Response of Net Primary Productivity of Zambezi teak forests to climate change along a rainfall gradient in Zambia

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Abstract. Understanding climate change effects on forests is important considering the role forests play in mitigating climate change. We studied the effects of changes in temperature, rainfall, atmospheric carbon dioxide (CO_2) concentration, solar radiation, and number of wet days (as a measure of rainfall intensity) on net primary productivity (NPP) of the Zambian Zambezi teak forests along a rainfall gradient. Using 1960-1989 as base-line, we projected changes in NPP for the end of the 21st century (2070-2099). We adapted the parameters of the dynamic vegetation model, LPJ-GUESS, to simulate the growth of Zambian forests at three sites along a moisture gradient receiving annual rainfall of between 700 mm to more than 1000 mm. The thus adjusted plant functional type was tested against measured data. We forced the model with contemporary climate data (1960-2005) and with climatic forecasts of an ensemble of five General Circulation Models (GCMs) following RCP 4.5 and RCP 8.5. We used local soil parameter values to characterize texture and measured local tree parameter values for maximum crown area, wood density, leaf longevity, and allometry. While increased CO_2 concentration enhances NPP at the wetter Kabompo and the intermediate Namwala sites, NPP decreases at the drier Sesheke site under both scenarios by the end of 21st century. The projected decreased NPP under RCP 8.5 at the Sesheke site results from the reduced rainfall. We thus demonstrated that differences in rainfall pattern influence the way in which climate change will affect forests resources. We also showed that using local parameter values is essential to obtaining reasonably reliable simulations.

1   Introduction

Globally, net primary productivity (NPP) plays a pivotal role in the carbon budget. Many authors have demonstrated the existence of a close relationship between shifts in NPP and dynamics in climatic variables (Delire et al., 2008; Pan et al., 2015). Without a doubt, patterns of terrestrial NPP may respond to changes in climatic variables. Therefore, inferring the NPP patterns and assessing the sensitivity of terrestrial NPP to global change and natural disturbance is essential because it deepens our understanding of ecosystem response to climate change. Future climate trends for most of the Zambezian phyto-region point in the direction of increased aridity. Therefore, the frequency and severity of drought events are expected to intensify under changing climate for most of southern Africa. Further, during the past half a century, available evidence show that the temperature increased by 0.5 °C in Africa and minimum temperatures rose more than maximum temperatures. Specifically, in southern Africa, the prediction is for a temperature rise by more than 3.4 ℃ above the 1981-2000 baseline towards the end of the 21st century (Niang et al., 2014). Both these climatic shifts may lead to increased ecosystem water stress and consequently a reduction in NPP in the Zambezian phytochorion.

However, these climatic variabilities may vary significantly in the way in which they impact forest growth and productivity. These variations may occur at spatial, ecosystem types, and climate zones (Wu et al., 2011). For example, while increased temperature stimulates plant growth up to its optimal temperature in some plants (Wu et al., 2011), it has also been demonstrated to exponentially stimulate autotrophic plant respiration (Burton et al., 2008; Wu et al., 2011). Therefore, the potential impacts of increasing temperature can either be enhanced or moderated and may depend on whether water availability decreases or increases (Chen et al., 2013). Without a doubt, reduced rainfall coupled with an increase in temperature is known to suppress NPP in most terrestrial ecosystems (Wu et al., 2011).

Although the Miombo woodlands chiefly dominate the Zambezian phytochorion, other important vegetation types therein play an important role in the lives of the local community as well as providing environmental services. The Zambezi teak forests are one such unique ecosystem that have come under intense human pressure in the most recent past (Matakala et al., 2015; Theilade et al., 2001). These forests are a source of valuable commercial timber produced from *Baikiaea Plurijuga*. The forests also provide employment through wood-based industries (Piearce, 1986a; Piearce, 1986c). Additionally, the Zambezi teak forests play a substantial role in mitigating climate change.

To examine the response of Net Primary Productivity to climate change in the Zambezian phytochorion, we studied the Zambezi teak forests in southern Africa. These forest type occur along a moderately steep rainfall gradient and as expected presents an exciting opportunity to make inference on ecosystem response to the changing climate. In this study, we applied the LPJ-GUESS model (Ahlström et al., 2012; Smith et al., 2001) to quantify the projected future effects of changes in temperature, rainfall, CO_2 concentration, solar radiation, and number of wet days on NPP under RCP 4.5 and RCP 8.5 scenarios. Our objective was to assess the NPP's future response of the Zambezi teak forests to climate change along a rainfall gradient in Zambia.

2   Materials and methods

2.1   Study sites

We carried out the study for the Zambian Zambezi teak forests at the Kabompo (14° 00.551S, 023° 35.106E), Namwala (15° 50.732S, 026° 28.927E), and Sesheke (17° 21.278S, 24° 22.560E) sites. At the Sesheke site, the Masese forest reserve was

5   assessed while at the Namwala site, we assessed the Ila forest reserve. At the Kabompo site, we studied the Kabompo and Zambezi forest reserves. While the Masese forest reserve is found in the drier agro-ecological zone I, the Kabompo and Zambezi forest reserves are located in the wetter ecological zone II. The Ila forest reserve at the Namwala site stretches along ecological zones I and II (Fig. 1 and Table 1).

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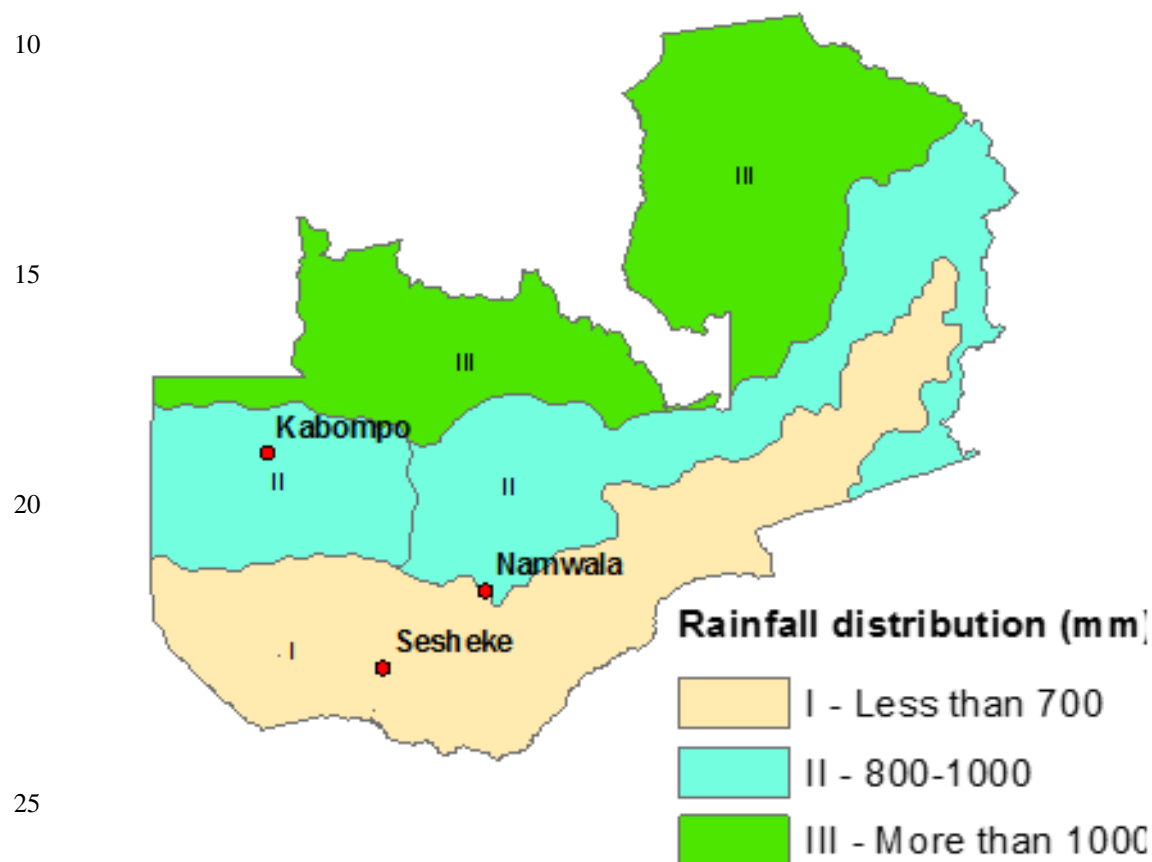
Figure 1. Rainfall pattern and distribution of study sites following the ecological zones I, II, and III (Wamunyima, 2014)

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Table 1. Climate and soil characteristics at Kabompo, Namwala, and Sesheke. For rainfall and temperature, the period covered for average values presented are given in brackets.

Parameter	Kabompo	Namwala	Sesheke
Coordinates	14°00.551S, 023°35.106E	15°50.732S, 026°28.927E	17°21.278S, 24°22.560E
Ecological zone	II	I and II	I
Total annual rainfall (mm)	983.46 (1944-2011)	905.20 (1944-2011)	643 (1947-2011)
Mean annual temperature (°C)	21.35 (1959-2003)	21.61 (1959-2011)	21.46 (1950-2011)
Nitrogen (%)	0.0404	0.0301	0.0300
Clay (%)	0.53	0.56	0.31
Silt (%)	0.54	0.55	0.43
Fine sand (%)	35.51	63.22	24.89
Course sand (%)	63.42	35.70	74.31
pH-H2O	5.55	5.74	5.86
Organic carbon (%)	0.77	0.73	0.90
Soil bulky density (g/m³)	1.54	1.53	1.87

2.2 LPJ-GUESS model description

LPJ-GUESS (Ahlström et al., 2012; Smith et al., 2001) is a dynamic vegetation model (DVM) optimised for local, regional, and global applications. The model uses temperature, precipitation, solar radiation, number of wet days, CO_2 concentrations, and soil texture as input variables to simulate the exchange of water and carbon between soils, plants, and the atmosphere. The ecosystem composition and structure is then determined for each simulated scale. One grid cell has a number of patches of approximately 0.1 ha in size (Smith et al., 2001). Each patch has a mixture of PFTs (Ahlström et al., 2012; Sitch et al., 2003), distinguished by their bioclimatic niche (distribution in climate space), growth form (tree or herb), leaf phenology (evergreen, summer green, or rain green), photosynthetic pathway (C3 or C4), and life history type (shade-tolerant or shade-intolerant). In a patch, each woody plant belongs to one PFT and has a unique set of parameters that control establishment, phenology, carbon allocation, allometry, survival response to low light conditions, scaling of photosynthesis and respiration rates, and the limits in climate space the PFT can occupy. In the model, leaf longevity has a direct relationship with carbon storage, and in LPJ-GUESS the relationship is implemented by relating the specific leaf area (SLA; m² kg C⁻¹) to leaf longevity (See Eq. (1)) according to the 'leaf economics spectrum' (Reich et al., 1997).

$$SLA \ = \ 0.2 \ \times \ e^{(6.15 \ - \ 0.46 \ \times \ \ln(12\alpha))} \tag{1}$$

where α is leaf longevity (in years).

Photosynthesis, stomatal conductance, plant water uptake and evapotranspiration are modelled concurrently on a daily time step by a coupled photosynthesis and water module, which was adapted from the BIOME3 model (Haxeltine and Prentice, 1996). Soils have an upper (0.0 m to 0.5 m) and a lower (0.5 m to 1.5 m) layer, identical in texture. Water enters the upper soil

layer through precipitation. Transpiration and evapotranspiration deplete the water content of the soil. Additional depletion of soil water may occur through percolation beyond the lower soil layer and out of reach by plant roots. Uptake by plants is partitioned according to the PFT specific fraction of roots situated in each layer (Smith et al., 2001).

Net Primary Productivity (NPP) is determined from Gross Primary Productivity (GPP) after accounting for maintenance and

5   growth respiration. The accrued NPP is allocated on an annual basis to leaves, sapwood and fine roots, enabling tree growth (Sitch et al., 2003). This allocation is adjusted such that the following four allometric equations, or "constraints", controlling the structural development of the average individual, remain satisfied: Leaf area to sapwood cross-sectional area relationship (McDowell et al., 2002) (See Eq. (2)), the functional balance constraint (See Eq. (3), the stem mechanics equation (Huang et al., 1992) (See Eq. (4)), and the crowding constraint (See Eq. (5)) (Reineke, 1933). In LPJ-GUESS model, crown area (m^2 per

10   individual) is determined from stem diameter (See Eq. (6)) and tree diameter is derived from the sapwood, heartwood, and wood density (See Eq. (7)).

Changes in PFT populations occur through the establishment and mortality of individuals. Bioclimatic limits (average climate of the last 30 years) determine which PFTs are able to establish under current climatic conditions, and establishment is implemented at the end of each simulation year for each PFT. Individual plants die due to stress, senescence, disturbance, and

15   fire. Fire depends on litter load, flammability and the available water content. Available water content is determined from the uppermost soil layer as a surrogate for the litter moisture content, which is not modelled explicitly (Thonicke et al., 2001). Biomass-destroying disturbances are simulated as a stochastic (random) process, affecting individual patches. The generic disturbances with a 100 year expected interval were prescribed. These kill all individuals on an affected patch, converting their biomass to litter (Smith et al., 2001). We used LPJ-GUESS version 3.0 and implemented a 'cohort mode' for our study

20   (Braakhekke et al., 2017; Smith et al., 2001). Though this model version accounts for nitrogen dynamics in soil and vegetation, we did not switch nitrogen on during our simulations.

$$LAI = K_{lasa} \times SA \tag{2}$$

$$C_{leaf} = K_{lr} x \, \omega \times C_{root} \tag{3}$$

$$H = K_{allom2} \times D^{K_{allom3}} \tag{4}$$

25    $$N \approx D^{-k_{rp}} \tag{5}$$

$$CA = K_{allom1} \times D^{K_{rp}} \tag{6}$$

$$D = \left[\frac{4 \, x \, (C_{sapwood} + C_{heartwood})}{WD \times \pi \times K_{allom2}}\right]^{1/(2+K_{allom3})} \tag{7}$$

Where K_{lasa}, K_{lr}, K_{rp}, K_{allom1}, K_{allom2}, and K_{allom3} are all constants, LAI is the leaf area index (m²), SA is the sapwood cross section area (m²), C_{leaf} is leaf carbon (kg C m²), C_{root} is root carbon (kg C m²), ω is the mean annual value of a drought-stress

30   factor which varies between 0 and 1 and higher values represent greater water availability. In our study we used a value of 0.35, which is the water stress threshold for leaf abscission (i.e. the point at which the leaves start shading). H stands for total tree height (m), D is tree diameter (m), N stands for population density (individuals per m²), CA is crown area (m²), CA$_{max}$ is

maximum crown area (m²), WD stands for wood density (kg C m⁻³), $C_{sapwood}$ is sapwood carbon (kg C m²), and $C_{heartwood}$ is heartwood carbon (kg C m²).

2.3   Data sources

We collected data on soil and vegetation parameters from the field survey (Ngoma et al., 2018a, b) while climate data was collected from local weather stations and the dataset of the Coupled Model Inter-comparison Project phase 5 (CMIP5). Forcing data on observed temperature rainfall, and cloud cover were collected from local weather stations within the respective ecological zones. We collected climate data from 15, 13, and 28 weather stations for Sesheke, Kabompo and Namwala sites respectively. The surveyed Ila forest reserve at the Namwala site stretches in zones I and II, thus climate data was averaged from all local weather stations in both zones. Contemporaneously number of wet days were downloaded from Climatic Research Unit (CRU) website (University of East Anglia Climatic Research Unit et al., 2015), while contemporaneously and projected temperature, rainfall, solar radiation and number of wet days were taken from CMIP5: CNRM-CM5.1 (Voldoire et al., 2013), EC-Earth (Hazeleger et al., 2011), HADGEM2-ES (Collins et al., 2011), IPSL-CM5A-LR (Dufresne et al., 2013), and MPI-ESM-LR (Giorgetta et al., 2016; Jungclaus et al., 2013) (See Table S2 for full names and details on resolutions of these models). We analysed soil parameters down to 1.5 m depth from the plots where we conducted vegetation survey (Ngoma et al., 2018a). We determined soil texture and bulk density following the method by Sarkar and Haldar (2005) and organic carbon by Walkley and Black (1934) (See Table S1 for details). Data on CO_2 concentration was taken from Representative Concentration Pathway (RCP) database: RCP 4.5 (Clarke et al., 2007; Smith and Wigley, 2006; Wise et al., 2009) and RCP 8.5 (Riahi et al., 2007).

We collected data on crown area, tree diameter, and total tree height from the field survey in our previous studies (Ngoma et al., 2018a, b), while data on leaf longevity was determined from Specific Leaf Area (SLA) (Reich et al., 1997) to parameterize LPJ-GUESS model. We determined SLA from tree leaves we collected from the trees that we felled to develop allometric equations (Ngoma et al., 2018a, b). Data on vegetation carbon and tree ring indices for LPJ-GUESS model validation was taken from the biomass (Ngoma et al., 2018a, b) and dendrochronological (Ngoma et al., 2017) studies respectively.

2.4   Description of the modelled climate data

We used the Representative Concentration Pathways 4.5 and 8.5 (RCP 4.5 and RCP 8.5) scenarios with an ensemble of five Global Circulation Models (GCMs): CNRM-CM5, EC-EARTH, HADGEM2-ES, IPSL-CM5A-LR, and MPI-ESM-LR (See Table 2 for full names). Using more than one scenario and the use of ensemble means reduces the uncertainty in projected climate data compared to a single model. The climate data was re-gridded from the original spatial resolution of the climate model to a resolution of 0.5° x 0.5°.

We applied the method by Piani et al. (2010) to bias-correct daily rainfall and temperature (minimum and maximum) values from the five GCMs against the WATCH Forcing Data (Weedon et al., 2011). The solar radiation data was bias-corrected following the method by Haddeland et al. (2012) using WATCH forcing data series (1971–2000) as a reference.

2.5 Climate change

5   In this study, we defined climate as the average weather pattern over a period of 30 years. Climate change was thus, defined as the difference between the climates of two periods. We used 1960-1989 as the baseline to determine the relative climate change for the end of the 21st century (2070-2099).

2.6 Description of the Zambezi teak forests.

Following the defined PFTs (Ahlström et al., 2012; Sitch et al., 2003), we used the "deciduous tropical broadleaved rain green"

10   PFT in our study. Deciduous tropical trees shed their leaves during the dry season (See Appendix A in Ngoma et al. (2017) for the Zambezi teak forests in different seasons of the year). Trees of the Zambezi teak forests tolerate shade. For example, seedlings of *Baikiaea plurijuga* need some shade to survive (PROTA4U, 2017). Shade tolerant species are able to dominate a closed-forest and seeds are able to germinate in a closed forest. For *Baikiaea plurijuga*, regeneration is mainly from seeds, though seedlings are usually destroyed by wild animals within the forests (Piearce, 1986a).

15   The Zambezi Teak forests are two storeyed forests with either a closed or open canopy (Mulolwa, 1986). They are composed of 80 species (Ngoma et al., 2018a, b) but *Baikiaea plurijuga* Harms is most abundant (i.e. 50 %) (Ngoma et al., 2018a, b; Ngoma et al., 2017). Trees of the Zambezi teak forests grow up to 20 m high and 120 cm in diameter (Piearce, 1986b). The forests have a deciduous shrub layer which is locally known as mutemwa and that grows up to 3 m to 6 m high. During the rainy season the forests have a ground layer of herbs and grasses (Mulolwa, 1986). These herbs and grasses have shallow root

20   systems that develop during the rainy season and die or become dormant during the dry season.

2.7 Model set-up

We initiated the model with a 1000 year spin-up at each site to allow the model time to reach equilibrium in all carbon pools. We spun-up the model with observed climate data from local weather stations and contemporaneously modelled climate data during the respective model runs. Observed climate data are temperature, rainfall, and cloud cover data observed from local

25   weather stations in the respective study sites, while contemporaneous data on CO_2 concentration were downloaded from the RCP database (RCP Database, 2018). Data on the number of wet days per month were downloaded from Centre for Environmental Data Analysis (University of East Anglia Climatic Research Unit et al., 2015). Contemporaneously modelled climate data are temperature, rainfall, number of wet days per month, and solar radiation averaged from the five GCMs described under section 2.4, and CO_2 concentration data downloaded from RCP data base (RCP Database, 2018).

30   Using observed local climate data, we forced LPJ-GUESS during the spin-up with repeated cycle of 30-year climate data for 1959-1988 and a constant CO_2 concentration of 316 ppm, corresponding to the observed value for 1959. After the 1000-year

spin-up period, the model was forced with a 53-year observed climate and CO_2 values, corresponding to the 1959-2011 period at Namwala and Sesheke sites. We forced the model with a 45-year observed climate and CO_2, corresponding to the 1959-2003 period at Kabompo site. CO_2 had reached 375 ppm and 390 ppm by 2003 and 2011 respectively.

Before forcing the model with projected climate data, we first spun-up the model with 30 years modelled climate data from

5   1960-1989 and a constant CO_2 of 317 ppm, corresponding to 1960. We then forced the model with 46-year contemporaneously modelled climate data for the period 1960-2005. We used CO_2 data for the same period of 1960-2005 and by 2005, CO_2 had reached 379 ppm.

After the spin-up period, and using observed local climate data at the respective sites as forcing, we performed a factorial experiment to determine the effects of various tree parameters (Table 2) and soil textures (Tables 1 and S1) on different model

10   output. We first ran the model with default tree parameters that were provided together with the model code (These are tree parameters from literature, but provided together with the model code. See Table 2). After identifying some limitations (Section 3.2), we tested the effects of local tree parameter values listed in Table 2 that coincided with the locations of our measurement plots (Ngoma et al., 2018a). We assessed effects of changing each parameter separately, and of changing all parameters combined at each site (Table 2). We further assessed the effects of soil by running the model with default soil parameters

15   (provided with the model code on a 0.5 x 0.5 global grid) and with local soil parameters derived from samples at the respective sites (Table S1). Results at each site were averaged for 45 years (1959-2003) at Kabompo and for 53 years (1959-2011) at the Namwala and Sesheke sites. Forcing the model with observed climate data, and using local tree and soil parameters, we compared the LPJ-GUESS simulated carbon stocks and NPP with measured carbon stock (Ngoma et al., 2018a, b) and tree-ring indices (Ngoma et al., 2017) respectively.

20   We performed a factorial experiment for projected effects of temperature, rainfall, CO_2 concentration, incoming solar radiation, and number of wet days per month for the end of the 21st century (2070-2099) following RCP 4.5 and RCP 8.5 scenarios. To isolate the contemporaneous effects of each of these climatic variables, the model was forced with the 1960-2005 values of the input climate variable of interest while keeping the 1960 values constant for the other input climatic variables. When assessing the projected effects, we forced the model with projected climate values for the period 2006-2099 of the input climate

25   variable of interest, while keeping the 2006 value constant for the other input climatic variables.

Table 2. Local and default tree parameter values used in LPJ-GUESS model. K_{rp}, K_{allom1}, K_{allom2}, and K_{allom3} are constants in allometric equations (See Section 2.2 and Smith et al. (2001). Default parameters were provided together with the model code (Smith et al. (2001)).

Site	K_{allom1}	K_{allom2}	K_{allom3}	K_{rp}	Maximum crown area (m²)	Wood density (kg m⁻³)	Leaf longevity (Years)
Default	250	60	0.67	1.60	50	200	0.50
Kabompo	279	21	0.48	1.11	336	790	0.95
Namwala	424	20	0.56	1.39	269	790	0.94
Sesheke	480	31	0.58	1.19	452	790	0.94

3 Results

3.1 Projected climate conditions: RCP 4.5 and RCP 8.5

Temperature (Fig. 2b) and incoming solar radiation (Fig. 2c) are projected to increase by the end of the 21st century (2070-2099) at all sites under both scenarios relative to 1960-1989. Temperature increases by 3°C at all sites by end of the 21st century

5 under RCP 4.5 while, under RCP 8.5, temperature is projected to increase by 5°C at the Kabompo and Namwala sites, and by 6°C at the Sesheke site.

Rainfall is projected to decrease by 33 mm and 23 mm at Kabompo and Sesheke respectively, and increase by 28 mm at Namwala under RCP 8.5 by 2099. Under RCP 4.5, rainfall will increase at Namwala and Sesheke and decrease at Kabompo by the end of 21st century (Fig. 2a). The number of wet days will decrease at all sites under both scenarios by end of the 21st

10 century (Fig. 2d). Carbon dioxide concentration is projected to almost double under RCP 8.5 by 2099 (Fig. 2e).
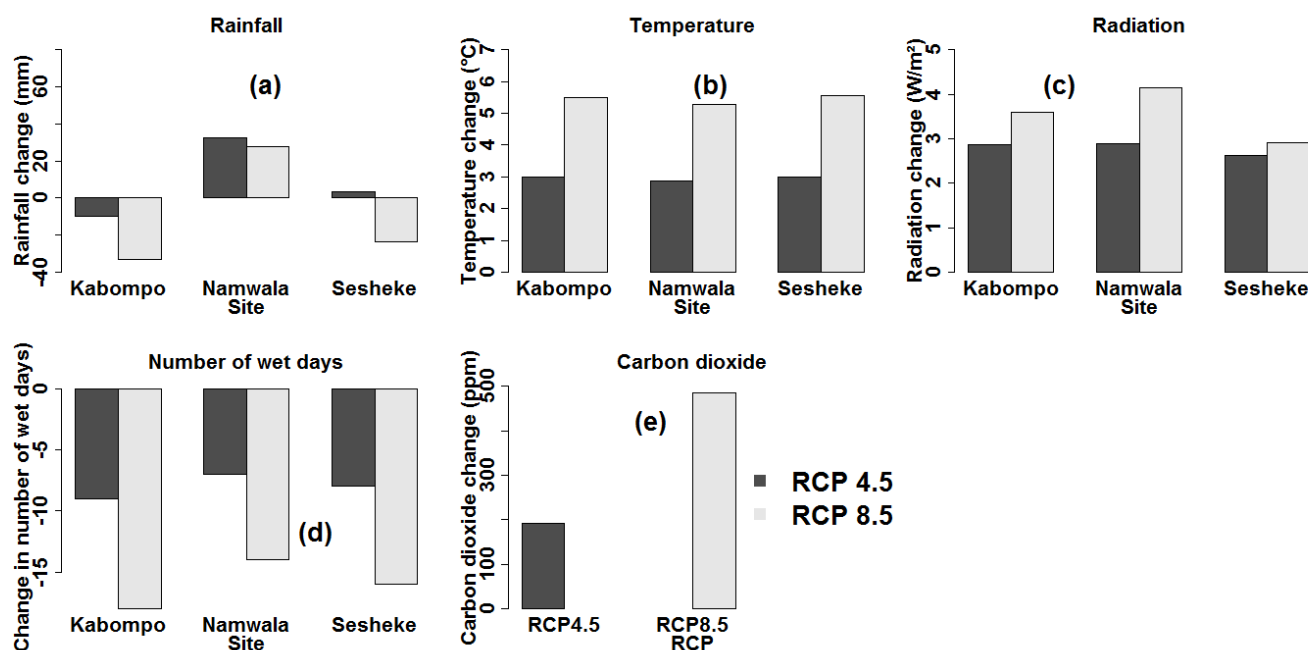
Figure 2. Projected changes in rainfall (a), temperature (b), incoming solar radiation (c), number of wet days (d), and carbondioxide concentration (e) under RCP 4.5 and RCP 8.5 by the end of 21st century. End of the 21st century is the period 2070-2099. Values were determined as means of the five GCMs and changes were determined with reference to 1960-1989 period as baseline. For sources of data, refer to Section 2.3.

3.2   LPJ-GUESS model validation

We forced LPJ-GUESS model with observed local climate data and used local tree (Table 2) and soil parameter values (Table S1) to validate the model. We validated the model by comparing standardised tree-ring indices to LPJ-GUESS simulated annual NPP, i.e. for the period 1970-2003 at the Kabompo site, and 1959-2011 at the Namwala and Sesheke sites. The

5   relationships were not significant at all the three sites (Fig. 3).
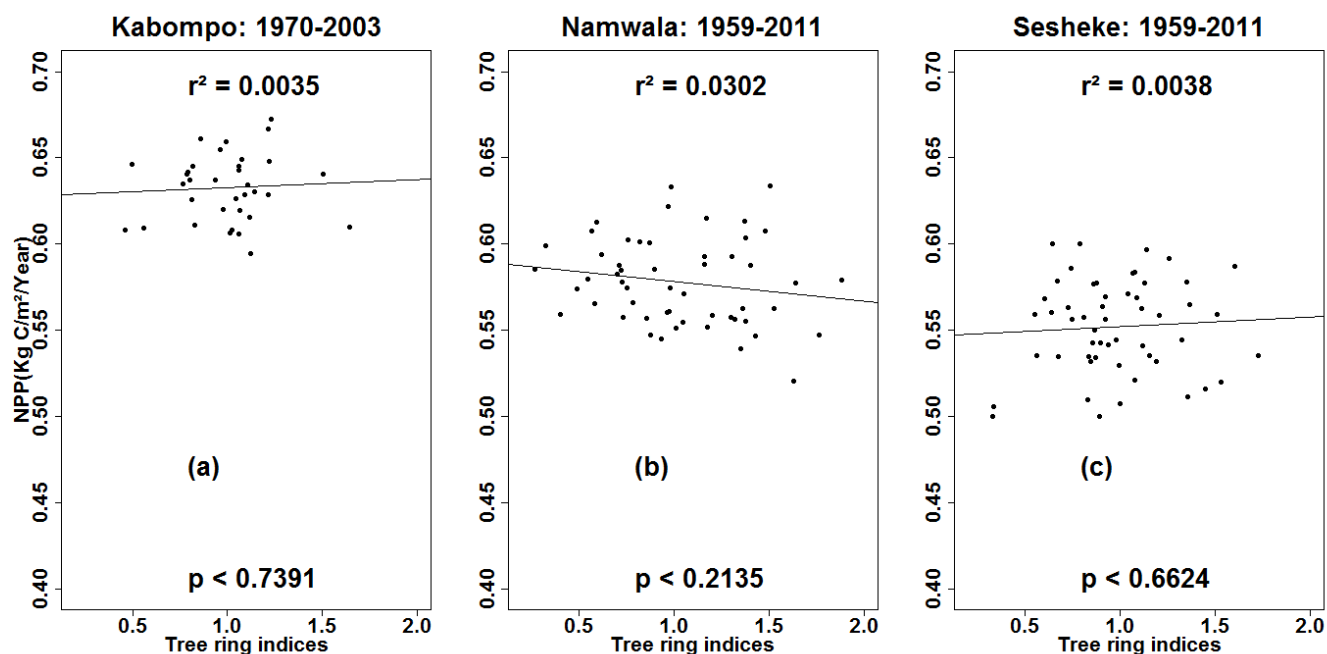
Figure 3. Correlations between LPJ-GUESS simulated NPP and tree-ring indices at Kabompo (a), Namwala (b), and Sesheke (c).

We also validated the model by comparing measured vegetation carbon with simulated vegetation carbon at the respective study sites. We forced the model with local climate data and ran it with default soil and tree parameters to assess its performance and the model over-estimated vegetation carbon stock at all sites by between 44 % and 145 %. However, replacing default

10   with local soil parameters (Table S1), maximum crown area, wood density, leaf longevity, and allometry (Table 2), the error reduced to 5 %, 47 %, and 17 % at the Kabompo, Namwala, and Sesheke sites compared to measured vegetation carbon (Fig. 4).
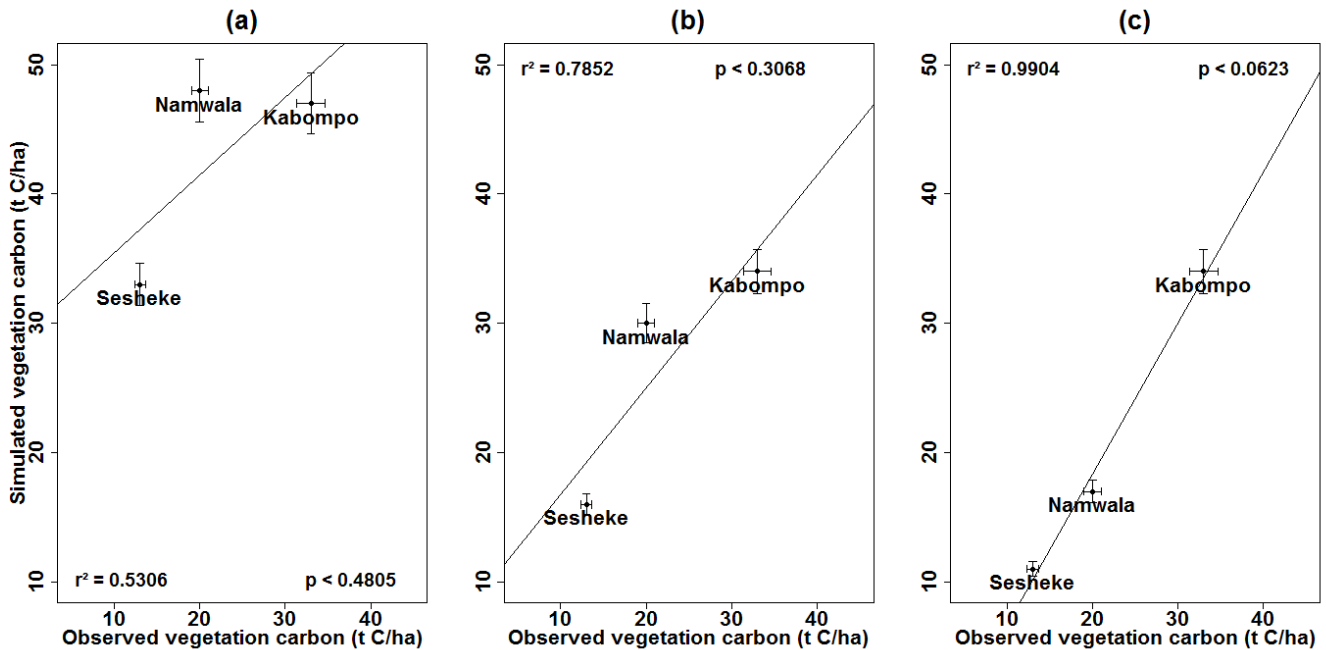
Figure 4. Measured versus LPJ-GUESS simulated vegetation carbon stock simulated with default soil parameters, default tree parameters, and observed local climate (a), local soil, local tree parameters, and observed local climate (b), and with local soil, local tree parameters, and modelled contemporaraneously climate (c).

We further assessed the LPJ-GUESS model performance by comparing measured and simulated tree heights and crown size. Using Eq. (4), tree heights estimated using default tree parameter values (Table 2) of K_{allom2} and K_{allom3} were taller than those estimated using local tree parameters of these same constants for the measured tree diameter at breast height (DBH) at all sites (Fig. 5). Applying the Mean Absolute Percentage Error (Sileshi, 2014) to indicate allometric model performance, tree heights were over-estimated by 111 % at Kabompo, 156 % at Namwala, and 56 % at Sesheke sites when we used default tree parameters values of K_{allom2} and K_{allom3} in the allometric equation compared to measured tree heights. Using local tree parameter values (Table 2), tree heights were over-estimated by 2 % and 1 % at Kabompo and Namwala and under-estimated by 8 % at Sesheke respectively. Thus, both default and local tree parameters over-estimated tree heights at Kabompo and Namwala compared to measured heights, though the over-estimation was largest with default parameters (Fig. 5).
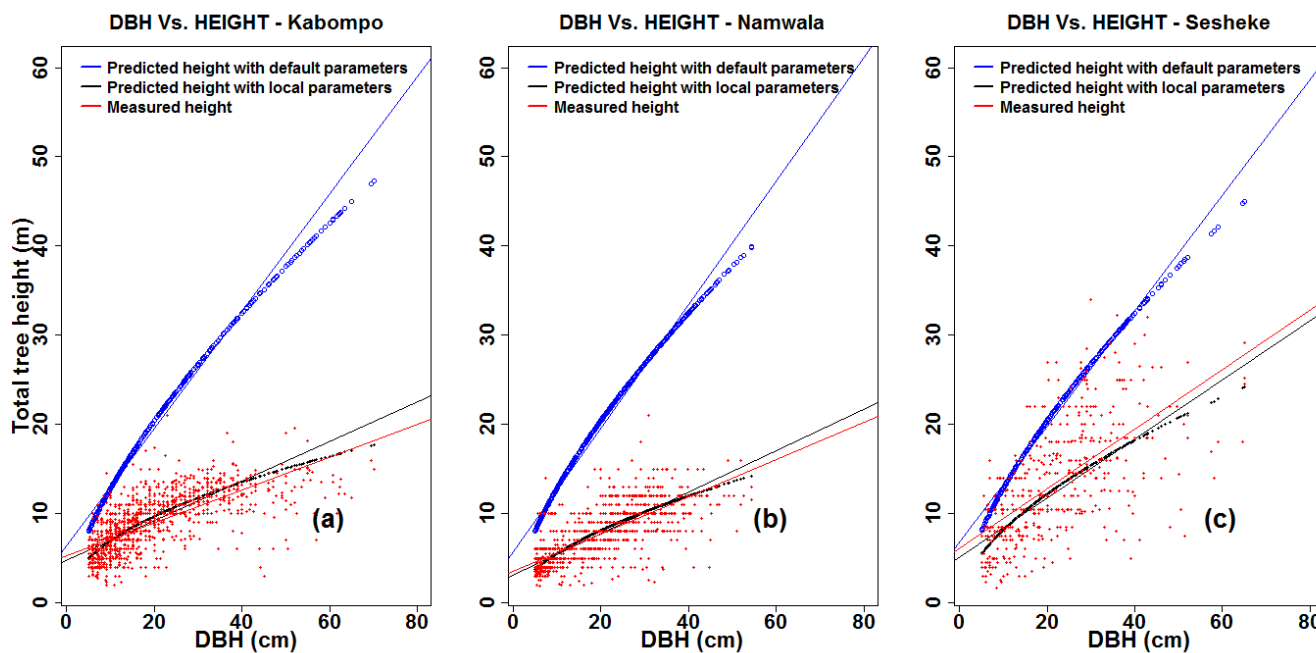
Figure 5. Measured and predicted total tree height, plotted against DBH at Kabompo (a), Namwala (b), and Sesheke (c).

The crown size, estimated with Eq. (6), was under-estimated by 61 % at Kabompo and Namwala and by 76 % at Sesheke when we used default tree parameters. However, with local tree parameters, the model under-estimated crown size by 15 %, 11 %, and 23 % at Kabompo, Namwala, and Sesheke, respectively compared to measured crown size (Fig. 6 and Table 2).
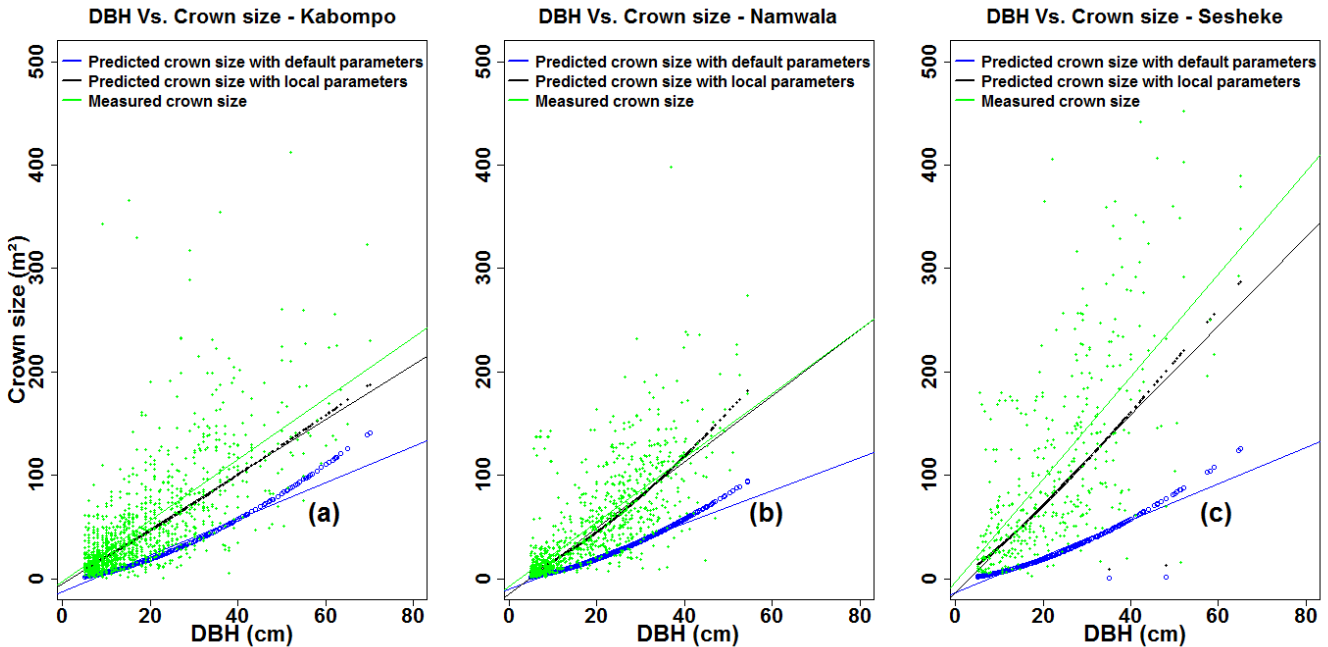
Figure 6. Measured and predicted crown size plotted against DBH at Kabompo (a), Namwala (b), and Sesheke (c).

3.3   Carbon stocks, LAI and NPP

Running the LPJ-GUESS model with local soil and tree parameters, and forcing it with local observed climate data for the
period 1960-2003, vegetation carbon stocks, and Leaf Area Index (LAI) were highest at Kabompo, and Sesheke had the lowest
values. The aggregated three carbon pools (vegetation, litter, and soil carbon) were highest at Kabompo and lowest at
Namwala. Vegetation carbon was lower when we forced the LPJ-GUESS model with contemporaneously modelled climate
data for the period 1960-2003 at all sites compared to the values simulated with observed local climate data. Vegetation carbon
stocks, LAI, and NPP simulated with both local soil and local tree parameters, and forcing the model with local climate data
were lower at all sites compared to values generated by default tree and soil parameters apart from at the Sesheke site where
NPP was higher by 0.0532 kg C m^{-2} year^{-1} (Fig. 7).
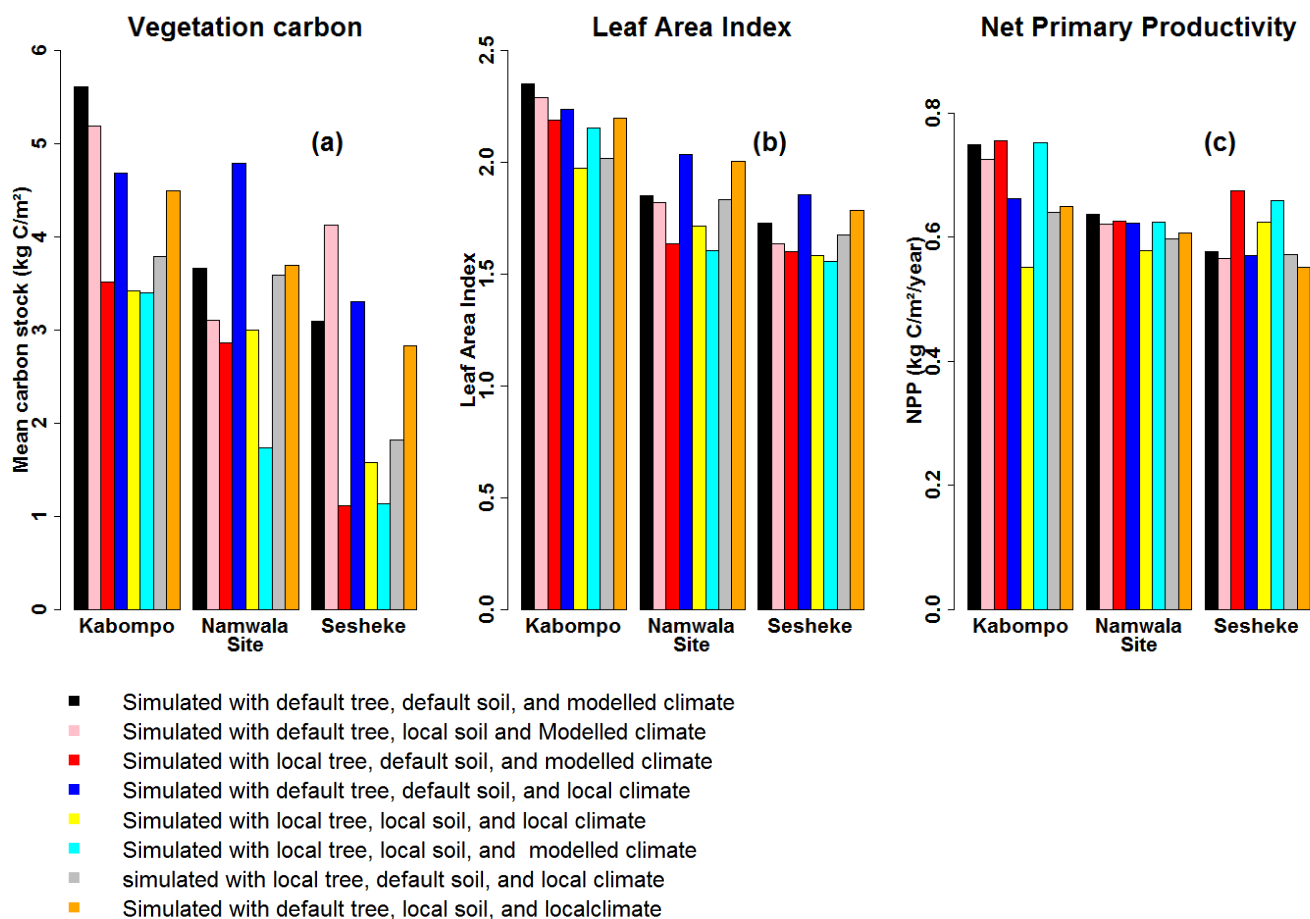
Figure 7. Mean annual vegetation carbon stocks (a), LAI (b), and NPP (c) simulated with local and default soil and tree parameter values, and forcing the model with local and modelled climate data. Simulations were done for the period 1959-2003.

3.4 Climate change effects on NPP

By the end of the 21st century, combined changes of all climatic variables is projected to increase NPP at all sites under both scenarios except at the Sesheke site where NPP reduces. NPP is projected to increase most at the Kabompo site under RCP 8.5 (Fig. 8). Increased CO_2 concentration is projected to positively have most effects on NPP at Kabompo and Namwala under both scenarios, while under RCP 8.5 decreased precipitation negatively affects NPP at Sesheke.
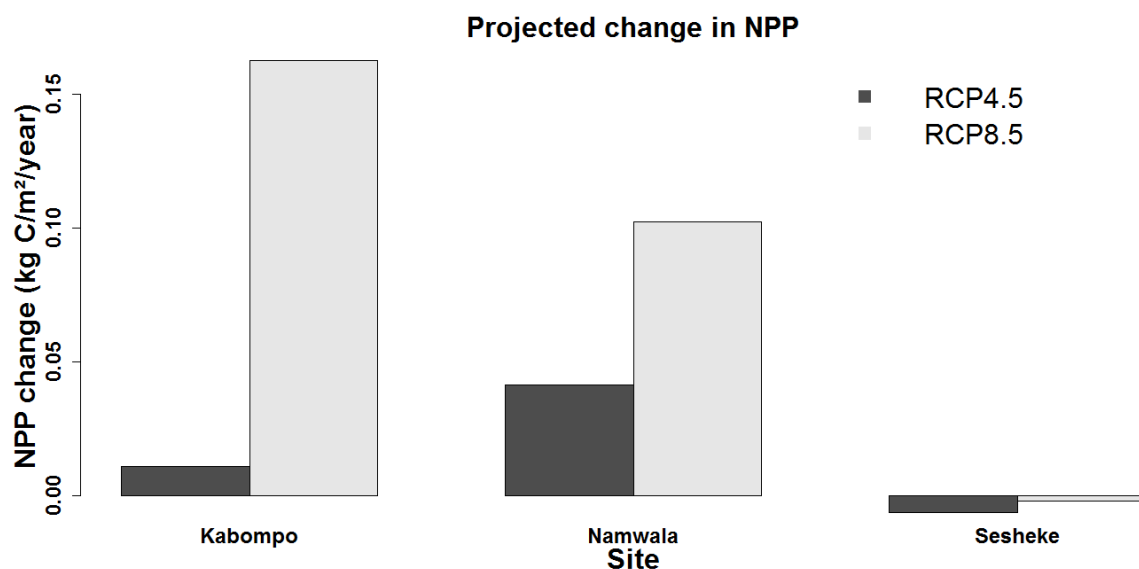
Figure 8. Projected changes in NPP at Kabompo, Namwala, and Sesheke resulting from combined changes in temperature, rainfall, CO_2 concentration, solar radiation and number of wet days by the end of the 21st century (2070-2099) with reference to 1960-1989 as the baseline.

4   Discussion

4.1   LPJ-GUESS model performance

We generated new soil texture and tree parameter values for maximum crown area, wood density, leaf longevity, and allometry, and results simulated with the LPJ-GUESS model improved when we used these local soil and tree parameter vales compared to using the default parameters. The over-estimation of vegetation carbon that resulted from using default soil parameter values indicates the differences in clay, silt, and sand proportions between default and local soils of the Zambezi teak forests. Our field measurements (Ngoma et al., 2018a, b) showed that trees were between 2 m and 21 m tall. The high default tree heights of between 8 m and 47 m led to over-estimating vegetation carbon by between 33 % and 92 %.

We found no correlation between LPJ-GUESS-simulated NPP and tree-ring indices at all sites. This lack of correlation hint at the limited amount of soil water that is available to trees in the model, given the standard 1.5 m maximum soil depth we adopted in our simulations. In the sites, trees access soil water down to more than 5 m depth according to the trees' rooting depth in the Zambezi teak forests (Childes, 1988; Högberg, 1984; Ngoma et al., 2018a, b). However, we adopted the standard 1.5 m soil depth in our model runs following the maximum soil depth from which we conducted soil assessment (Table S1). The limited amount of soil water availability in LPJ-GUESS model was clearly indicated by the non- significant correlations between NPP and rainfall at all sites (Fig. S2) as oppose to the significant positive relationship we recorded between tree ring

indices and rainfall (Fig. S2 (a) and (i)). The significant positive relationship between tree ring indices and rainfall of previous two years at Seseke (Fig. S2 (i)) indicates a carry-over effects of rainfall on trees' productivity, an aspect not addressed in LPJ-GUESS model. This lack of representation of carry-over effects of rainfall in Dynamic Global Vegetation Models (DGVM's) on trees' productivity was also reported by other researchers (Babst et al., 2013). Thus, apart from the limited water

5   accessibility in the model, the lack of representation of carry-over effects of previous year's rainfall limits NPP's growth in LPJ-GUESS model resulting in lack of correlation between LPJ-GUESS-simulated NPP and tree-ring indices. This opens the novel concept to improve and validate LPJ-GUESS model.

4.2   NPP's climate response

We projected an increase in NPP at Kabompo and Namwala caused by increasing CO_2 concentration and temperature. The

10   positive temperature and CO_2 effects were clearly observed from the high positive correlations between NPP and temperature (Fig. S5), and NPP and CO_2 (Fig. S4). However, the positive temperature effects could just be up to an optimal temperature level. For tropical trees, carbon uptake reduces with leaf temperature of above 31 °C (Doughty and Goulden, 2008). Activity of photosynthetic enzymes also reduces (Farquhar et al., 1980) resulting in reduced NPP.

The projected NPP increase at Kabompo and Namwala is in the same direction as the results reported by other researchers

15   (Alo and Wang, 2008; Mohammed et al., 2018; Pan et al., 2015) for some parts of Africa (Table 3). Some modelling studies on tropical forests (Braakhekke et al., 2017; Ciais et al., 2009; Doherty et al., 2010; Melillo et al., 1993; Midgley et al., 2005; Pan et al., 2015; Thuiller et al., 2006) also reported high positive effects of increased CO_2 concentration on forests' productivity. However other researchers report that herbaceous plants and deciduous trees sometimes acclimate to increased CO_2 concentration by reducing photosynthetic capacity and stomatal conductance (Ellsworth, 1999; Mooney et al., 1999). As

20   a results, the required nitrogen and water needed to fix a given amount of carbon is reduced (Chapin et al., 2007), though in some cases, acclimation has no effect on photosynthetic rate and stomata conductance (Curtis and Wang, 1998). It is therefore, not clear to what extent modelling results are realistically since CO_2 enrichment experiments are lacking in the tropics. Little is known about the response of tropical forests to increased CO_2 concentration (Thomas et al., 2008). In our study, the correlations between tree ring indices and CO_2 concentration were not significant at all sites (Fig. S3), contrary to modelling

25   results, indicating the need for more research.

The projected decreased NPP under RCP 8.5 at the Seseke site results from high negative effects of the projected reduced rainfall coupled with increased temperature. NPP of the drier areas is mainly influenced by water by enhancing the water use efficiency of vegetation (Yu and Chen, 2016). Reduced rainfall decreases soil water availability needed by the plants. High temperature enhances evapotranspiration resulting in reduced soil moisture (Miyashita et al., 2005). When soil water decreases,

30   the stomata close to restrict water loss. The closure of stomata prevents the movement of carbon into the plant, resulting in reduced NPP (McGuire and Joyce, 2005). Decreased soil water also limits nutrient absorption (e.g. Nitrogen) by the roots and transportation to the plants. Increased temperature enhances plant respiration thereby reducing photosynthetic activities

(Burton et al., 2008; Wu et al., 2011). The projected reduced number of wet days likely have more effects on NPP at Sesheke under RCP 4.5 by the year 2099. The projected NPP decrease at Sesheke is in the same direction as the findings of Delire et al. (2008) who reported an NPP reduction of 12 % for the savanna forests by 2080. Alo and Wang (2008) also projected NPP decrease in west and southern Africa.

5 The differences in NPP response to climate change at each of the study sites is especially caused by variability in rainfall and nutrient distribution (Fig. 1 and Table 1). Though the photosynthesis process is dependent on CO_2 concentration, plant's response to increasing CO_2 is limited by the availability of soil water and nutrients. Thus, plants growing in poor nutrient condition respond less to rising CO_2 concentration (Lloyd and Farquhar, 1996). This could be the case with the reduced NPP response at Sesheke where nitrogen content is lower than at Kabompo and Namwala (Table 1) despite the increasing projected

10 CO_2 concentration. However, deciduous trees sometimes acclimate to increased CO_2 concentration by reducing photosynthetic capacity and stomatal conductance (Ellsworth, 1999; Mooney et al., 1999). As a result, the required nitrogen and water needed to fix a given amount of carbon is reduced (Chapin et al., 2007), resulting in decreased NPP.

Table 3. Projected changes in NPP: Current study compared to literature

Change in NPP (%)	Forest biome	Study site	Period covered	Applied model	Reference	Comments
-16.98	Tropical evergreen forest/woodland	Central and West Africa	1950-2000 to 2070-2099	IBIS	(Delire et al., 2008)	Used CRU data for control results
-24.18	Tropical deciduous forest/woodland					
-6.06	Savanna					
10.00	Grassland/steppe					
0.00	Open shrubland					
-50.00	Desert					
-18.47	Tropical evergreen forest/woodland	Central and West Africa	1961-1990 to 2070-2099	IBIS	(Delire et al., 2008)	Used climate data from Mark et al. (1999) for control results - Both rainfall and temperature changed
-26.03	Tropical deciduous forest/woodland					
-15.12	Savanna					
12.99	Grassland/steppe					
-6.78	Open shrubland					
-16.67	Desert					
28.11	All biomes	East Africa	1981–2000 and 2080–2099	LPJ DGVM	(Doherty et al., 2010)	Difference sources f climate data (Refer to the article)
1.50	**Deciduous forests**	**Kabompo - Zambia - Southern Africa**	**1960-1989 and 2070 - 2099**	**LPJ GUESS**	**Current study**	**RCP4.5**
6.70	**Deciduous forests**	**Namwala - Zambia - Southern Africa**	**1960-1989 and 2070 - 2099**	**LPJ GUESS**	**Current study**	**RCP4.5**
-0.90	**Deciduous forests**	**Sesheke - Zambia - Southern Africa**	**1960-1989 and 2070 - 2099**	**LPJ GUESS**	**Current study**	**RCP4.5**
21.70	**Deciduous forests**	**Kabompo - Zambia - Southern Africa**	**1960-1989 and 2070 - 2099**	**LPJ GUESS**	**Current study**	**RCP8.5**

16.40	Deciduous forests	Namwala - Zambia - Southern Africa	1960-1989 and 2070 - 2099	LPJ GUESS	Current study	RCP8.5
-0.30	Deciduous forests	Sesheke - Zambia - Southern Africa	1960-1989 and 2070 - 2099	LPJ GUESS	Current study	RCP8.5

Symbol	Meaning of symbol
LPJ-DGVM	Lund-Potsdam-Jena Dynamic Global Vegetation Model
IBIS	Integrated Biosphere Simulator
JULES	Joint UK Land Environment Simulator
LPJ-GUESS	Lund-Potsdam-Jena General Ecosystem Simulator
ORCHIDEE	ORganizing Carbon and Hydrology in Dynamic EcosytEms
CEVSA	Carbon Exchange between Vegetation, Soil, and the Atmosphere
DLEM	Dynamic Land Ecosystem Model

The different NPP response to climate change at the three sites could also be attributed to differences in species composition and the variable responses of these distinct tree species to the environment caused by variation in there physiological properties. While 9 % of the total tree species are common in all the three sites, 25 % of the total surveyed species are found at Kabompo,

5   38 % at Namwala and 16 % at Sesheke only (Ngoma et al., 2018b).

Although we projected different NPP patterns at the three study sites, these projections depend on the accuracy of climate data. In our study, we averaged climate data from five GCMs considering the different climatic values generated by each GCM. The use of ensembles improves the modelling of climate data compared to a single model, thereby reducing the uncertainty that might be caused by sources of climate data.

10   Generally, there are some similarities in the results we generated in our study with literature (Tables 3) for similar forest types. The differences in actual values hint on the differences in models applied and the extent of area coverage. For example, while we conducted our study at local level, other researchers conducted similar studies at regional level (Doherty et al., 2010). Studies conducted at regional level constitute average results of different biomes while our study covered one biome only at all the three sites. Other factors such as species composition and soils also differ between our study sites and study sites of

15   other researchers. We compared our results to few studies due to limited literature on modelling studies reported for African biomes. Also, studies using the same model as our study (LPJ- GUESS) are limited in Africa. We could not find any studies applying LPJ- GUESS model at local level in Africa as most studies are conducted at global level (Cao and Woodward, 1998; Schaphoff et al., 2006). Availability of such studies would give much insight on our results. This therefore presents an opportunity to focus modelling research in Africa so as to determine the potential response of the different biomes to climate

20   change.

4.3   Conclusions

We generated new soil texture and tree parameter values for maximum crown area, wood density, leaf longevity, and allometry. The results simulated with the LPJ-GUESS model improved when we used these newly generated local parameters. NPP is projected to increase at the wetter Kabompo and intermediate Namwala sites under both scenarios especially caused by the

25   increased carbon dioxide concentration by the end of 21st century, while at the drier Sesheke site, NPP will decrease by the

end of the 21st century under both scenarios. The projected decreased NPP under RCP8.5 at the Sesheke site results from the reduced rainfall. We thus demonstrated that differences in rainfall pattern influence the way in which climate change will affect forests resources. We also showed that using local parameter values is essential to obtaining reasonably reliable simulations.

5 *Data availability*: Refer to section 2.3 of this paper for sources of various data used in this article

Author contribution: Justine Ngoma, Bart Kruijt, Eddy Moors, Royd Vinya, and Rik Leemans conceived the idea and designed the study; Justine Ngoma prepared the paper, Justine Ngoma and Maarten C. Braakhekke analysed NPP data, Justine Ngoma and Iwan Supit analysed climate data; James H. Speer together with all other authors provided editorial comments, interpreted and discussed the results.

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