**Abstract**

Pollen data collected in Africa at high (Kuruyange, valley swamp, Burundi) and low altitude (Lake Victoria; Ngamakala, pond, Congo) showed that after 6 ky Before Present (BP), pollen of deciduous trees increase their relative percentage, thus suggesting the beginning of a drier climate and/or an increase in the length of the dry season. Until now, pollen-climate transfer functions only investigated mean annual precipitation, hence omitting the potential effect of a change in precipitation seasonality. In the present study, we use an equilibrium biosphere model (i.e. BIOME3.5) to estimate the sensitivity of equatorial African vegetation to such changes at specific sites. Climatic scenarios, differing only in the monthly distribution of the current annual amount of precipitations, are examined at the above three locations in equatorial Africa. Soil characteristics, monthly temperatures and cloudiness are kept constant at their present day values. Good agreement is shown between model simulations and current biomes assemblages, as inferred from pollen data. Traditionally, the increase of the deciduous forest component in the palaeodata around 6 ky has been interpreted as the beginning of the drier climate period. However, our results demonstrate that a change in the seasonal distribution of precipitation could also induce the observed changes in vegetation types. This study confirms the importance of taking into account seasonal changes in the hydrological balance when palaeoecologists wish to reconstruct vegetation composition or to infer quantitative climate parameters, such as temperature and precipitation, from pollen or vegetation proxy.

## 1 Introduction

One of the fundamental assumptions in plant ecology is that on continental or global scales, the distribution and composition of vegetation is strongly controlled by climate (Woodward, 1987; Stephenson, 1990) through the key processes of photosynthesis, respiration and transpiration. Thus, the relation between vegetation compo-

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sition and climate is often described in a simple way using annual descriptors such as temperature and precipitation (Bonnefille et al., 1990). However, precipitation regimes are characterised by two main aspects (mean and variability) and the duration and intensity of the dry season(s) has to be considered in defining the suitable bioclimatic limits of a vegetation type (Street-Perrott and Perrott, 1993).

The modern mega-climate of Africa is quite simple due to the simple topography of the continent. Climatic zones related to the upper-level circulation tend to occur as symmetrical belts on either side of the equator (Thompson, 1965). Consequently two symmetric gradients of temperature and humidity spread from the equator. The tropical climate is governed by the seasonal movement of the meteorological equator (i.e. inter-tropical convergence zone (ITCZ)), in response to changes in the location of maximum solar heating. The ITCZ migrates northward to ca. 15–24_ N in June to August, and Southward to ca. 8_ N in West Africa and to ca. 16_ S in East Africa in December and February, respectively (Hastenrath, 1988). The equatorial zone is therefore characterized by a double rainfall maximum. In East Africa, the altitudinal effect on climate associated with the local topography (Mt Kenya, 5197 m; Mt Ruwenzori, 5120 m; Kilimandjaro, 5899 m; Mt Rungwe, 3176 m) is superimposed to this simple pattern and results in a linear decrease of the temperature with altitude but a complex distribution of rainfall (Osmaston, 1989).

During the period between 12 000 and 6000 years before present (radiocarbon age), insolation had a higher seasonal contrast compared to present day values due to solar radiation changes associated with orbital parameter changes (Kutzbach and Street-Perrott, 1985) thus inducing some changes in the seasonal pattern of the precipitation at a regional scale. Results of the COHMAP modelling project (Kutzbach et al., 1993) showed higher July precipitation across a part of Africa due to the intensification of the summer monsoon. For instance, between 30_ S and 30_ N in Africa at 12 ky BP (respectively 6 ky BP), simulations show an increase of the July precipitation of ca 4mmday$^{-1}$ (respectively ca 2mmday$^{-1}$).

In contrast? In the equatorial highlands of central East Africa during the early Holocene (10–7 ky

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BP), the reconstructed mean annual precipitation is 30mmyr$^{-1}$ (−2%) below presentday value with several positive shifts (Bonnefille and Chali´e, 2000). Moreover, pollen

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**Comment [Bart1]:** Here, “mean and variability” are referring to the mean and variations with the year, right? Perhaps say “month-to-month variations within the year” to avoid ambiguity with the notion of interannual variability of precipitation, which has a big impact on vegetation.

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**Comment [Bart2]:** Linear? Really? Or just a general decrease?

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**Comment [Bart4]:** This is the case for the northern hemisphere, but not the southern. The important thing is that the seaonality of insolation, was different in both hemispheres relative to present, and in turn, this likely had an impact on the seasonality of precipitation, particularly in monsoonal climates.

records show large variations of vegetation during the Holocene as a consequence of precipitation changes (Bonnefille et al., 1990; Vincens et al., 1993).

Until now, only annual precipitation has been estimated (Bonnefille et al., 1990; Vincens et al., 1993; Peyron et al., 2000, e.g.) from palaeodata. It has been shown (Barboni et al., 2003) that the seasonality of the precipitation (as represented by the duration of the dry season) in the tropical region of SW India has a strong impact on modern pollen-taxa distributions. The first attempts to estimate the total duration of the rainy season(s) by transfer functions (Chalie´ , 1992) need to be improved. Indeed, pollen data does not allow us to unambiguously reconstruct environmental conditions much different from the modern ones, particularly when low atmospheric $CO_2$ concentration prevail, because from the reconstructions are ultimately based on the best analogues available within modern data (Guiot, 1990). One way to slacken this constraint is to use mechanistic models to simulate present and past vegetation distributions. This type of models describes explicitly photosynthetic processes and hydrological cycles according to empirical laws and experimental measurements.

In this paper, we focus on the mean monthly precipitation and we analyse different scenarios for? this parameter and its impact on equatorial African ecosystems at the century time scale. For such time scales, vegetation and climate can be considered as being in steady state equilibrium (Webb, 1986). Therefore, changes in vegetation composition, in response to a modification of the precipitation regime, may be evaluated with the equilibrium biosphere model BIOME 3.5 (Haxeltine and Prentice, 1996). This model is applied at three sites along an equatorial transect, in different botanical contexts in order to simulate a set of diversified ecosystem responses. The three selected sites show consistent pollen records of past vegetation. They all show a tropical forest established at the beginning of the Holocene, and taxonomic changes during the mid-Holocene that have been interpreted as a consequence of hydrologic changes (annual rainfall amount and/or seasonal precipitation change) (Kendall, 1969; Elenga

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et al., 1994; Jolly et al., 1994).

## 2 Methods

### 2.1 BIOME3.5

BIOME3.5 is an advanced version of the BIOME3 terrestrial biosphere model (Haxeltine and Prentice, 1996) including improved descriptions of competition, phenology, photosynthesis and respiration (Kaplan, personal communication). This model describes the potential vegetation present at a site following an essential logic. First, the model selects the plant functional types (PFTs, assemblage of species which have the same response to environmental factors) likely to be present on the site according to their physiological, phenological and bioclimatic characteristics and the site specific climatic conditions. For each of the selected PFTs, maximum sustainable leaf area index (LAI) and net primary production (NPP), are calculated using a coupled carbon and water fluxes model. NPP values are then compared independently for trees and grasses to select the dominant PFT. Simulation of competition between trees and grass is based on NPP and LAI values. Vegetation is described as monthly/annual values of LAI and NPP for the dominant PFT and secondary PFTs. These outputs can be classified into biome types according to the dominance and assemblages of PFTs and a classification scheme (Haxeltine and Prentice, 1996). Model inputs are expressed as latitude, atmospheric $CO_2$ content, soil texture (Zoble, 1986; map of soil from the FAO Unesco, 1974) and monthly mean values of temperature, precipitation and cloudiness. BIOME3.5 is not the latest version of BIOME3 model. BIOME4 (Kaplan et al., 2002) is also available for the scientific community, but it does not differ from this previous version in its representation of tropical vegetation. We continued to use the early version in conformity with Guiot et al. (2000).

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### 2.2 Validation of BIOME3.5

A qualitative and quantitative comparison at a global scale of BIOME3 simulations of the present-day vegetation with a digitised global map of potential natural vegetation showed that the model successfully reproduces the broad-scale pattern (Haxeltine and Prentice, 1996). Another comparison was made between predicted NPP and a set of NPP data measured by Leith (1975) showed a fair agreement between the predicted NPP and measured

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**Comment [Bart6]:** Maybe explain this a bit more—if (low) CO2 values are constraining the vegetation one way or another, then the use of modern analogues alone will a) be limited by the simple absence of appropriate analogues, or b) be systematically wrong, because, say, the CO2 effect will be inferred through the analogues as a climatic effect.

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**Comment [Bart7]:** holding temperature and CO2 levels constant? Question: Does Biome 3.5 allow for any modification of top of the atmosphere incoming shortwave radiation, or does it simply use cloudiness anomalies to modify present-day insolation?

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NPP, yielding a correlation coefficient of 0.74 (Haxeltine and Prentice, 1996). However, even if BIOME3 can be considered robust in the intertropical area (Jolly and Haxeltine, 1997), it tends to underestimate NPP values above 1100 $gCm^{-2} yr^{-1}$ The same bias has been observed for a large number of other global NPP models (Moore III et al., 1995). BIOME3.5 was not changed for the intertropical biomes.

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## 2.3 Sites description

The selected sites are located on an African equatorial transect (Fig. 1) characterised by constant temperatures during the year (Fig. 2). We chose Ngamakala (Congo, 4_40 S, 15_230 E, 400m; Elenga et al., 1994), Lake Victoria (Pilkinton bay, Uganda, 0_190 N, 33_200 E, 1134 m; Kendall, 1969) and Kuruyange (Burundi, 3_350 S, 29_410 E 2000 m; Bonnefille et al., 1991; Jolly and Bonnefille, 1991; Jolly et al., 1994). The 3 sites present high values of annual precipitation and annual mean temperature (Ngamalakala: 1620 mm, 24.1 _C; Lake Victoria: 1175 mm, 22.3_C; Kuruyange: 1470 mm, 17.4_C) which are considered as non-limiting conditions for the current vegetation composition. According to (White, 1983), Ngamakala present-day vegetation belongs to the Guineo-Congolian domain. Kuruyange, a swamp today anthropised, is located in the afromontane domain with a mosaic of East African evergreen bushland and secondary Acacia wooded grassland near the transitional rain forest (White, 1983). The surrounding vegetation of Pilkington Bay is a mixed mosaic of semi-deciduous or deciduous forest and savanna.

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## 2.4 Climate data

For each site, relevant climatic data at each site are obtained by interpolation from a database of global climatic variables (Leemans and Cramer, 1991) using an artificial neural network (ANN), (Peyron et al., 2000).

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Temperature, cloudiness and soil texture are maintained constant at their current site values in the simulations. It may appear unrealistic to change the precipitation distribution cloudiness constant. However, changes in cloudiness are difficult to estimate because co-variations between precipitation and cloudiness are poorly understood in this context (Gregory and Morris, 1996). Moreover, we aim at deciphering the ecosystem response to one specific parameter under investigation (rainfall seasonality), hence primarily producing sensitivity experiments rather than fully realistic experiments. Only the distribution and the magnitude of the monthly precipitation during the year are modified, keeping constant the annual amount of precipitation.

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**Comment [Bart9]:** Again I wonder whether there was any perturbation of insolation considered.

The construction of the precipitation scenarios can be described in three steps:

1. Automatic identification of the months with extreme precipitation (minimum or maximum) is done on the modern mean monthly precipitation distribution curve for each studied site.
2. The amount of precipitation for one of the extremes is set by increments from −120mm to 120mm by 20mm steps. This step is a compromise between the number of scenarios and the calculation time. As the intertropical region is characterised by two wet seasons, the amount of precipitation is modified for the four extreme months.
3. The monthly amounts of precipitation for the months located between two extreme months are linearly interpolated as following:

**Comment [Bart10]:** Wouldn't it be more realistic to use some kind of sinusoidal function?

$$\acute{E}P_j = \frac{\acute{E}P^2_{ex} - \acute{E}P^1_{ex}}{m^2_{ex} - m^1_{ex}} \times \left[ m_j - m^1_{ex} \right] + \acute{E}P^1_{ex} \quad (1)$$

where the extreme months encompassing month $m(j)$ are noted $m_{ex}(1)$ and $m_{ex}(2)$, their increments being É$P_{ex}(1)$ and É$P_{ex}(2)$. $P(j)$ is the modern precipitation of month $j$ and É$P(j)$ is its increment . When the amount of precipitation for the extreme months varies simultaneously, we simulate for 12 increments, $12^4$=20 736 new precipitation distributions. For each of the 4 modified months, there are 12 possibilities to obtain a new distribution of precipitation. The new distribution must have an annual amount of precipitation more or less equal to those of the actual precipitation Pan on the site. Strictly, the new distribution $P_{0an}$ is such that $|P_{0an}-P_{an}|<100$ mm. This strong constraint highly reduces the number of tested distributions. For example, when it is applied on the Kuruyange site, the number of simulated distributions is 4124. Simulation of the vegetation is performed in each of the new precipitation scenario, using BIOME3.5.

## 2.5 Variables selected to describe the vegetation change

The NPP value of each PFT present in the grid cell is used to describe the vegetation. We express the seasonal precipitation signal with simple parameters (number of dry days, sum of the daily amount of precipitation). We use the "highest number of consecutive dry days" (called driest-season variable, in days) as a discriminant variable.

**Comment [Bart11]:** Could this variable be given a more specific name, like "dry-season length" (which is what I think it is measuring).

A month is defined as "dry" when the monthly amount of precipitation is lower than 30mm (K¨oppen, 1884). This variable requires a daily time-step data to calculate and is obtained by a linear interpolation:

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– For a month $i$ , the amount of precipitation $P(m_i)$ is attributed to the day representing the middle of the month ($md_i$) considered (Haxeltine and Prentice, 1996).

**Comment [Bart12]:** How are days measured? As "Julian" dates from the beginning of the year?

– For days between two consecutive middle days, precipitation at day $j$+1 is obtained from precipitation at day $j$ as follows:

$$P_{j+1} = P_j + \frac{P_{i+1} - P_i}{(md_{i+1} - md_i)_2} \quad (2)$$



To characterise the seasonal variation, we calculate the standard deviation around the annual mean to take into account the amplitude of the change.

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## 2.6 Relationship between seasonality and biome

Different precipitation scenarios, built as explained above, allow simulation of the corresponding biome type at each location. For a given range of the driest-season variable, the frequency of appearance of the simulated biome type is calculated as the ratio of the number of occurrence of a given biome type to the total number of simulations for this range. Simulated biome type can be classified by decreasing moisture (Fig. 3) as follows:

**Comment [Bart13]:** precipitation amount?

– Tropical Evergreen Forest: TrEF
– Tropical Semi-Deciduous Forest: TrsDF
– Tropical Deciduous Forest/ Woodland: TrDF/W
– Tropical Savanna: TrSa

The biomes TrEF, TrsDF and TrDF/W are all dominated by the "tropical raingreen trees" PFT and only differ by the number of "greendays", i.e. days when a foliage cover is present.

## 2.7 Altitudinal effect

**Comment [Bart14]:** I agree with Colin Prentice's assessment of this section.

We also evaluate the impact of the atmospheric pressure decrease at higher altitude. At Kuruyange (2000 m) we test the effect of a seasonal change in the precipitation with two distinct [$CO_2$] concentrations: (1) [$CO_2$] at sea-level pressure and (2) estimated [$CO_2$], taking into account atmospheric pressure decrease due to altitudinal effect. We aim at testing if (and how) this lower [$CO_2$] may change the vegetation response and sensitivity to a same seasonal variation in the precipitation distribution. Estimates of



the atmospheric pressure were calculated according to an empirical relationship (Triplet and Roche, 1977) as following:

$$p(z) = p(z_0) - 0.08z \quad (3)$$

with $p$ representing the pressure (in hPa), $z$, the altitude (in m), and $p(z_0)$_1000 hPa being the atmospheric pressure at the sea level. Thus, in first order, when altitude is taken into account at Kuruyange, the partial pressure in $CO_2$ decreases with a constant

$CO_2$ atmospheric concentration.

## 3 Results

Under the current precipitation distribution, at each of the three sites the simulated biome is TrsDF, a mixed forest characterised by evergreen and deciduous trees. When we vary the precipitation regime according to the rules given above, four types of biomes are simulated, but with varying frequencies (Fig. 3). At Ngamakala, independently of the precipitation distribution, the modern biome TrsDF is the most frequent (60% of the total number of simulated biome), followed by the drier TrDF/W (37%). For Lake Victoria, the most frequent biome is drier than the modern one (65% TrDF/W), and the modern biome TrsDF is the second-most frequent (32%). For Kuruyange, the vegetation has a particularly strong response to variations of precipitation seasonality. Indeed, the modern biome type is TrsDF dominant (45%) but two other types are important: a wetter biome TrEF (32%) or a drier one TrDF/W (23%). PFTs potentially present at each site are of three types: tropical raingreen trees (trt), tropical/warm or temperate grass (trg/teg) and woody desert plant type $C_3$ and $C_4$ (wod). At Kuruyange, teg replaces trg. Generally, the dominant PFT is trt whatever the site chosen, except some rare cases where it is trg.

Figure 4 gives the value of NPP of the three PFTs for the Ngamakala site as a function of the driest-season variable, each point representing one scenario of precipitation. It is noticeable that NPP values vary more as a function of the PFT and vary less, and



differently as a function of the driest-season variable. The trt PFT has a NPP value decreasing from 2000 $gCm^{-2} yr^{-1}$ to 1400 $gCm^{-2} yr^{-1}$ for a driest-season longer than 100 days. For the trg PFT, the NPP values seem to be almost constant and equal to 1800 $gCm^{-2} yr^{-1}$, despite a small discontinuity around 40 dry days. The dispersion of the NPP values is related to the number of significatively different scenarios considered for each value of the driest-season variables.

Figure 5a represents the frequency of appearance of each biome type as a function of the variation class of the driest-season variable for Ngamakala. Our results show two distinct transitions, where the first is less marked than the second. Between 20 and 100 consecutive dry days, the probability of simulating a semi-deciduous biome is almost equal to one. As the number of dry days increases above 100 days, the probability of simulating a deciduous biome reaches a maximum. Note that the shift between TrsDF and TrDF/W biomes is simulated as a fairly radical change, simulated strictly for a driest season between 100 and 120 days. For this site, the savanna biome type rarely occurs. At Lake Victoria, only one transition occurs between a semi-deciduous forest and a deciduous one (Fig. 5b). This transition takes place between 60 and 100 dry days and reveals progressive, especially if compared to the change observed in Ngamakala. The tropical savanna is also simulated, but its occurrence is always low.

At Kuruyange, located at 2000 m, BIOME3.5 simulates two distinct transitions (Fig. 5c). Between 0 to 100 consecutive dry days, the model simulates an evergreen forest. Afterward, the biome type is semi-deciduous until 140 dry days. Finally, the frequency of the deciduous forest is high above 140 dry days. We notice that the range of the driest-season parameter is rather narrow when the semi-deciduous biome dominates.

The results are significantly different when we take into account the decrease of pressure with elevation (Fig. 5d). The range where the modern biome is potentially present increases from days 100 to 140 to days 40 to 120. Moreover, all the transitions shift to lower critical values.

In Fig. 6, we investigate the development of the NPP of the three PFTs as a function of



the standard deviation (sigma) of the number of consecutive dry days. Sigma is related to the seasonal range of the monthly precipitation. These two variables appear to be sufficient to summarize the precipitation distribution. This figure allows us to study in detail the distribution of trt (Fig. 6a) and trg (Fig. 6b) in Ngamakala and of trg (Fig. 6c and d) in the two other sites.

## 4 Discussion

Under water stress, the model predicts that all PFTs undergo a general decrease of their respective NPP values. A first question to ask is whether the simulated physiological response

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is realistic. In term of absolute NPP, BIOME3.5 underestimates systematically ecosystem NPP above 1000 $gCm^{-2}$ $yr^{-1}$ (Haxeltine and Prentice, 1996). In our simulation design, values of NPP are often higher than 1500 $gCm^{-2}$ $yr^{-1}$. Thus, due to the characteristics of BIOME3.5, one cannot expect the simulation of realistic NPP values. However, because of the process-based characteristics of the model, we believe that the simulated response in terms of trend is realistic. All the PFTs are stressed (marked by a general decrease of the mean NPP value above a PFT-specific threshold) by an increase of the dry season length. The differential response illustrates that grasses have a better adaptation capacity to water stress than woody plants. These differences could be interpreted by a different growth scheme for plants corresponding to these two PFTs, with a "short" longevity (i.e., a better yield for a broad climatic spectrum) for grass type.

The biome type TrsDF has a broader occurrence versus driest-season parameter compared to the evergreen forests (Fig. 5c and d). Studies on the effect of the atmospheric [$CO_2$] show that $C_3$ cultural plants decrease their photosynthetic rate when $CO_2$ pressure is reduced, inducing a decrease of NPP. When we run BIOME3.5 with decreasing $CO_2$ partial pressure (increasing altitude), we observe a decrease in both the NPP and Leaf Area Index values (i.e. foliage covers). In BIOME3.5, the PFT is selected using climatic constraints without taking into account the altitude, i.e. the $CO_2$

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partial pressure. Therefore, to improve vegetation simulation, it would be better to select potentially present PFT(s) after NPP and LAI calculations which would take into account the atmospheric $CO_2$ concentration.

At the biome level, ecosystem transitions are simulated as a function of the intensity of the driest season. These transitions are characterised by vegetation change from a tropical semi-deciduous forest biome to a tropical deciduous forest biome. At present-day, BIOME3.5 simulates a semi-deciduous forest at the three studied sites with a length of the driest season of 3, 84 and 96 days at Lake Victoria, Ngamakala and Kuruyange, respectively. This study shows that even if we keep constant the total annual amount of precipitation, a seasonal change is able to produce major biome changes. The change toward drier biomes appears around 110, 80 and 100/150 days, respectively, of driest season at Ngamakala, Lake Victoria and Kuruyange without altitude effect. We note that the simulated vegetation change due only to the change of the seasonality of precipitation is more important than the changes observed in the palaeodata during the Holocene at the three sites (Kendall, 1969; Bonnefille et al., 1991; Elenga et al., 1994; Jolly et al., 1994). Our simulations demonstrate that we have to take into account the seasonal distribution of precipitation when reconstructing past climates. Reconstruction of mean annual climatic variables (Bonnefille et al., 1990; Peyron et al., 2000; Bonnefille and Chalié, 2000; Peyron et al., 2006) in tropical areas must be completed by considering the precipitation seasonal distribution. If BIOME3.5 output correctly matches palaeodata, the next step will consist in developing an objective and automatic procedure to determine which climatic scenario is the most probable.

BIOME3.5 does not include dynamic processes by which vegetation structure and composition adapt to abiotic changes and perturbations. Therefore, these successions occur from one steady state to another. The succession representation is limited because it is difficult to synthesize the particular signal or change in the distribution of precipitation which is responsible for the transition. Indeed, no unique relationship exists between the consecutive number of dry days and the simulation of a particular biome type.

Figure 6 helps us to understand the sensitivity of NPP of different PFTs to the num-

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ber of consecutive dry days and to seasonal amplitude of the precipitation. It shows complex behavior for individual PFTs and in general, only a NPP decrease for extreme values of the variable is predictable. The change in NPP for tropical raingreen trees (Fig. 6a) shows that this PFT is sensitive to these two precipitation variables and has a threshold effect at Kuruyange. The 3-D pictures show that a seasonal change of precipitation has different impacts on different PFTs, and that this impact is site dependent. All PFTs are affected by water stress expressed as differential decrease of their NPP and LAI. These variables are correlated, but driest season is the parameter that directly affects the vegetation by a NPP decrease.

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**Comment [Bart19]:** Are you saying that the absolute values may not be realistic, but the changes or anomalies are?

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**Comment [Bart22]:** Does this mean "The simulated changes in response to changes of precipitation seasonality is larger than observed changes in vegetation during the Holocene?

**Comment [Bart23]:** augmented?

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One of the parameters that we fixed is the 20mm step of variation of the monthly precipitation chosen to vary between −120mm and 120 mm. Thus, some distributions are rejected as realistic distributions compared to the modern one. However, this method allows us to include some scenarios that are still? rather realistic when compared to the actual distribution, while keeping a reasonable calculation time. Otherwise, a stochastic scenario selection would perhaps be more appropriate to drastically change these distributions (Gritti et al., unpublished). The main advantage of the method applied here is that the four extreme months produce a maximum of two dry seasons, corresponding to the present climate in the studied region. Moreover, when an extreme month has a negative precipitation value, for example when it is an actual minimum month incremented by negative number, the method used here fixes this value to zero. An improvement could be to increment the adjacent months to increase the dry season around this actual minimum. The annual amount of precipitation, which has to be kept "constant", was set equal to the current modern annual amount plus or minus 100 mm. This value was retained empirically and a better approximation could be chosen by using an estimate of the interannual variation of the annual amount of precipitation at the nearest meteorological stations.

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Regarding the threshold on the monthly amount of precipitation used to define a dry month, the literature is abundant. The value of 30mm used here is perhaps the oldest definition of a dry month (Köppen, 1884) and, according to Aubréville and Chevalier

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(1949), 30mm is "certainly under the true value, but this corresponds to a certainty". The calculation of the number of dry days could be improved by using the xerothermic Gaussen index (Gaussen and Bagnouls, 1953) which takes into account relative humidity. Moreover, while the processes considered in biospheric models are highly nonlinear, some of them have characteristic times substantially shorter than one month. The use of monthly average data as model forcing is thus not a priori justified and may lead to non-negligible errors on the model output variables (Hubert et al., 1998).

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Regarding the spatial dimensions of this study, the climate has been interpolated for this particular location from a method that has been proved efficient (Peyron et al., 2000). The processes taken into account in the model are adapted to a global description. Therefore, some necessary assumptions, when used at the local scale, are certainly too simple. For example, the depth of the vegetation roots is fixed at 1.5m in BIOME3.5, whereas in the tropics the roots system can reach 68m deep (Canadell et al., 1996). The error could be assessed with a complete comparison method between regional simulated vegetation and pollen records. Moreover, the model is an equilibrium biosphere model and in order to simulate a real vegetation succession, a dynamical tool would be more accurate (Gritti et al., unpublished).

**Comment [Bart26]:** experimental design employing?

## 5 Conclusions

The effect of a change in the seasonaly distribution of precipitation on the vegetation has been tested with an equilibrium vegetation model because current palaeoclimatology methods cannot take into account this parameter. Our simulations confirm that at all sites, located near the Equator, a substantial increase of the consecutive dry days number could lead to a change in the tropical forest composition and structure. Such changes are as important as those observed in the pollen diagrams during the Holocene. The impact on the vegetation depends on the PFT and the location. A smooth seasonal change in the precipitation as used in this study can induce one or several well marked biome "successions". The change toward a drier biome, i.e. from a semi-deciduous to a deciduous one for example, appears,

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respectively at 110, 80 and 150 days of driest season at Ngamakala, Lake Victoria and Kuruyange. The NPP value of each PFT potentially present at the tropical location is affected by the seasonality of precipitation.

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**Comment [Bart27]:** in order to investigate the sensitivity? of current climate-reconstruction methods which focus on annual-mean values of climate variables.

**Comment [Bart28]:** Earlier you said the simulated change were more important.

**Comment [Bart29]:** It's not so much the location, but the present climate and vegetation at a location.

**Comment [Bart30]:** transitions?

Finally, our study indicates that in the future, sensitivity analyses of models will be very useful to test explicit or often implicit hypotheses assumed by palaeoecologists. Here, without a modelling approach it would be impossible to estimate the potential impact of a change in the seasonality of the precipitation at a specified location. In natural conditions, it is rare to find exact analogues (same mean annual temperature, annual precipitation, soil, altitude, latitude,. . . ) with only a change in the precipitation distribution. This lack of analogues allows for the common assumption by palaeoclimatologists

**Comment [Bart31]:** Oh-oh. I think you might get some "push-back" by palaeo*climatologists*, who might argue that it's their palaeo*ecologist* colleagues that make those bad assumptions.

that a change of vegetation is only due to a change of the annual amount of precipitation. Our study demonstrates the importance of seasonal distribution of precipitation in pollen-derived climate reconstructions. A way to integrate such changes is the inverse modelling iterative procedure developed by Guiot et al. (1999, 2000) and extensively applied to Africa by Wu et al. (2007a,b). This approach allows the reconstruction of the most probable climate of the Mediterranean Basin and of Eurasia under lowered $CO_2$ concentration at the last glacial maximum from pollen data, with a first attempt to integrate a seasonal change in the precipitation distribution.

**Deleted:** It could reconstruct

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**Fig. 1.** Sites location and current observed vegetation formations.

**Fig. 2.** Temperature (lines) and precipitation (bars) distribution for the three studied sites.
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**Fig. 3.** Synthesis of the Biome types simulated for each site. In red, Tropical Evergreen Forest biome; dark green, Tropical Semi-Deciduous Forest biome; light green, Tropical Deciduous Forest/Woodland biome; yellow, Tropical Savanna.
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**Fig. 4.** Evolution of the NPP for different PFTs, as a function of the variable driest season (number of consecutive days) for Ngamakala (400 m). Solid circle, tropical/warm grass PFT (trg); Open lozenge, tropical raingreen trees PFT (trt); Open triangle, woody desert plant type C3 and C4 PFT (wod).
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**Fig. 5.** Biome types and seasonal changes. In red, Tropical Evergreen Forest biome; in dark green, Tropical Semi-Deciduous Forest biome; in light green, Tropical Deciduous Forest/ Woodland biome; in yellow, Tropical Savanna for **(A)** Ngamakala (Congo) **(B)** Lake Victoria (Uganda) **(C)** Kuruyange (Burundi) with atmospheric pressure measured at the sea level **(D)** Kuruyange (Burundi), with atmospheric pressure at 2000 m, calculated, applying an empirical correction to take into account the altitudinal effect.

Fig. 6.
**Fig. 6.** Sensitivity test in a tridimensional representation ($gCm^{-2} yr^{-1}$), number of consecutive dry days, sigma of the prescribed precipitation distribution), at Ngamakala for tropical trees **(A)** and tropical grasses **(B)**, and at Kuruyange **(C)** and at Lake Victoria **(D)** for tropical grasses. Dashed line with solid circle corresponds to NPP value obtained with the modern precipitation distribution.
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