The sum of transpiration and interception is limited by the potential evapotranspiration (PET in mm). PET is the maximum amount of water that would be transpired and evaporated if there were enough water available. Daily PET is calculated with the modified Penman–Monteith equation, which has often been applied to tropical vegetation (Allen et al., 1998; Fisher et al., 2009; Monteith, 1965). For more details concerning the water use efficiency concept and calculating the PET see Appendix B.

Most parameters of the soil water module (porosity, field capacity, permanent wilting point, residual water content, conductivity and pore size distribution) depend on soil type. There exist no detailed soil measurements for this poorly studied region in Madagascar – only the local soil texture is known. Therefore, the missing values were estimated from the literature on tropical forests (soil texture: sandy loam; Larcher, 2001; Liang et al., 1994; Maidment, 1993). Also the water use efficiency (WUE) for the transpiration values is relatively uncertain. Therefore we have conducted a sensitivity analysis for WUE (see Appendix B). All compiled parameter values can be found in Appendix A.

2.4. The precipitation module

To investigate different rainfall scenarios, daily precipitation values were simulated. We follow the approach of Kumagai, who assumed that the frequency (time between two rainfall events: S in days) and amounts of daily rainfall (A in mm) could be expressed as independent random variables (Kumagai et al., 2004). For both, an exponential distribution is assumed. Because of seasonal variations and inter-annual variability, we divided the year into periods of three months. The two distributions were parameterized individually for each period i . The interval between precipitation events (S), expressed as an exponential distribution, is given by a probability density function

$$f_S(x) = s_i \cdot \exp(-s_i \cdot x), \quad x > 0, \quad (8)$$

where $1/s_i$ is the average number of days between two rainfalls in period i . When rainfall occurs, the amount of precipitation (A) is also assumed to be an independent random variable, expressed by an exponential probability density function

$$f_A(x) = a_i \cdot \exp(-a_i \cdot x), \quad x > 0 \quad (9)$$

where $1/a_i$ is the average amount of precipitation on a rainy day. The sum of rainy days and dry days gives the total number of days in one period i . For calibration, we used daily meteorological data of the last 40 years from the town of Toamasina, which is located near the study site (National Climatic Data Center, <ftp://ftp.ncdc.noaa.gov/pub/data/gsod/>). The parameter values of the precipitation module are listed in Table A.3 in Appendix A.

2.5. The carbon flux module

A first carbon module approach has been presented and tested successfully for tropical forests in South-East Asia by Pinard and Cropper (2000). In this study, we implemented a new carbon module to the forest model FORMIX3. Forest carbon stocks were simulated in three separate pools: the aboveground biomass pool (AGB in $\text{Mg}_c \text{ha}^{-1}$, Mg_c = mega grams carbon), the deadwood pool (D in $\text{Mg}_c \text{ha}^{-1}$, including litter), and the soil carbon pool (S in $\text{Mg}_c \text{ha}^{-1}$). The annual input to the deadwood pool is driven by tree mortality (M in $\text{Mg}_{\text{odm}} \text{ha}^{-1}$). Microorganisms decompose the deadwood to soil (decomposition rate $d_{D \rightarrow S}$). During the deadwood decomposition process, they emit carbon into the atmosphere ($d_{D \rightarrow A}$). The change in the deadwood pool is calculated as follows:

$$\frac{dD}{dt} = M - d_{D \rightarrow A} \cdot D - d_{D \rightarrow S} \cdot D \quad (10)$$

Due to respiration, the soil carbon pool (S) also emits carbon into the atmosphere ($d_{S \rightarrow A}$):

$$\frac{dS}{dt} = d_{D \rightarrow S} \cdot D - d_{S \rightarrow A} \cdot S \quad (11)$$

The net ecosystem exchange (NEE in $\text{Mg}_c \text{ha}^{-1} \text{yr}^{-1}$) of the forest is calculated here as difference between carbon storage by photosynthetic production (P_B in $\text{Mg}_{\text{odm}} \text{ha}^{-1} \text{yr}^{-1}$) and carbon emission due to autotrophic respiration (R in $\text{Mg}_{\text{odm}} \text{ha}^{-1} \text{yr}^{-1}$), decomposition of deadwood, and soil respiration.

$$NEE = P_B - R - d_{D \rightarrow A} \cdot D - d_{S \rightarrow A} \cdot S \quad (12)$$

The specific transition rates between the forest, deadwood and soil pools are documented in Table A.3 in Appendix A. Here, positive NEE values indicate that the carbon stock in the forest is increasing.

2.6. Simulation experiments

In this study we used simulations with the extended FORMIX3 model to explore the sensitivity of the investigated Malagasy forest to different precipitation regimes. Using *in situ* field measurements from a tropical forest in eastern Madagascar, a parameterization of the FORMIX3 model was developed and tested for the region in a first step (see Appendix A). Unknown parameter values (e.g., number of seeds) were determined with a calibration process by comparing the aboveground biomass, species composition, and tree density of a simulated mature forest with field data from the study region (Armstrong et al., 2011). For decision making concerning the unknown model parameters we minimized the mean square error between field data and the averaged equilibrium state of the corresponding simulated value (Bennett et al., 2013).

For the analysis of a mature forest, we simulated 1 ha of forest succession over 600 years. All calculated output values are mean values over 10 simulation runs and over the last 400–600 years of the forest succession simulation, based on the assumption that the model in that period is in the equilibrium/climax state.

We analysed 14 different precipitation levels by varying the mean annual precipitation between 800 mm yr⁻¹ and 3400 mm yr⁻¹ (increment 200 mm yr⁻¹). The range includes the current mean annual precipitation (3000 mm), the regional IPCC forecasts of approximately 20% reduction in mean annual precipitation (2400 mm) as well as the extreme scenario of 60% reduction in mean annual precipitation (1200 mm). Such an extreme reduction is unlikely to occur for mean annual precipitation, but is realistic for sporadic El Niño events, which occur every two to seven years (Bates et al., 2008; Dunham et al., 2011; Ingram and Dawson, 2005; Malhi and Wright, 2004; Pachauri and Reisinger, 2008). However, we intentionally chose a broad range of mean annual precipitation values to analyse in detail how forest dynamics and carbon stocks respond to long-term shifts in mean annual rainfall in our model.

3. Results

The calibrated model was able to reproduce the observed biomass and PFT composition very well (Appendix A). In the following we present results with respect to the response of forest dynamics and carbon stocks to variations in mean annual precipitation.

3.1. Impact of precipitation on aboveground biomass and forest productivity

Under current rainfall conditions, the simulated overall aboveground biomass was observed to be 800 Mg_{odm} ha⁻¹ (mean over years 400–600, see Fig. 2a). This value corresponds well to field data (see Appendix A and Fig. 2a). When annual rainfall was reduced by 20% (IPCC scenario), the forest lost only 1% of its biomass (Fig. 2b). The biomass loss was 22% when annual precipitation was reduced by 60% (Extreme scenario).

The impact of reduced rainfall on forest biomass differed between tree species groups (Fig. 2b). In the simulated unstressed forest, shade-tolerant trees accounted for nearly 70% of the overall

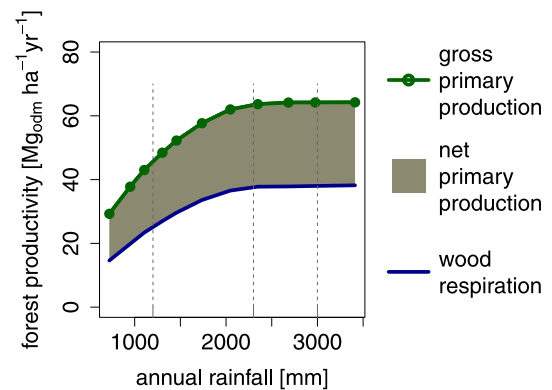


Fig. 3. Mean forest productivity (GPP, NPP) and autotrophic respiration for a simulated mature forest depending on different rainfall scenarios. The dotted lines represent from left the Extreme scenario (–60%), the IPCC scenario (–20%) and the Current scenario.

aboveground biomass (which corresponds well to field data – see Appendix A). In the Extreme scenario this fraction was reduced to 52%. The fraction of intermediate tolerant trees increased from 29% to 47%. The percentage of shade-intolerant tree species (pioneers) was below 1% for all rainfall scenarios. In general, the species composition shifted towards species with intermediate light tolerance when the precipitation was reduced.

For a mature forest the simulation predicted a gross primary production of 64 Mg_{odm} ha⁻¹ yr⁻¹ under current rainfall conditions. The net primary production was estimated at 26 Mg_{odm} ha⁻¹ yr⁻¹, autotrophic respiration at 38 Mg_{odm} ha⁻¹ yr⁻¹ (maintenance and growth respiration of the trees). In the IPCC scenario no reduction of GPP or respiration was observed (Fig. 3). However, when annual rainfall was reduced by 60% (Extreme scenario), gross primary production decreased by 33%, net primary production decreased by 25% and respiration decreased by 38%.

3.2. Impact of precipitation on net ecosystem exchange (NEE) and carbon pools

For the current level of annual rainfall, the forest stored up to +15.0 Mg_c ha⁻¹ yr⁻¹ in the first 100 years of the simulated regeneration started from bare ground (carbon sink, Fig. 4a). Our simulations show that the modelled, unstressed Malagasy forest reached a stable equilibrium (and, therefore, stable carbon flux)

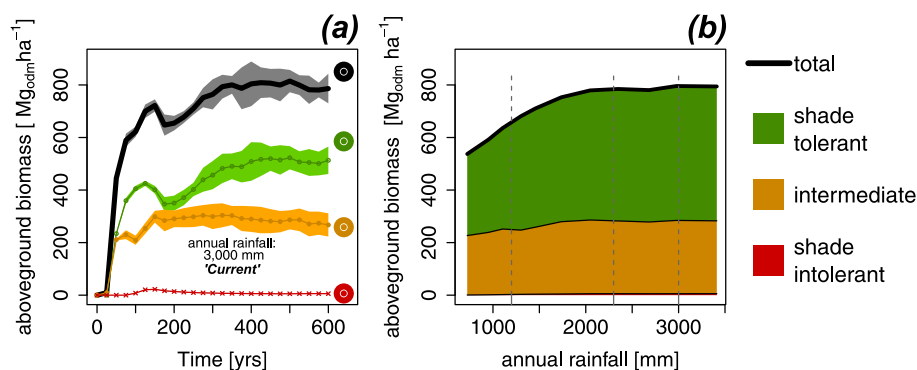


Fig. 2. Aboveground biomass for a simulated mature forest depending on different rainfall scenarios. (a) Simulated aboveground biomass over a period of 600 years using the current annual rainfall for Madagascar (3000 mm). The dots represent the field measurements of the forest in Madagascar. (b) Average species composition and total aboveground forest biomass as a function of mean annual precipitation. The species composition is calculated as a fraction of total aboveground biomass. We distinguished three species groups with different light demands (shade-tolerant/climax species, shade-intolerant/pioneer species, tree species with intermediate shade tolerance). The dotted lines represent from left the Extreme scenario (–60%), the IPCC scenario (–20%) and the Current rainfall scenario.

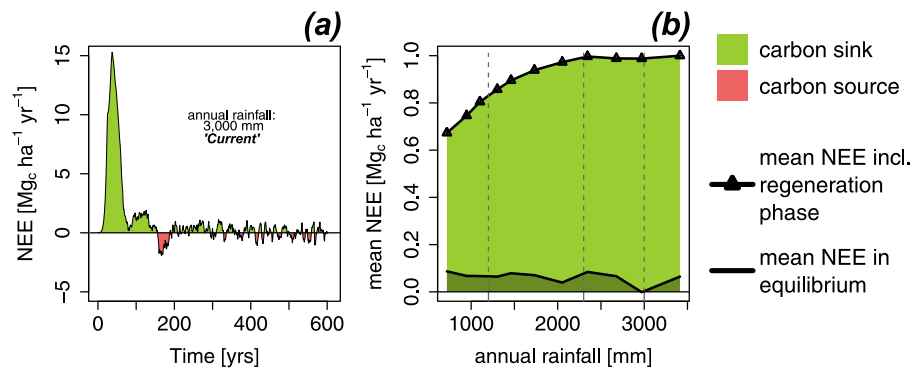


Fig. 4. Net ecosystem exchange NEE for a simulated mature forest depending on different rainfall scenarios. (a) Simulated NEE over a period of 600 years using the current annual rainfall for Madagascar (3000 mm). In the first 100 years of the regeneration phase the forest stores most of the carbon. (b) Mean NEE for a simulated mature forest as a function of annual rainfall. Presented are the mean NEE over the whole simulation period of 600 years, inclusive of the regeneration phase. The second line is the mean NEE without the regeneration phase (only values between years 400 and 600 of the simulation). Positive values indicate that the forest stores carbon.

after 200 years (Fig. 4a). In this state, the average NEE was nearly zero and fluctuated between -1.0 and $+1.0 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$. If annual rainfall was reduced by 20% (IPCC scenario), the mean NEE over the whole succession period showed a reduction of 5% (Fig. 4b). However, an annual rainfall reduction of 60% (Extreme scenario) caused a reduction in the NEE of 25% ($0.75 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$). The mean NEE of a mature forest (average over the last 400 years of the simulation) is in all rainfall scenarios nearly zero.

In our forest succession simulation, the total carbon stored in the forest was 550 Mg_c per hectare under current rainfall conditions (including living biomass, deadwood pool, and soil carbon). $71 \text{ Mg}_c \text{ ha}^{-1}$ were stored in the deadwood pool and $64 \text{ Mg}_c \text{ ha}^{-1}$ in the soil carbon pool. According to the IPCC scenario (rainfall -20%), carbon storage in the aboveground living biomass, deadwood pool and soil pool was relatively stable (reduction of 2%). However, carbon storage decreased in the Extreme scenario (rainfall -60%) by 22% in the aboveground living biomass and by 25% in the soil and in the deadwood pools, respectively (Fig. 5).

4. Discussion

In the IPCC 2007 report (Pachauri and Reisinger, 2008), a rainfall decline of approximately 20% is predicted for Madagascar for 2100. Based on our simulation results, the overall impact of 20% reduced rainfall on the studied tropical forest in Madagascar will be low to moderate. Specifically, the effect on forest biomass, production, and net ecosystem exchange (NEE) will be low. Our simulations suggest

that with a reduction of 20% in mean annual precipitation, the soil water content is still high enough to support unstressed tree growth.

We also investigated the effect of higher rainfall reductions. To summarize the simulation results, the impact of reduced precipitation on the Malagasy study forest can be divided into two classes. If precipitation is greater than 2100 mm per year, the effect of reduced rainfall on forest dynamics is low. However, annual rainfall levels below 2100 mm (-30% of the current value) would change forest structure considerably. Below this threshold, biomass, productivity, and NEE will be significantly reduced. Reducing the annual precipitation by 50% (1500 mm), for instance, decreases the aboveground NPP and lowers the carbon stocks by about 20%, respectively. Please notice that an annual rainfall of 1500 mm is still very high compared to the precipitation in other regions. To a certain extent, it appears that for the scenarios with strong precipitation reduction, the forest buffers the effects of reduced rainfall by decreasing LAI and transpiration (Lischke and Zierl, 2002).

The slowdown of tree growth in our reduced rainfall simulations fits well to throughfall exclusion experiments for tropical forests in Indonesia (Schuldt et al., 2011). By reducing the soil water content by up to 30%, they found that annual stem diameter growth decreased by 30% (Schuldt et al., 2011). In our Extreme simulation scenario, the soil water content was reduced by 22% and the resulting net primary production (NPP), which is to some extent correlated with tree diameter growth, was reduced by 25%.

In another throughfall exclusion experiment in the Amazon, precipitation was reduced by 50%, aboveground NPP declined by 25% (Nepstad et al., 2002). In our simulation, the aboveground NPP was reduced by one fifth when we reduced the rainfall by 50%. A second experiment in the Amazon investigated a rainfall reduction of 35–41% (Brando et al., 2008), resulting in a reduction of 21% in aboveground NPP. For a rainfall reduction of 40% in our simulated forest the NPP declined by 15%. The reduction of NPP in our simulation is thus comparable to the results in the throughfall exclusion experiments.

In the Amazon, Malhi et al. (2004) analysed the aboveground wood productivity of Neotropical forest plots. The aboveground coarse wood productivity varies by more than a factor of three: from $1.5 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$ (1000 mm annual rainfall) to $5.5 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$ (4000 mm annual rainfall). Our study shows a comparable relationship between rainfall and net primary production (NPP, as a proxy for aboveground wood productivity without mortality): NPP varies between $5 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$ (800 mm annual rainfall) and $12 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$ (3500 mm annual rainfall). The productivity is much higher compared to the analysis in the

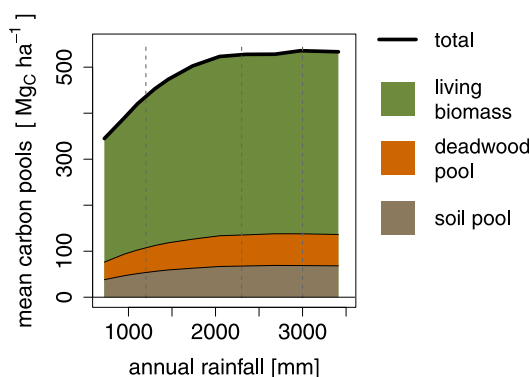


Fig. 5. Simulated mean carbon storage of a mature forest including living biomass, soil carbon and dead wood as a function of annual rainfall. The dotted lines represent from left the Extreme scenario (-60%), the IPCC scenario (-20%) and the Current scenario.

Amazon. This is mainly due to the higher aboveground biomass stocks (see Appendix A).

It is challenging to discuss under which conditions tropical forests act as a carbon sink or a carbon source. Grant et al. (2009) found in a simulation study large carbon sinks, up to $6 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$ in the first decades of succession and reported that the forest need 100 years to reach carbon neutrality ($+1 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$) after a clear-cut. Due to higher carbon pools compared to other forests, our investigated forest stored more carbon after a clear-cut and had a longer regeneration phase (200 years). The mean NEE of our simulated mature forest (average over the last 200 years of the simulation) was in all rainfall scenarios nearly zero and the standard deviation remained stable over precipitation scenarios ($1 \text{ Mg}_c \text{ ha}^{-1} \text{ yr}^{-1}$).

It is obvious that throughfall experiments in tropical regions can be done only for a limited number of sites. Forest models can play an important role in realizing virtual experiments as they synthesize current knowledge on forest ecology. This simulation study has shown that the used forest model reproduce similar results compared to several throughfall experiments. Nevertheless, we also want to discuss possible weaknesses of modelling methods used here. A larger effort is the development of a parameterization of a specific forest type, especially for tropical forests with a large number of tree species. We developed a method that most of forest model parameters can be derived directly from forest inventory data. Nevertheless, for some parameters and processes additional information is needed, e.g. the soil parameters were compiled from the literature due to missing in-situ soil measurements in the investigated region. For the calculation of the forest water balance we used an approach based on constant water use efficiency (WUE). Some studies have shown that plants can increase their WUE at the beginning of a drought period. Currently it is not known how relevant this effect is for tropical forests (and if it differs between tree species). Thus, we did not included such effect in the here presented study. Nevertheless, we explored the influence of different WUE values in a sensitivity analysis (see Appendix B). This sensitivity analysis has shown that for a plausible range of WUE values, the main forest attributes did not change significantly. The second point is that this study focused on the analysis of changes in the yearly annual rainfall. To explore the impact of droughts, it would be interesting to analyse in future studies the effect of the variability within a year. For a better understanding of the impact of El Nino oscillation, we investigated additional scenarios in which drought events occurred every six years over a period of four months with a 60% reduction in precipitation. In these scenarios we did not find a significant shift in forest structure or in carbon pools (compared to the scenario with current rainfall conditions). During this short-term reduction in precipitation, the soil water content was still high enough resulting in nearly unbiased tree growth. That the simulated short-term droughts did not show any effects on forest dynamic could be caused by the used aggregations in the soil water module (only one soil layer, no differences in rooting depth, no differentiation in soil water uptake between tree species). However, in combination with the monthly time step used in our simulation, we believe that these simplifications are only of minor importance for the mentioned analysis concerning long-term shifts in precipitation regimes.

In general, our study provides an example of how forest models can be used to increase the understanding of potential climate change on forest dynamics and carbon stocks. While we focussed here on changes of mean annual precipitation, we suggest that future studies should also address the consequences of changes in rainfall variability. Based on thorough understanding of the effects of single environmental drivers, forest models can also be applied

to assess the interactions of several environmental drivers, e.g. of changing precipitation, temperature and CO_2 .

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Appendix A–C. Supplementary material

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.envsoft.2013.10.026>.

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