Ecological Complexity 24 (2015) 46–56

Contents lists available at ScienceDirect

Ecological Complexity

journal homepage: www.elsevier.com/locate/ecocom

Original Research Article

# Assessing the effect of climate change on carbon sequestration in a Mexican dry forest in the Yucatan Peninsula

Z. Dai [a,b,*], K.D. Johnson [a], R.A. Birdsey [a], J.L. Hernandez-Stefanoni [c], J.M. Dupuy [c]

[a] USDA Forest Service, 11 Campus Blvd, Suite 200, Newtown Square, PA 19073, USA
[b] Commission for Environmental Cooperation, 393 rue St-Jacques Ouest, bureau 200, Montreal, QC H2Y 1N9, Canada
[c] Centro de Investigación Científica de Yucatán A.C., Unidad de Recursos Naturales, Calle 43# 130. Colonia Chuburná de Hidalgo, C.P. 97200, Mérida, Yucatán, Mexico

ARTICLE INFO

*Article history:*
Received 20 May 2015
Received in revised form 18 September 2015
Accepted 21 September 2015
Available online

*Keywords:*
Secondary forest
Karstic landscape
Biomass
Soil carbon pool
Forest-DNDC
Biome-BGC

ABSTRACT

Assessing the effect of climate change on carbon sequestration in tropical forest ecosystems is important to inform monitoring, reporting, and verification (MRV) for reducing deforestation and forest degradation (REDD), and to effectively assess forest management options under climate change. Two process-based models, Forest-DNDC and Biome-BGC, with different spatial modeling scales were evaluated to estimate the potential effect of climate change on carbon sequestration in a tropical dry semi-deciduous forest in the Yucatan Peninsula of Mexico. The results from the simulations using the two models show that carbon sequestration in this dry forest is highly sensitive to warming. Carbon uptake in this forest may increase or decrease slightly with a corresponding increase or decrease in precipitation; however, with an increase in temperature, carbon uptake may decrease significantly, showing that warming may be the main climate factor that impacts carbon storage in this tropical dry forest. Model performance evaluation indicates that both models may be used to estimate C stocks, but DNDC may be better than BGC for assessing the effect of climate change on C dynamics.



## 1. Introduction

Carbon (C) sequestration in forest ecosystems benefits the natural environment and contributes to the mitigation of global warming because forests are an important terrestrial C sink (Miehle et al., 2006; Trettin et al., 2006; Birdsey et al., 2007; Pan et al., 2011; Charman et al., 2013). The responses of terrestrial ecosystems to global warming can vary regionally. For example, projections from global climate models indicate the potential for more rain in middle and high latitude zones (Wentz et al., 2007; Zhang et al., 2007; Lambert et al., 2008), but not for low latitude areas (Zhang et al., 2007) and parts of subtropical areas (Dai et al., 2011). Understanding the regional differences in the response of forest ecosystems to global warming is fundamental to assess the role of forest ecosystems in reducing atmospheric $CO_2$ concentrations.

Climate change may have had a significant role in the collapse of the ancient Maya civilization in Mexico. Analyses of oxygen isotopes and chemical components in historical sediments in the Yucatan Peninsula indicate that historical air temperature and precipitation fluctuated greatly between 1300 and 1100 year BP (800–1000 A.D.), resulting in multiyear droughts (Hodell et al., 1995; Curtis et al., 1996; Haug et al., 2003; Medina-Elizalde and Rohling, 2012). These records imply that the current global warming trend may cause strong and long drought periods in the future, especially if rain decreases in this area (Zhang et al., 2007).

Understanding C dynamics in forest ecosystems is critical for assessing the impacts of deforestation and forest degradation, both of which are common in the tropical dry forests of Mexico. Specifically, quantifying C pools and sequestration rates (i.e. net $CO_2$ flux) informs strategies for Monitoring, Reporting and Verification (MRV) and reducing deforestation and forest degradation (REDD). The most common direct way to measure C sequestration is by using eddy flux measurement technology for small areas (Baldocchi, 2003; Hutley et al., 2005; Barr et al., 2006; Oren et al., 2006; Kurbatova et al., 2008). However, these studies have found that $CO_2$ fluxes are highly dependent on changing environmental factors, including topography, climate, hydrology, soil, vegetation and various disturbances (Pietch et al., 2003; He et al., 2012; Pacific et al., 2009). Therefore, flux measurements are inadequate by themselves to account for landscape heterogeneity

* Corresponding author at: USDA Forest Service, 11 Campus Blvd, Suite 200, Newtown Square, PA 19073, USA.
*E-mail address:* zdai@fs.fed.us (Z. Dai).

http://dx.doi.org/10.1016/j.ecocom.2015.09.004
1476-945X/

and extrapolation over large regions. Additionally, spatially explicit and long-term carbon dynamics using only eddy flux measurements or field measurements are limited by personnel, equipment, and funds. These issues can be overcome with ecosystem models developed from expert knowledge of ecosystem processes, long-term experiences, and observations. Recent applications of biogeochemical carbon models for assessing forests response to land use change and natural and human disturbances highlight the merits of these methods (Miehle et al., 2006; He et al., 2012; Chen et al., 2003; Hanson et al., 2004; Mo et al., 2008; Hlasny et al., 2011; Miao et al., 2011; Dai et al., 2013). Thus, ecosystem models are important tools for understanding the responses of forests to climate change, and for assessing long-term C dynamics at the landscape level to aid in forest management decisions.

Many ecosystem C models such as MAESTRO (Wang and Jarvis, 1990) and Biome-BGC (Thornton et al., 2002), have been used for simulating C dynamics in forest ecosystems. Miehle et al. (2006) compared the performance of five forest C models, i.e., 3-PG (Landsberg and Waring, 1997), BIOMASS (Hingston et al., 1998), CABALA (Battaglia et al., 2004), Forest-DNDC (Li et al., 2000), and PROMOD (Battaglia and Sands, 1997), using observations from 93 plantations across southeastern Australia. Their results showed that most models performed reasonably well to predict forest C accumulation, and that, in particular, CABALA and Forest-DNDC performed better than others based on the model performance efficiency. Differences in performance efficiencies among models can be substantial, and in at least one study of 13 models (Hanson et al., 2004), efficiencies ranged from 0.17 to 0.73 for daily net ecosystem exchange (NEE), at least partly due to model structure. Also, since there are a variety of model structures developed from different natural environments, it is sometimes unclear which models are most appropriate for new environments. To help address these uncertainties, it is beneficial to experiment with more than one model, which allows for additional model evaluations against field observations and also evaluations of agreement between modeled output trends. In this study we chose to apply two models, Forest-DNDC which requires more data inputs and has a more sophisticated soils submodel, and Biome-BGC which has a simpler structure and is more widely applied.

Most of Mexico is located in the northern tropical zone, with a high diversity of forest types ranging from deciduous to evergreen based primarily on moisture availability. Responses of these forests to climate change are likely to be very different. For example, the climatic and hydrogeological conditions in the Yucatan Peninsula are very different from the rest of the country (Perry et al., 2003; Brienen et al., 2009; Dai et al., 2014). Global warming may increase air temperature in this area at a rate of $\geq$0.1 °C per decade (based on data beginning in 1960; Met Office, 2011), but may not bring more rain (Zhang et al., 2007), potentially impacting the carbon dynamics in these dry tropical forest ecosystems (Brienen et al., 2009). In addition, Mexican tropical dry forests cover more area, and are more threatened by climate change than other tropical ecosystems (Hernandez-Stefanoni et al., 2011; Dupuy et al., 2012). Accordingly, it is important to consider the responses of carbon dynamics in tropical dry forests when exploring climate change mitigation options.

The aims of this study were threefold: (1) to evaluate the Forest-DNDC and Biome-BGC models for a Yucatan dry semi-deciduous forest using biomass, soil and climate observations, (2) to apply the two models for estimating the effect of climate change on carbon dynamics in the forest, and (3) to evaluate the performance of the models. To achieve the first and third objectives we used field observations from 276 plots from Kaxil Kiuic in the Yucatan Peninsula collected by Hernandez-Stefanoni et al. (2011) and Dupuy et al. (2012). Four quantitative model performance evaluation variables were also used to evaluate the model performance. To achieve the second objective, a daily climate dataset for a 43-year period (1970–2012) was used, based on the climate data recorded at six weather stations in this area.

## 2. Data and methods

### 2.1. Study site

This site is located in the Yucatan Peninsula, Mexico, 20.02–20.16°N and 89.39–89.60°W (Fig. 1). It is a tropical dry semi-deciduous forest landscape of about 350 km$^2$, which is mainly comprised of forestlands (93.9%) with scattered croplands (about 5.35%) and urban areas (about 0.75%) at present (Fig. 2). The land use has historically been swidden agriculture for over two thousand years (Hernandez-Stefanoni et al., 2011; Dupuy et al., 2012; Rico-Gray and Garcia-Franco, 1991; Turner et al., 2001). The current forest is regenerated after deforestation and cropland abandonment.

The landscape topography consists of mosaics of low and moderate hills with small flat areas. The slope ranges between 0 and 90%, with an average slope of 7%. The elevation ranges from 70 to 176 m above mean sea level, with a mean of 116 m. The climate is tropical, with a summer rain period from June to October and a dry season between November and May. The mean annual precipitation is 1190 mm during the 38-year period from 1970 to 2007, based on the available climate data observed at the weather

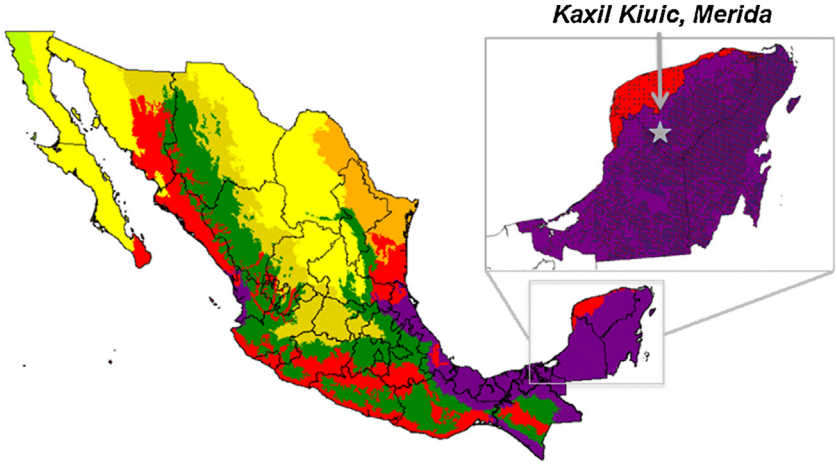


**Fig. 1.** Kaxil Kiuic forest in the Yucatan Peninsula, Mexico.

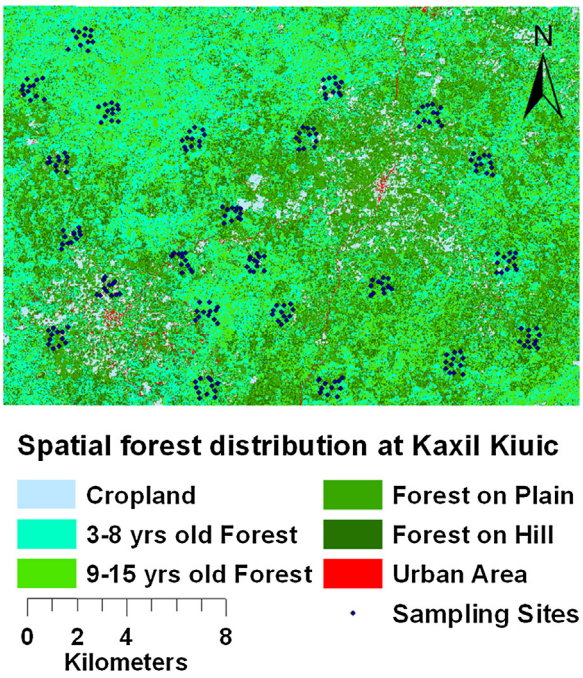


**Fig. 2.** Measurement sites for biomass and soils, and vegetation distribution in 2005 derived from a SPOT 5 satellite image of January 2005 (Hernandez-Stefanoni et al., 2011).

stations in the study area, obtained from the Mexican meteorological network (CONAGUA, 2012; http://smn.cna.gob.mx/). Mean temperature for the 38-year period is 26.5°.

The soils developed from limestone parent material with neutral pH, ranging from 5.5 to 7.8 with a mean of 7.2 (Dupuy et al., 2012). Clay content varies widely, ranging from 21 to 84% in rock-free soil, with a mean of 49%. The main soil types range from sandy clay to clay but a few soils are loam. The stone content in most soils is high, varying from 0 to 90%, with an average of 29% and rock-free soil occurs only rarely. Soil organic matter (SOM) ranges from 2.5 to 72.0% in rock-free soil, with a mean of 23%, based on soil sample analysis (Dupuy et al., 2012). There is no surface drainage system (no rivers or streams) in this area because of stony and thin soils (ranging from several centimeters to a meter in depth) over porous limestone bedrock that allows rainwater to quickly move into the aquifer (Perry et al., 2003; Allen and Rincon, 2003).

Vegetation in the forest is naturally regenerated from either deforestation or cropland abandonment. Most stands were 7–74 years old in 2012 based on the inventory conducted in 2008–2009 (Hernandez-Stefanoni et al., 2011); mean stand age is 27. Canopy stature is generally low, 8–13 m in height, with occasional emergent trees exceeding 13 m in some old forest plots (>50 years) (Hernandez-Stefanoni et al., 2011). Stem density of woody plants ≥1 cm in DBH (diameter at breast height) ranged from 2550 to 24 550 individuals with a mean of 11 165 trees $ha^{-1}$. Stem density of trees >5 cm in DBH ranged from 0 to 4950 with an average of 1654 stems $ha^{-1}$, and for trees $1 \leq DBH \leq 5$ cm, it ranged from 1400 to 24 000 with a mean of 9511 individuals $ha^{-1}$. The diversity of plant species in this study area is relatively high although the richness may be low compared to humid tropical forests in Mexico. There were 123 species of trees >5 cm in DBH and 41 species of trees 1–5 cm in 2008–2009. The main species are *Bursera simaruba* (Burseraceae), *Lysiloma latisiliquum*, *Caesalpinia gaumeri*, *Piscidia piscipula*, *Mimosa bahamensis* and *Lonchocarpus xuul* (Fabaceae), *Neomisllspaughia emarginata* and *Gymnopodium floribundum* (Polygonaceae), and *Thouinia paucidentata* (Sapindaceae) (Dupuy et al., 2012).

### 2.2. Field measurements and data collection

Forest stand biomass in the 350 $km^2$ of the study area was estimated using 276 sample plots (Fig. 2). Twenty three landscape units were first delineated in order to account for the whole range of forest fragmentation and to evaluate the influence of landscape structure on species richness and biomass in this forest landscape (Hernandez-Stefanoni et al., 2011). Each landscape unit was about 1 $km^2$, in which twelve plots were installed using a stratified sampling design representing different secondary forest cover classes to collect soil samples and measure tree height (TH, m) and diameter at breast height (DBH, cm). Plot size was 200 $m^2$ to estimate the biomass of trees >5 cm in DBH; a concentric 50 $m^2$ subplot was designed to measure TH and DBH of trees $1 \leq DBH \leq 5$ cm (Hernandez-Stefanoni et al., 2011). The biomass of trees ≥10 cm in DBH was estimated using the equation developed by Cairns et al. (2003), and modified by Urquiza-Haas et al. (2007), whereas the equation used to calculate the biomass of trees <10 cm in DBH was developed by Hughes et al. (1999), and modified by Chave et al. (2003). The modifications to both equations involved weighing each general equation using species-specific data on wood specific gravity for common woody species to improve the accuracy of biomass estimates. The total biomass in each plot was estimated by summing the individual tree estimates to Mg $ha^{-1}$. As many trees in this forest have no annual rings, stand age of each plot was estimated by interviewing the land owners or users (Hernandez-Stefanoni et al., 2011). Landowners were generally older (40 years) than the mean stand age (23 years) to improve the accuracy of this approach.

Daily minimum and maximum temperature and daily precipitation were obtained from six weather stations in this area. Five had a recording period from 1969 to 2007 with some data missing, and the other one had a short climate recording period, from 2006 to 2012, with some data missing. Because of data missing for different times at different stations, the data were integrated into one dataset for a 43-year period from 1970 to 2012 for this study.

Soil samples were collected from the inventory plots using three 10-cm-deep soil samples at the center, northern and southern edges. Soil organic matter (SOM), pH, and texture were analyzed; the detailed method was reported by Dupuy et al. (2012).

### 2.3. Two process-based carbon models

Two models, Forest-DNDC (DNDC) and Biome-BGC (BGC), were used to assess the potential impact of climate change on C stocks in the study area. Although both models are process-based, there are some differences between them. The BGC model is widely used to quantify C dynamics in forests (Tatarinov and Cienciala, 2006; Chiesi et al., 2007; Wang et al., 2009) and the version used in this study is a point scale model utilizing spatial mean conditions of soil and vegetation and simplified processes to simulate C in forest ecosystems. The model simulates the mean fluxes and states of C, nitrogen (N) and water. Plant physiological processes in BGC respond to diurnal variations in environmental conditions, mainly temperature, precipitation, short wave radiation and vapor pressure deficit. BGC simulates daily soil moisture variations based on precipitation and evapotranspiration. The C and N dynamics in soils are simulated daily based on the simulated soil conditions. The model parameterization and algorithms of BGC can be found online: http://www.ntsg.umt.edu/project/. The main parameters used in BGC and DNDC are presented in Tables 1a and 1b. Table 1a shows the values used by BGC for only one plot, because it needs 276 datasets for this study. Table 1b shows the ranges of the values used by DNDC because this model uses spatial datasets.

**Table 1a**
Partial parameters for Biome-BGC.[a]

| Parameter | Value | Parameter | Value |
|---|---|---|---|
| Offset for maximum temperature (°C) | 0.0 | Offset for minimum temperature (°C) | 0.0 |
| Multiplier for precipitation | 1.0 | Multiplier for VPD | 0.0 |
| Multiplier for short wave radiation | 1.0 | Atmospheric $CO_2$ concentration (ppv) | 370 |
| Soil depth (m) | 0.3 | Sand in soil (%) | 35 |
| Silt in soil (%) | 20.0 | Clay in soil (%) | 45 |
| Site elevation (m) | 85 | Latitude (°N) | 20.1 |
| Albedo at the site (DIM) | 0.18 | Atmospheric N deposition ($kg\,N\,m^{-2}\,year^{-1}$) | 0.0001 |
| Soil water content ($cm^3\,cm^{-3}$) | 0.5 | First-year maximum leaf C ($kg\,C\,m^{-2}$) | 0.001 |
| First-year maximum stem C | 0.1 | Coarse woody debris C ($kg\,C\,m^{-2}$) | 0 |
| Litter C in labile pool | 0.041 | Litter C in unshielded pool ($kg\,C\,m^{-2}$) | 0.041 |
| Litter C in shielded pool | 0.041 | Litter C in lignin pool ($kg\,C\,m^{-2}$) | 0.284 |
| SOC1 ($kg\,C\,m^{-2}$) | 0.699 | SOC2 ($kg\,C\,m^{-2}$) | 1.398 |
| SOC3 ($kg\,C\,m^{-2}$) | 2.097 | SOC4 ($kg\,C\,m^{-2}$) | 7.97 |
| Litter N in labile pool ($kg\,N\,m^{-2}$) | 0.001 | Soil N in mineral pool ($kg\,N\,m^{-2}$) | 0.041 |
| FTGP (proportion) | 0.2 | FLGS (proportion) | 0.2 |
| AFLRT ($year^{-1}$) | 1.0 | Annual live wood turnover fraction ($year^{-1}$) | 0.7 |
| Annual fire mortality fraction | 0.0 | Ratio of new fine root C to new leaf C | 1.0 |
| Ratio of new stem C to new leaf C | 1.0 | Ratio of new root to new stem | 0.23 |
| Current growth proportion | 0.5 | C:N of leaf | 35 |
| C:N of leaf litter after translocation | 49 | C:N of fine root | 60 |
| C:N of live wood | 70 | C:N of dead wood | 442 |
| Leaf litter labile proportion | 0.39 | Leaf litter cellulose proportion | 0.44 |
| Leaf litter lignin proportion | 0.17 | Fine root labile proportion | 0.3 |
| Fine root cellulose proportion | 0.45 | Fine root lignin proportion | 0.25 |
| Dead wood cellulose proportion | 0.76 | Dead wood lignin proportion | 0.24 |
| CWIC ($LAI^{-1}\,d^{-1}$) | 0.041 | Canopy light extinction coefficient | 0.7 |
| All-sided to projected leaf area ratio | 2.0 | CASLA ($m^2\,(kg\,C)^{-1}$) | 12.0 |
| Ratio of shaded SLA to sunlight SLA | 2.0 | Fraction of leaf N in rubisco | 0.08 |
| Maximum stomatal conductance ($s^{-1}$) | 0.005 | Cuticular conductance ($m\,s^{-1}$) | 0.00001 |
| LWPSS (MPa) | −0.6 | LWPCS (MPa) | −2.3 |
| VPDSS (Pa) | 930 | VPDCS (Pa) | 4100 |
| Boundary layer conductance ($m\,s^{-1}$) | 0.01 | | |

SLA, specific leaf area; SOC1, soil C in microbial recycling fast pool; SOC2, soil C in medium microbial recycling pool; SOC3, soil C in slow microbial recycling pool; SOC4, soil C in recalcitrant pool; FTGP, transfer growth as fraction of growing season; FLGS, litterfall as fraction of growing season; AFLRT, annual leaf and fine root turnover fraction; CASLA, canopy average specific leaf area; CWIC, canopy water intercept coefficient; LWPSS, leaf water potential at start of stomatal conductance reduction; LWPCS, leaf water potential at completion of stomatal conductance reduction; VPDSS, vapor pressure deficit at start of stomatal conductance reduction; VPDCS, vapor pressure deficit at completion of stomatal conductance reduction.

[a] These data are only for a plot; there are some differences among plots. Climate data, such as daily precipitation, temperature, radiation and vapor pressure deficit, are not included.

DNDC simulates forest growth and C and N dynamics in forest ecosystems and emissions of trace gases such as $CO_2$, $CH_4$ and $N_2O$ based on the balance of water, light, and nutrients in forest ecosystems (Li et al., 2000; Stange et al., 2000; Miehle et al., 2006). Vegetation is divided into three layers, i.e., over-story, understory and ground-growth. The vegetation of each layer is simulated based on competition for energy and nutrients. Like BGC, DNDC simulates plant physiological process responses to variations in environmental conditions. However, DNDC does so mostly on an hourly rather than daily basis. The soil profile is divided into multiple layers, 1–5 cm in thickness; soil conditions and the dynamics of C and N in each soil layer are also modeled hourly. This model has been widely tested and used for estimating greenhouse gas (GHG) emissions from forested wetland and upland ecosystems and assessing C sequestration in a wide range of climatic conditions, including boreal and tropical (Stange et al., 2000; Zhang et al., 2002; Li et al., 2004; Kiese et al., 2005; Kesik et al., 2006; Kurbatova et al., 2008; Dai et al., 2012). The model structure, algorithms, and parameterization can be found in the model manual (http://www.dndc.sr.unh.edu) and publications (Li et al., 2000, 2004; Stange et al., 2000; Zhang et al., 2002; Dai et al., 2012).

### 2.4. Model setup and validation

Both models were evaluated using biomass estimates from 276 plots within the Kaxil Kiuic forest in the Yucatan Peninsula, Mexico (see Section 2.2). Model performance was evaluated employing four widely used quantitative methods (Dai et al., 2011): the coefficient of determination ($R^2$, squared correlation coefficient), model performance efficiency ($E$) (Nash and Sutcliffe, 1970), percent bias (PBIAS), and the RRS [the ratio of the root mean squared error (RMSE) to SD (standard deviation)] (Moriasi et al., 2007). We used $E$, PBIAS, and RRS in addition to $R^2$ because $R^2$ by itself may not accurately indicate bias (Moriasi et al., 2007). Moreover, favorable results from the four statistics together indicate that a model has performed well.

The key variable used to evaluate model performance is $E$ ($-\infty$, 1), and it is calculated as

$$E = 1 - \frac{\sum (x_i - y_i)^2}{\sum (x_i - \bar{x})^2} \quad (1)$$

where $x_i$, $\bar{x}$ and $y_i$ are observed values, observed mean and simulated results, respectively. The evaluation variables, PBIAS and RRS, are computed, respectively, as

$$\mathrm{PBIAS} = \frac{\sum (x_i - y_i)}{\sum x_i} \times 100 \quad (2)$$

$$\mathrm{RRS} = \frac{\mathrm{RMSE}}{\mathrm{SD}} \quad (3)$$

where SD is the observation standard deviation; RMSE is the root mean squared error, the equation is

$$\mathrm{RMSE} = \sqrt{\frac{\sum (x_i - y_i)^2}{n}} \quad (4)$$

**Table 1b**
Key parameters for Forest-DNDC.

| Parameter | Value | Parameter | Value |
|---|---|---|---|
| Initial leaf N (%) | 1.2–1.5 | ADD at start of leaf growth[a] | 900 |
| AmaxA ($\mu mol\, g^{-1}\, s^{-1}$) | −40 to −46 | ADD at start of wood growth | 900 |
| AmaxB | 66–76 | ADD at end of leaf growth | 8000 |
| OPT (°C) | 25 | ADD at end of wood growth | 8000 |
| MinPT (°C) | 2 | Leaf N translocation rate | 0.5 |
| MaxPT (°C) | 45 | Senescence start day | 300 |
| DAF | 0.76 | Leaf C/N | 30–35 |
| Growth respiration fraction | 0.2 | Wood C/N | 100–150 |
| Dark respiration fraction | 0.1 | Leaf retention years | 1.2–1.6 |
| WMRF | 0.07 | C reserve fraction | 0.75 |
| RMRF | 1.0 | C fraction of dry matter | 0.5 |
| Light half saturation constant | 180–200 | Specific leaf weight (SLW, $g\, m^{-2}$) | 160–180 |
| Respiration Q10 | 2.0 | Ratio of change in SLW (0–1) | 0.0–0.1 |
| Canopy light attenuation | 0.5–0.58 | Minimum wood/leaf | 1.4–1.6 |
| Water use efficiency | 13.5–15 | Leaf geometry | 2 |
| VDP1 | 0.05 | Maximum N storage ($kg\, N\, ha^{-1}$) | 200 |
| VPD2 | 2.0 | Maximum wood growth rate | 1.0 |
| Maximum leaf growth rate ($\%\, year^{-1}$) | 0.9 | | |
| Spatial soil, climate, hydraulic and geographical parameters[b] | | | |
| SOC in organic layers (%) | | Daily maximum temperature (°C) | |
| SOC in mineral layers (%) | | Daily minimum temperature (°C) | |
| Depth of organic layers (cm, ≤150) | | Over-story age | 3–75 |
| Depth of mineral layers (cm, ≤150) | | Understory age | 3–75 |
| Clay content in organic layer (%) | | Coefficient of stem density (0–1) | 0.2–1.0 |
| Clay content in mineral layer (%) | | Capacities of organic layer (0–1) | |
| pH of organic layer | | Capacities of mineral layer (0–1) | |
| pH of mineral layer | | HC of organic layer ($cm\, h^{-1}$) | |
| Stone content in organic layer (0–1) | | HC of mineral layer ($cm\, h^{-1}$) | |
| Stone content in mineral layers (0–1) | | Wilting points of organic layer (0–1) | |
| Humads fraction in organic layer (0–1) | | Wilting points of mineral layer (0–1) | |
| Humads fraction in mineral layer (0–1) | | | |
| Daily snow ($kg\, m^{-2}$) | | Elevation (m above mean sea level) | 70–176 |
| Daily precipitation (mm) | | Latitude (decimal degrees) | 20–20.16 |

[a] AmaxA, intercept of photosynthetic curve; AmaxB, slope of photosynthetic curve; OPT, optimal photosynthetic temperature; MinPT, minimum photosynthetic temperature; MaxPT, maximum photosynthetic temperature; DAF, daily Amax as a fraction of instantaneous Amax; WMRF, wood maintenance respiration fraction; RMRF, root maintenance respiration fraction; VPD1, intercept of vapor pressure deficit; VPD2, slope of vapor pressure deficit; HC, hydraulic conductivity; ADD, accumulative degree day.
[b] Soil data were observed (see Dupuy et al., 2012); daily climate data were obtained from 6 weather stations for a period of 43 years.

where $n$ is the number of samples, or the pairs of the observed and simulated values; and the $R^2$ is

$$R^2 = \left( \frac{\sum (x_i - \bar{x})(y_i - \bar{y})}{\sqrt{\sum (x_i - \bar{x})^2 \sum (y_i - \bar{y})^2}} \right) \quad (5)$$

To evaluate the two models, biomass outputs (in $Mg\, ha^{-1}$) were compared to the plot-level field estimates of each of the 276 plots. Each plot's simulation was run until it reached its known stand age to a maximum of 75 years (the age of the oldest trees in Kaxil Kiuic forest). We assumed that the current forest is regenerated from swidden agriculture. This is because the Yucatan Peninsula has a long history of ancient Mayan settlements dating over 2000 years, during which time shifting cultivation has been the main practice impacting the forests (Rico-Gray and Garcia-Franco, 1991). Forest stand age and soil conditions used for model parameterizations were based on the observations and estimations conducted by Hernandez-Stefanoni et al. (2011) and Dupuy et al. (2012) in 2008–2009. Because there was no available climate data for the period from 1938 to 1969, we repeated the data from 1970 to 2002 to replace the missing historical data.

## 3. Model applications

After the BGC and DNDC models were evaluated, they were used to assess the potential effect of climate change on C stocks using a range of climate change scenarios (Table 2) (Special Report on Emission Scenarios) (IPCC, 2001). The temperature change ranged from 1 to 6 °C in the 21st Century given by six emissions marker scenarios (IPCC, 2007), and either more rain or less rain in low latitude areas (Wentz et al., 2007; Zhang et al., 2007; Lambert

**Table 2**
Scenarios for simulating carbon sequestration response to climate change.[a]

| Climate change | Simulation code | Description |
|---|---|---|
| Precipitation increase | S-PI | Precipitation would increase by 20% without considering changes in other climate conditions |
| Precipitation decrease | S-PD | Precipitation would decrease by 10% without considering changes in other climate conditions |
| Temperature increase | S-T | Daily mean air temperature would increase by 2 °C without considering that the temperature rise could bring more rain, or global warming does not bring more rain to this forest |
| Global warming bringing more rain | S-TP | Temperature would increase by 2 °C and precipitation would increase by $10\%\, °C^{-1}$ of temperature increase, or global warming brings more rain to this forest |
| Baseline | S-BL | The 75-year period climate dataset used for model validation was utilized as baseline |

[a] All climate change scenarios were designed based on the observed climate conditions for a 43-year period from 1970 to 2012.

et al., 2008). Additionally, a baseline scenario (S-BL) was simulated using the same climate conditions as in the model evaluation. In contrast to the model evaluation component, each of the 276 plots was simulated for 75 years, regardless of its stand age, and the mean result from all the plots was reported. Similarly, all the vegetation and soil conditions were kept constant for each scenario and no disturbance effects were added.

## 4. Data analysis and statistical test

Annual results from both models under different climate change scenarios, including baseline, were used to analyze the effect of climate change on carbon sequestration in the secondary tropical dry forest. The differences (changes) between each scenario and the baseline for aboveground biomass, NPP and soil carbon pool were used to assess the effect of climate change. To evaluate the potential effects of climate change on carbon sequestration in this forest, we compared annual changes for the baseline with those for each scenario using *F*-tests and Pearson correlation analyses.

## 5. Results

### 5.1. Model validation and evaluation

Both models BGC and DNDC were compared with the observed biomass from 276 circular plots in Kaxil Kiuic forest. Fig. 3a shows that the biomass simulated by DNDC was significantly correlated with the observed values ($R^2 = 0.83$, $P \ll 0.001$); the slope of the regression model between observed and simulated values was close to 1.0 ($b = 1.03$), and the intercept ($a = 1.33$) was only about 3% of the observed average. Fig. 3b indicates that the biomass simulated by BGC was significantly correlated with the observed values ($R^2 = 0.59$, $P \ll 0.001$) with a reasonable slope ($b = 0.93$) and intercept ($a = 3.03$, about 6.5% of the observed average) of the regression model between observed and simulated values. These qualitative metrics show that both DNDC and BGC can be used to assess C stocks in Kaxil Kiuic forest in the Yucatan Peninsula, Mexico.

The results of the four model evaluation variables are presented in Table 3. The $E$ ($\geq$0.40) and $R^2$ ($\geq$0.59) from BGC evaluation show that BGC can perform well to assess C stocks for Kaxil Kiuic forest. However, DNDC has a better performance with $E \geq 0.79$ and $R^2 \geq 0.83$. Similarly, the error between the observation and simulation for BGC was about two times larger than DNDC in both the size classes analyzed (Table 3).

### 5.2. Aboveground biomass response to climate change

The changes (differences between each scenario and baseline) in aboveground biomass under the four climate change scenarios (S-PI, S-PD, S-T and S-TP) (see Table 2) simulated by DNDC and BGC

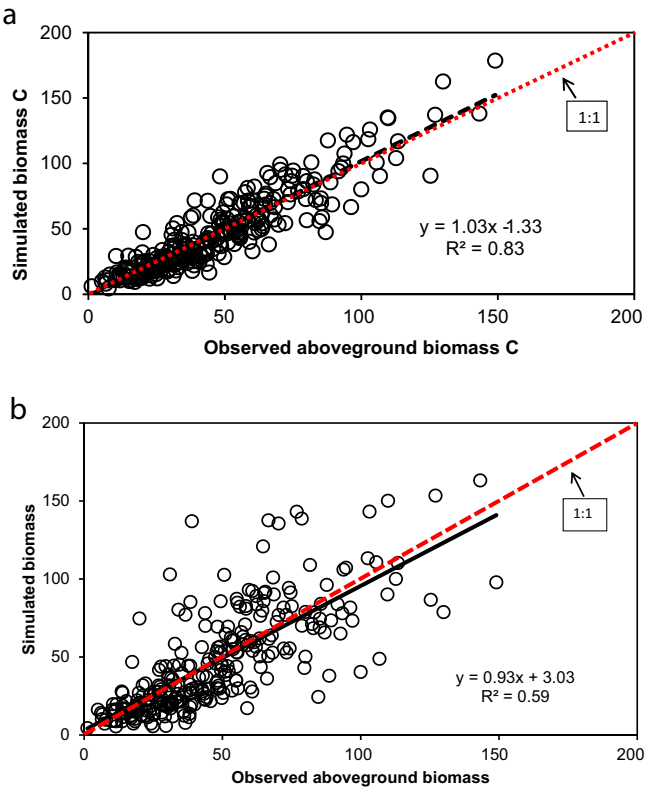


**Fig. 3.** (a) The total aboveground wood biomass C (Mg ha$^{-1}$) observed vs. simulated using Forest-DNDC for the 276 plots in the tropical dry forest at Kaxil Kiuic in Yucatan Peninsula, Mexico. (b) The aboveground wood biomass C (Mg ha$^{-1}$) observed vs. simulated by using Biome-BGC for the 276 plots in the tropical dry forest at Kaxil Kiuic in Yucatan Peninsula, Mexico.

are presented in Fig. 4a and Table 4. The results show that, under a 20% increase in precipitation, biomass would increase significantly and linearly ($R^2 > 0.96$, $n = 75$, $P \ll 0.001$), and would produce an increase in net C storage in this forest. However, the two models suggested very different rates of increase: 145 kg C ha$^{-1}$ year$^{-1}$ for BGC and 16 kg C ha$^{-1}$ year$^{-1}$ for DNDC, respectively. Accordingly, the mean cumulative biomass increment (difference between S-PI and S-BL) for these two models over the 75-year period was also quite different: 5.77 Mg C ha$^{-1}$ for BGC and 0.68 Mg C ha$^{-1}$ for DNDC, respectively.

Biomass decreased significantly and linearly in both models due to temperature increase (S-T) over the 75-year period ($R^2 > 0.98$, $n = 75$, $P \ll 0.001$), but the rates of change were different (Fig. 4a and Table 4). Biomass decreased at a rate of 208 kg C ha$^{-1}$ year$^{-1}$

**Table 3**
Results from model performance evaluation.[a]

| Biome-BGC (≥5 cm) | | Biome-BGC (≥1 cm) | | Forest-DNDC (≥5 cm) | | Forest-DNDC (≥1 cm) | |
|---|---|---|---|---|---|---|---|
| Variable | Value | Variable | Value | Variable | Value | Variable | Value |
| $R^2$ | 0.61 | $R^2$ | 0.59 | $R^2$ | 0.89 | $R^2$ | 0.83 |
| $E$ | 0.54 | $E$ | 0.40 | $E$ | 0.88 | $E$ | 0.79 |
| PBIAS | 8.87 | PBIAS | −0.99 | PBIAS | 0.36 | PBIAS | 0.14 |
| RRS | 0.67 | RRS | 0.78 | RRS | 0.34 | RRS | 0.46 |
| $a$ | 0.79 | $a$ | 0.93 | $a$ | 0.91 | $a$ | 1.03 |
| $b$ | 10.59 | $b$ | 3.03 | $b$ | 3.24 | $b$ | −1.33 |

[a] $R^2$ is the coefficient of determination; $E$ is the model performance efficiency (Nash and Sutcliffe, 1970); PBIAS is the percent bias; RRS is the ratio of the root mean squared error (RMSE) to SD (standard deviation); $a$ and $b$ are the slope and intercept of the regression model between observation and simulation, respectively; (≥1 cm) and (>5 cm) represent tree size in diameter at breast height; model performance rating ranges are: $0.25 \leq E < 0.5$ (satisfactory), $0.5 \leq E < 0.75$ (good), and $E \geq 0.75$ (excellent); a PBIAS between −25 and 25 and a RRS of less than 0.7 are considered satisfactory (Moriasi et al., 2007).

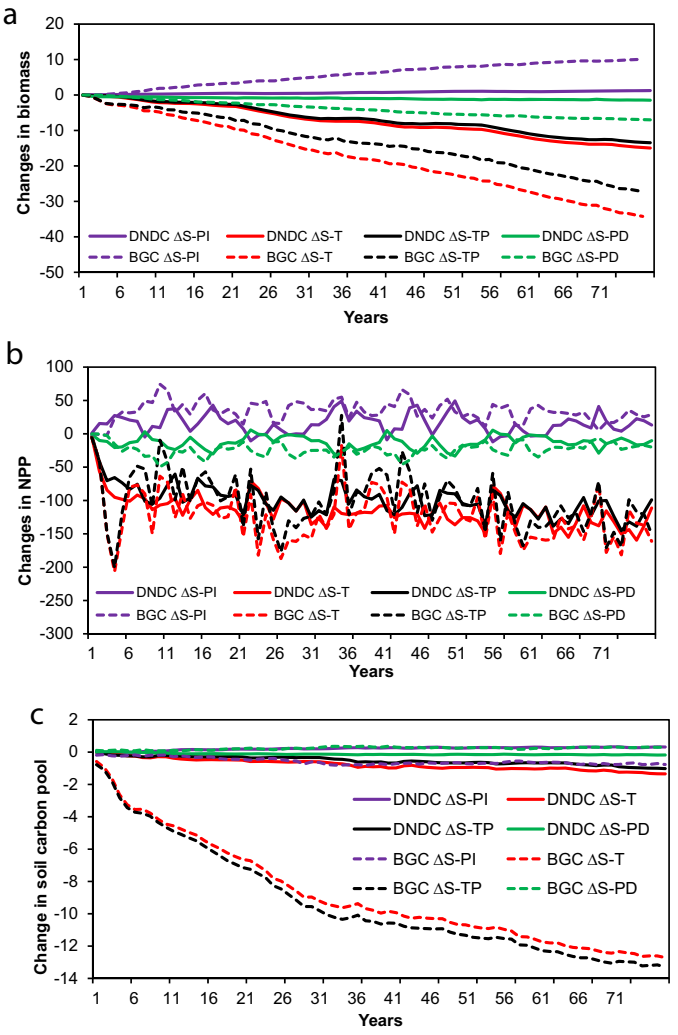


**Fig. 4.** (a) Potential effects of climate change on C storage in forest stands (Mg C $ha^{-1}$) in Kaxil Kiuic forest simulated by Forest-DNDC and Biome-BGC, respectively; ΔS-PI, ΔS-PD, ΔS-T, and ΔS-TP reflect the changes in aboveground biomass corresponding to baseline scenario (S-BL) under precipitation increase, precipitation decrease, temperature increase and an increase in both temperature and precipitation, respectively. (b) Potential effects of climate change on net primary production (NPP, g $m^{-2}$) in Kaxil Kiuic forest simulated by Forest-DNDC and Biome-BGC, respectively; ΔS-PI, ΔS-PD, ΔS-T, and ΔS-TP reflect the changes in net primary product corresponding to baseline scenario (S-BL) under precipitation increase, precipitation decrease, temperature increase and an increase in both temperature and precipitation, respectively. (c) Effects of climate change on soil carbon pool (Mg C $ha^{-1}$) simulated by Forest-DNDC and Biome-BGC, respectively; ΔS-PI, ΔS-PD, ΔS-T, and ΔS-TP reflect the changes in organic carbon in mineral soil layer corresponding to baseline scenario (S-BL) under precipitation increase, precipitation decrease, temperature increase and an increase in both temperature and precipitation, respectively.

for DNDC and 460 kg C $ha^{-1}$ $year^{-1}$ for BGC. Moreover, mean cumulative decrease in biomass under S-T in the 75-year period was 7.5 and 17.7 Mg C $ha^{-1}$ simulated by DNDC and BGC, respectively.

Similarly, biomass decreased significantly ($R^2 > 0.98$, $n = 75$, $P \ll 0.001$) at a linear rate of 189 kg C $ha^{-1}$ $year^{-1}$ for DNDC and 358 kg C $ha^{-1}$ $year^{-1}$ for BGC under S-TP; thus, in the 75-year period, mean biomass under S-TP was 6.7 and 13.5 Mg C $ha^{-1}$ lower compared to the S-BL simulated by DNDC and BGC, respectively. The results from both models indicated that the impact of S-TP on biomass in this forest was slightly smaller than the sum of the two independent impacts of S-T and S-PI.

### 5.3. Net primary production response to climate change

The changes in net primary production (NPP) under different scenarios are presented in Fig. 4b and Table 4. Both models identified an insignificant change in NPP under S-PI and S-PD in the 75-year period. However, NPP significantly decreased linearly under S-T ($P < 0.01$) and S-TP ($P < 0.001$), although the decrease rates were small: 0.66 g $m^{-2}$ $year^{-1}$ under S-T and 0.70 g $m^{-2}$ $year^{-1}$ under S-TP for DNDC, and 0.57 and 0.73 g $m^{-2}$ $year^{-1}$ for BGC, respectively. The differences in NPP under the four climate change scenarios simulated by DNDC and BGC were small.

### 5.4. Effect of climate change on the soil carbon pool

There were large differences in the results of BGC and DNDC for assessing the impact of climate change on soil C pools, including organic C in forest floor (litter and duff) and mineral soil, although both models suggested an influence of climate change (Fig. 4c and Table 4). The results from DNDC suggested a modest impact of climate change while BGC suggested a larger influence.

DNDC suggested a linear increase in soil organic carbon (SOC) by 4.0 kg C $ha^{-1}$ $year^{-1}$ under S-PI, and a decrease by 1.9, 15.0 and 10.9 kg C $ha^{-1}$ $year^{-1}$ under S-PD, S-T and S-TP, respectively. The cumulative changes (difference between scenario and baseline) in SOC in the 75-year period simulated by DNDC under the four scenarios were 0.22, −0.12, −0.77 and −0.52 Mg C $ha^{-1}$ under S-PI, S-PD, S-T and S-TP, respectively (Fig. 4c). The results from DNDC indicated that a precipitation increase (S-PI) can slightly increase C storage in soils in this forest, but suggested that a small decrease in the soil C pool would result under S-PD, S-T and S-TP.

Results from BGC suggested a linearly decreasing trend in SOC in this forest under S-T and S-TP, of about 146.7 and 141.7 kg C $ha^{-1}$ $year^{-1}$, respectively. The large SOC decrease rate for BGC produced a high cumulative SOC loss in the 75-year period, of about 8.85 and 9.37 Mg C $ha^{-1}$ under S-T and S-TP, respectively. The results from BGC suggest that warming may heavily result in a substantial SOC loss from this forest ecosystem.

The simulated results using BGC for assessing the changes in SOC under S-PI and S-PD were opposite to the results from DNDC. BGC suggested a linear decrease in SOC at a rate of 7.5 kg C $ha^{-1}$ $year^{-1}$ under S-PI and a linear increase in SOC at a rate of 2.6 kg C $ha^{-1}$ $year^{-1}$ under S-PD, thus, the cumulative SOC decreased by 0.57 Mg C $ha^{-1}$ in the 75-year period under S-PI and increased by 0.24 Mg C $ha^{-1}$ in the same period under S-PD, respectively.

## 6. Discussion

### 6.1. Model validation

The results of the model validation for BGC and DNDC (Table 3) using observations indicate that both models can be used to assess C storage in the Kaxil Kiuic forest with adequate model performance efficiency ($E \geq 0.25$). However, based on the model performance rating ranges (see the annotation for Table 3) suggested by Moriasi et al. (2007), there are some differences between the two models for assessing C sequestration. BGC performed well ($0.25 < E < 0.75$), whereas DNDC performed excellently ($E > 0.75$) (Table 3). From the model evaluation, DNDC appears to function better than BGC for estimating C dynamics in this forest since model performance efficiency of DNDC ($E \geq 0.79$) is larger than that of BGC ($\geq 0.40$) and the error between the measurement and simulation of BGC is larger than the error of DNDC. Moreover, all model performance evaluation variables (Table 3), including RRS, PBIAS and $R^2$, indicate that DNDC may be

**Table 4**
Changes (differences between climate change scenarios and baseline) in biomass, NPP, LAI, and soil C pools for the two models under different climate change scenarios.[a]

| Item | Forest-DNDC | | | | Biome-BGC | | | |
|---|---|---|---|---|---|---|---|---|
| Scenario | S-PI | S-PD | S-T | S-TP | S-PI | S-PD | S-T | S-TP |
| Biomass | 16$^{***}$ | −13.6$^{***}$ | −208$^{***}$ | −189$^{***}$ | 145$^{***}$ | −98.8$^{***}$ | −460$^{***}$ | −358$^{***}$ |
| Mean biomass | 0.68 | −0.97 | −7.53 | −6.73 | 5.77 | −3.96 | −17.71 | −13.53 |
| NPP | 0.05$^{*}$ | −0.0005$^{\S}$ | −0.66$^{***}$ | −0.70$^{***}$ | 0.11$^{*}$ | 0.07$^{\S}$ | −0.57$^{**}$ | −0.73$^{***}$ |
| Mean NPP | 15.2 | −12.5 | −114.81 | −99.82 | 33.76 | 23.6 | −124.21 | −101.40 |
| LAI | 6.00$^{*}$ | −0.0005$^{*}$ | −1.00$^{*}$ | −1.00$^{*}$ | −3.00$^{*}$ | 0.0002 | −23.0$^{**}$ | −29.0$^{**}$ |
| Mean LAI | 0.14 | −0.096 | −0.15 | 0.02 | 0.14 | −0.094 | −0.48 | −0.39 |
| SOC | 4.0$^{***}$ | −1.9$^{**}$ | −15.0$^{***}$ | −10.9$^{***}$ | −7.5$^{***}$ | 2.6$^{**}$ | −141.7$^{***}$ | −146.7$^{***}$ |
| Mean SOC | 217.9 | −122.0 | −774.1 | −524.7 | −566.2 | 235.0 | −8849.8 | −9365.1 |

[a] Units: biomass, kg C ha$^{-1}$ year$^{-1}$; mean biomass, Mg C ha$^{-1}$; NPP, g m$^{-2}$ year$^{-1}$; mean NPP, g m$^{-2}$; LAI, m$^2$ m$^{-2}$ year$^{-1}$ × 10$^{-4}$; mean LAI, m$^2$ m$^{-2}$; SOC (soil organic carbon), kg C ha$^{-1}$ year$^{-1}$; mean SOC, kg C ha$^{-1}$.
$^{*}$ $P \geq 0.05$.
$^{**}$ $P < 0.01$.
$^{***}$ $P < 0.001$.
$^{\S}$ $P \geq 0.1$.

more suitable to estimate C stocks and the effect of climate change on C dynamics in the Kaxil Kiuic forest and similar forests in this area.

According to the model performance evaluation, BGC can be adequately used to assess the effect of climate change on C storage in aboveground biomass for this forest, but it may not be suitable for assessing the effect of climate change on soil C because this model may overestimate SOC loss due to warming. The differences in C sequestration results between the two models are likely related to their different approaches in modeling vegetation and soil processes. DNDC uses a multilayer soil model to simulate hourly changes in soil moisture, micro-organismic activities, SOM decomposition, and C and N dynamics in each of the soil layers; DNDC also uses a multilayer vegetation model to simulate plant photosynthesis and canopy evapotranspiration. In contrast, BGC employs single layer models to simulate daily changes for these processes.

In addition to using multilayer models, DNDC considers the effect of soil rock content on water movement in soils, whereas BGC does not. All soil parameters for BGC are rock-free. However, the effect of rock abundance should not be overlooked in this forest, where some soils are composed of as much as 90% rocks. The movement of soil water is different in stony soils developed over limestone bedrock and hills compared to rock-free soils. BGC simulates soil moisture based only on physiochemical properties of rock-free soils. It is the difference in simulating soil moisture between the two models that causes a difference in simulated changes in soil C pools under climate change. Thus, the large changes in soil C pools yielded by BGC may be over-estimates, whereas the small changes yielded by DNDC seem to be more feasible.

### 6.2. Carbon sequestration response to precipitation change

The simulated results from DNDC and BGC under S-PI and S-PD indicate that C sequestration increases with an increase in precipitation and decreases with a decrease in precipitation although the results differed between BGC and DNDC. DNDC suggests that S-PI would add about 0.68 Mg C ha$^{-1}$ to biomass and 0.22 Mg C ha$^{-1}$ to SOC pools, respectively, in the 75-year period, for a total increase of 0.90 Mg C ha$^{-1}$; whereas S-PD would decrease C storage by 1.09 Mg C ha$^{-1}$. The results from BGC under S-PI showed that biomass would increase by 5.77 Mg C ha$^{-1}$, but SOC would decrease by 0.57 Mg C ha$^{-1}$, for a total net increase of 5.20 Mg C ha$^{-1}$ in the 75-year period. Carbon storage in the forest would decrease by 3.72 Mg C ha$^{-1}$ under S-PD according to BGC. The difference in C sequestration estimates between these two models is principally related to the divergence in simulation methods for soils, mentioned above.

Although C sequestration in the dry forest can increase with an increase in precipitation, this scenario may not add a large amount of stored C. This is due to the hydrogeology of a hilly limestone landscape, a tropical climate with a long dry period from November to May, and thin and stony soils (Brienen et al., 2009; Allen and Rincon, 2003), such that a modest increase in precipitation cannot substantially improve the soil moisture regime. Accordingly, the results from DNDC seem to be more feasible than those from BGC for assessing C dynamics in the soil in this forest ecosystem under climate change.

The small biomass increase under S-PI may also be related to the large annual precipitation fluctuation in this area, ranging from 639 to 2091 mm in the 75-year period. The effect of an increase in precipitation on biomass under S-PI depended on the value of precipitation, with a critical value of about 1200 mm (Fig. 5a). When annual precipitation is above this critical value, biomass will show a negligible increase with an increase in annual precipitation. Below this critical value, the lower the annual precipitation is, the larger the increase in biomass with an increase in annual precipitation.

Mean annual precipitation intensity (mm per rain event calculated using historical observations) can significantly affect biomass storage in this forest. With higher mean precipitation intensity, biomass increases less with an increase in precipitation (Fig. 5b) ($R^2$ = 0.1596, $n$ = 75, $P < 0.001$), indicating that increasing annual precipitation cannot substantially raise biomass storage in the years with high mean annual precipitation intensity, such as 1990 with 2091 mm precipitation and a mean intensity of 26.1 mm per rain. In contrast, biomass can increase with an increase in precipitation intensity in the years with low precipitation, such as 1980 with 904 mm precipitation and a mean intensity of 9.5 mm per rain. Thus, biomass increased substantially in 1980, but little in 1990. There may be two factors associated with the impact of precipitation intensity on biomass. One is that high precipitation intensity may be accompanied by a strong storm that is not uncommon in this area. The other is that the thin soils covering bedrock and higher evapotranspiration than precipitation results in only modest biomass increase with an increase in precipitation intensity.

Historical changes in annual precipitation frequency (number of rain days per year based on the observations) can also influence biomass storage. Biomass increased with an increase in the number of annual rain days (quadratic; $P < 0.05$) (Fig. 5c). However, when the number of rain days was larger than 110, biomass hardly increased. This is because years with many rain

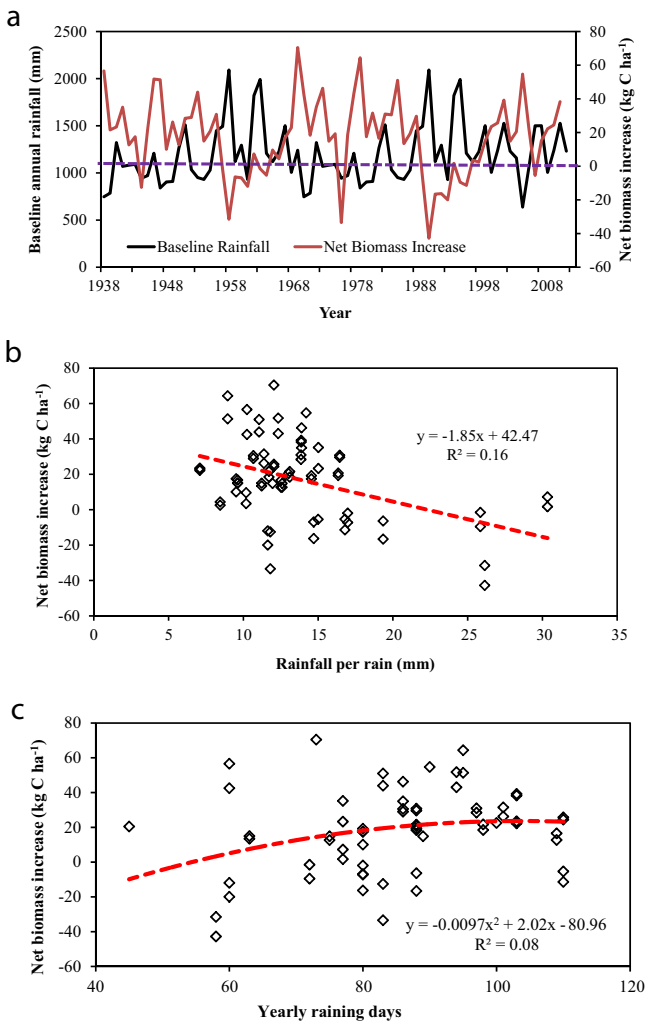


**Fig. 5.** (a) Annual precipitation and simulated net biomass increase under S-PI; dash line: possible critical value of precipitation, i.e., biomass may increase substantially with an increase in precipitation if it is under the critical level. (b) Impact of mean precipitation intensity (rainfall per rain) on biomass increase with an increase in precipitation in Kaxil Kiuic forest. (c) Impact of annual rain days on biomass increase with an increase in precipitation in Kaxil Kiuic forest.

days also tend to have high annual precipitation, such as in 1999 when the rainy season (May–October) accounted for 71% of the rain days and 90% of the total precipitation. Accordingly, increasing precipitation frequency could not add a large amount of biomass to this forest in that year with high rainfall.

### 6.3. Effect of temperature rise on carbon sequestration

Increasing temperature can substantially influence C sequestration in this tropical dry forest. The results from both models indicated that there would be significant decreases in biomass and soil organic C (forest floor and mineral soil), and small decreases in NPP under S-T although the models differed in the decrease rates predicted (Fig. 4 and Table 4). The C in biomass and soils would decrease after the 75-year period by 8.2 Mg C $ha^{-1}$ according to DNDC, and 26.6 Mg C $ha^{-1}$ according to BGC. This is about 0.109 and 0.355 Mg C $ha^{-1}$ $year^{-1}$ less than the current C rate for DNDC and BGC, respectively (current rate = 2.300 - Mg C $ha^{-1}$ $year^{-1}$ and a mean stand age of 27 in 2012), indicating that this tropical dry forest is sensitive to warming.

The high sensitivity to warming is related to the hydrogeology and imbalance between precipitation and evapotranspiration demands (Bauer-Gottwein et al., 2011). Precipitation is less than the potential evapotranspiration, about 80% based on Bauer-Gottwein et al. (2011). Accordingly, an increase in daily air temperature without additional rain can lead to longer and/or more serious droughts such that C sequestration can be reduced. However, BGC likely overestimated the C loss to warming and is mainly related to its estimated soil moisture regime, as discussed above.

The results of the S-TP simulations for both models show that the C dynamics in the Kaxil Kiuic forest would change in response to combined increase in precipitation and temperature. The results from DNDC showed that the S-TP scenario (temperature increase by 2 °C and precipitation increase by 10% $°C^{-1}$) can add only slightly more C to forest biomass (about 120 kg C $ha^{-1}$ in the 75-year period) than the sum of the independent impacts of S-PI (precipitation increase by 20%) and S-T (temperature rise by 2 °C). However, C sequestration in this forest ecosystem under S-TP was substantially less than the baseline scenario, indicating that the enhancing effect of precipitation cannot compensate for the reduction in C sequestration due to warming. The results from the simulations under S-TP and S-T showed that temperature might be the main factor leading to a decrease in C storage in biomass and a key factor impacting C stocks. As mentioned earlier, this may be due to an imbalance between precipitation and evapotranspiration demands, since precipitation is less than potential evapotranspiration in this area (Bauer-Gottwein et al., 2011).

The simulated results of this study are consistent with findings that historical climate fluctuations led to multiyear droughts in Mexico, which droughts played an important role in the classic Maya civilization collapse in the Yucatan Peninsula (Hodell et al., 1995, 2001; Curtis et al., 1996; Haug et al., 2003). This implies that global warming may produce more droughts in this tropical forest, and that, although global warming can bring more rain at a rate of 10% $°C^{-1}$ to this area, C storage capacity in this forest could still be compromised.

Additionally, global warming could also affect plant species composition in this tropical forest, although it was not the focus of this study, by favoring species with functional traits that enable them to reduce heat load, such as small or compound leaves and pulvination that allow shifting leaf angles (e.g. Fabaceae legumes) (Lebrija-Trejos et al., 2010). Drought-tolerant species that that have deep roots (e.g. many species of lianas and shrubs) or high water storage capacity (e.g. cacti and succulent plants) may also be favored under warmer temperatures (Paz et al., 2015). In contrast, species having opposite functional traits (e.g. palms (Arecaceae), aroids (Araceae), and most herbaceous species) may be disadvantaged and may even become locally threatened.

## 7. Conclusions and perspectives

The model validation for BGC and DNDC shows that these two models can be used to estimate C storage in stands of tropical dry semi-deciduous forests in the Yucatan Peninsula of Mexico. However, the performance evaluation indicates that DNDC may be better than BGC for assessing the C dynamics and the effect of climate change on the C dynamics due not only to higher modeling efficiency ($E \geq 0.79$ vs. $E \geq 0.4$), but also smaller error, especially for assessing C dynamics in soils for this dry tropical area. The main reason for this difference in model performance is that BGC uses a single-layer soil model so that the SOM decomposition rate may be over predicted for this dry forest with thin and stony soils covering limestone bedrock.

The results of the two models for assessing the effect of climate change on C stocks show that this tropical dry semi-deciduous forest is highly sensitive to climate change, especially warmer temperatures. An increase in precipitation by 20% may lead to only

a small increase in C sequestration, which is principally related to our assumption of an increase only in precipitation intensity. This precipitation intensity increase may not influence soil moisture for a long time due to the hydrogeological conditions of limestone parent materials, a hilly landscape and a tropical climate; thus, an increase in precipitation intensity can only cause a substantial increase in biomass in years with low precipitation. However, we presently have insufficient observations to develop a scenario for assessing the effect of an increase in precipitation frequency on C sequestration.

Biomass decreases substantially due to warming, even with an additional rainfall, indicating that warming is the main factor that impacts C sequestration. C storage may therefore decrease at a rate of about 189 kg C $ha^{-1}$ $year^{-1}$ under temperature increases of 2 °C while bringing an additional 10% of rain per °C, and at a rate of 207 kg C $ha^{-1}$ $year^{-1}$ without additional rain. The potential consequence is that longer and/or more serious droughts during the plant growth periods (rainy season) may lead to a substantial decrease in C storage. Projecting this result to the future, global warming can be expected to decrease C sequestration in this forest type under these particular hydrogeological conditions, thereby reducing the capacity of this forest to mitigate global warming by sequestering atmospheric $CO_2$. Furthermore, global warming may also lead to shifts in forest species composition, by favoring species with functional traits that enable them to better cope with heat load and/or drought, while disfavoring species with opposite functional traits. Eventually, the vegetation cover type in this area may shift from current semi-deciduous tropical forest to deciduous forest due to longer and/or more intense drought and heat load caused by warming.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecocom.2015.09.004.

## References


Allen, M.F., Rincon, E., 2003. The changing global environment and the lowland Maya: past patterns and current dynamics. In: Gomez-Pompa, A., Allen, M.F., Fedick, S.L., Jimenez-Osornio, J.J. (Eds.), The Lowland Maya Area: Three Millennia at the Human-Wildland Interface. Food Products Press, Binghamton, New York, pp. 13–29.

Baldocchi, D.D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Global Change Biol. 9, 479–492.

Barr, A.G., Morgenstern, K., Black, T.A., McCaughey, J.H., Nesic, Z., 2006. Surface energy balance closure by the eddy-covariance method above three boreal forest stands and implications for the measurement of the $CO_2$ flux. Agric. For. Meteorol. 140, 322–337.

Battaglia, M., Sands, P., 1997. Modeling site productivity of *Eucalyptus globulus* in response to climatic and site factors. Aust. J. Plant Physiol. 24, 831–850.

Battaglia, M., Sands, P., White, D., Mummery, D., 2004. CABALA: a linked carbon, water and nitrogen model of forest growth for silvicultural decision support. For. Ecol. Manag. 193, 251–282.

Bauer-Gottwein, P., Gondwe, B.R.N., Charvet, G., Marin, L.E., Rebolledo-Vieyra, M., Merediz-Alonso, G., 2011. Review: the Yucatan Peninsula karst aquifer, Mexico. Hydrogeol. J., http://dx.doi.org/10.1007/s10040-010-0699-5.

Birdsey, R.A., Jenkins, J.C., Johnson, M., Huber-Sannwald, E., Amiro, B., de Jong, B., Barra, J.D.E., French, N., Garcia-Oliva, F., Harmon, M.E., Heath, L.S., Jaramillo, V.J., Johnson, K., Law, B.E., Marin-Spiotta, E., Masera, O., Neilson, R., Pan, Y., Pregitzer, K.S., 2007. North American forests. In: King, A.W., Dilling, L., Zimmerman, G.P., Fairman, D.M., Houghton, R.A., Marland, G., Rose, A.Z., Wilbanks, T.J. (Eds.), The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle, a Report by the US Climate Change Science Program and the Subcommittee on Global Change Research. National Oceanic and Atmospheric Administration, National Climate Data Center, Asheville, NC, pp. 117–126.

Brienen, R.J.W., Lebrija-Trejos, E., Zuidema, P.A., Martinez-Ramos, M., 2009. Climate-growth analysis for a Mexican dry forest tree shows strong impact of sea surface temperatures and predicts future growth declines. Global Change Biol., http://dx.doi.org/10.111/j.1365-2486.2009.02059x.

Cairns, M.A., Olmsted, I., Granados, J., Argaez, J., 2003. Composition and above-ground tree biomass of a dry semi-evergreen forest on Mexico's Yucatan Peninsula. For. Ecol. Manag. 186, 125–132.

Charman, D.J., Beilman, D.W., Blaauw, M., Booth, R.K., Brewer, S., Chambers, F.M., Christen, J.A., Gallego-Sala, A., Harrison, S.P., Hughes, P.D.M., Jackson, S.T., Korhola, A.K., Mauquoy, D., Mitchell, F.J.G., Prentice, I.C., van der Linden, M., De Vleeschouwer, F., Yu, Z.C., Alm, J., Bauer, I.E., Corish, Y.M., Garneau, M., Hohl, V., Huang, Y., Karofeld, E., Le Roux, G., Loisel, J., Moschen, R., Nichols, J.E., Nieminen, T.M., MacDonald, G.M., Phadtare, N.R., Rausch, N., Dillasoo, U., Swingdles, G.T., Tuittila, E.-S., Ukommaanaho, L., Valiranta, M., Van bellen, S., Van Geel, B., Vitt, D.H., Zhao, Y., 2013. Climate-related changes in peatland carbon accumulation during the millennium. Biogeosciences 10, 929–944, http://dx.doi.org/10.5194/bg-10929-2013.

Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B., Hubbell, S.P., 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. J. Ecol. 91, 240–252.

Chen, J.M., Ju, W., Cihlar, J., Price, D., Liu, J., Chen, W., Pan, J., Balck, A., Barr, A., 2003. Spatial distribution of carbon sources and sinks in Canada's forests. Tellus 55B, 622–641.

Chiesi, M., Maselli, F., Moriondo, M., Fibbi, L., Bindi, M., Running, S.W., 2007. Application of Biome-BGC to simulate Mediterranean forest processes. Ecol. Model. 206, 179–190.

Comision Nacional Del Agua (CONAGUA), 2012. Climatic means by station. http://smn.cna.gob.mx/ (accessed November 2012).

Curtis, J.H., Hodell, D.A., Brenner, M., 1996. Climate variability on the Yucatan Peninsula (Mexico) during the past 3500 years, and implications for Maya cultural evolution. Quat. Res. 46, 37–47.

Dai, Z., Amatya, D.M., Sun, G., Trettin, C.C., Li, C., Li, H., 2011. Climate variability and its impact on forest hydrology on South Carolina coastal plain, USA. Atmosphere 2, 330–357, http://dx.doi.org/10.3390/atmos2030330.

Dai, Z., Trettin, C.C., Li, C., Li, H., Sun, G., Amatya, D.M., 2012. Effect of assessment scale on spatial and temporal variations in $CH_4$, $CO_2$ and $N_2O$ fluxes in a forested watershed. Water Air Soil Pollut. 223, 253–265, http://dx.doi.org/10.1007/s11270-011-0855-0.

Dai, Z., Trettin, C.C., Li, C., Sun, G., Amatya, D.M., Li, H., 2013. Modeling the impacts of climate variability and hurricane on carbon sequestration in a coastal forested wetland in South Carolina. Nat. Sci. 5, 375–388, http://dx.doi.org/10.4236/ns.2013.53051.

Dai, Z., Birdsey, R.A., Johnson, K.D., Dupuy, J.M., Hernandez-Stefanoni, J.L., Richardson, K., 2014. Modeling carbon stocks in a secondary tropical dry forest in the Yucatan Peninsula, Mexico. Water Air Soil Pollut. 225, http://dx.doi.org/10.1007/s11270-014-1925-x.

Dupuy, J.M., Hernandez-Stefanoni, J.L., Hernandez-Juarez, R.A., Tetetia-Rangel, E., Lopez-Martinez, J.O., Leyequien-Abaca, E., Tun-Dzul, F.J., May-Pat, F., 2012. Patterns and correlates of tropical dry forest structure and composition in highly replicated chronosequence in Yucatan, Mexico. Biotropica 44, 151–162.

Hanson, P.J., Amthor, J.S., Wullschleger, S.D., Wilson, K.B., Grant, R.F., Hartley, A., Hui, D., Hunt, E.R., Johnson Jr., D.W., Kimball, J.S., King, A.W., Lou, Y., McNulty, S.G., Sun, G., Thornton, P.E., Wang, S., Williams, M., Baldocchi, D.D., Cushman, R.M., 2004. Oak forest carbon and water simulations: model intercomparisons and evaluations against independent data. Ecol. Monogr. 74, 443–489.

Haug, G.H., Gunther, D., Peterson, L.C., Sigman, D.M., Hughen, K.A., Aeschlimann, B., 2003. Climate and the collapse of Maya civilization. Science 299, 1731–1735.

He, L., Chen, J.M., Pan, Y., Birdsey, R., Kattge, J., 2012. Relationship between net primary productivity and forest stand age in U.S. forests. Global Biogeochem. Cycles 26, GB3009, http://dx.doi.org/10.1029/2010GB003942.

Hernandez-Stefanoni, J.L., Dupuy, J.M., Tun-Dzul, F., May-Pat, F., 2011. Influence of landscape structure and stand age on species density and biomass of a tropical dry forest across spatial scales. Landsc. Ecol. 26, 355–370, http://dx.doi.org/10.1007/s10980-010-9561-3.

Hingston, F.J., Galbraith, J.H., Dimmock, G.M., 1998. Application of the process-based model BIOMASS to *Eucalyptus globulus* ssp. Globulus plantations on ex-farmland in southwestern Australia. I. Water use by trees and assessing risk of losses due to draught. For. Ecol. Manag. 106, 141–156.

Hlasny, T., Barcza, Z., Fabrika, M., Balazs, B., Churkina, G., Pajtik, J., Sedmak, R., Turcani, M., 2011. Climate change impacts on growth and carbon balance of forests in Central Europe. Clim. Res. 47, 219–236.

Hodell, D.A., Curtis, J.H., Brenner, M., 1995. Possible role of climate in the collapse of classic Maya civilization. Nature 375, 391–394.

Hodell, D.A., Brenner, M., Curtis, J.H., Guilderson, T., 2001. Solar forcing of drought frequency in the Maya lowlands. Science 292, 1367–1370.

Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. Ecology 80, 1892–1907.

Hutley, L.B., Leuning, R., Beringer, J., Cleugh, H.A., 2005. The utility of the eddy covariance techniques as a tool in carbon accounting: tropical savanna as a case study. Aust. J. Bot. 53, 663–675.

IPCC Climate Change, 2001. The scientific basis. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., Van der Linden, P.J., Dai, X., Maskell, K., Johnson, C.A. (Eds.), Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom, pp. 6–7.

IPCC Climate Change, 2007. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tigno, M.R, Miller, H.L. (Eds.), The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change IPCC, Paris, France.

Kesik, M., Bruggemann, N., Forkel, R., Kiese, R., Knoche, R., Li, C., Seufert, G., Simpson, D., Butterbach-Bahl, K., 2006. Future scenarios of $N_2O$ and NO emissions from European forest soils. J. Geophys. Res. 111, G02018, http://dx.doi.org/10.1029/2005JG000115.

Kiese, R., Li, C., Hilbert, D.W., Papen, H., Butterbach-Bahl, K., 2005. Regional application of PnET-DNDC for estimating the $N_2O$ source strength of tropic rainforests in the Wet Tropics of Australia. Global Change Biol. 11, 128–144.

Kurbatova, J., Li, C., Varlagin, A., Xiao, X., Vygodskaya, N., 2008. Modeling carbon dynamics in two adjacent spruce forests with different soil conditions in Russia. Biogeosciences 5, 969–980.

Lambert, F.H., Stine, A.R., Krakauer, N.Y., Chiang, J.C.H., 2008. How much will precipitation increase with global warming? EOS 89 (May (21)), 193.

Landsberg, J.J., Waring, R.H., 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. Manag. 95, 209–228.

Lebrija-Trejos, E., Pérez-García, E.A., Meave, J.A., Bongers, F., Poorter, L., 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. Ecology 91, 386–398.

Li, C., Aber, J., Stange, F., Butter-Bahl, K., Papen, H., 2000. A process-oriented model of $N_2O$ and NO emissions from forest soils. 1. Model development. J. Geophys. Res. Atmos. 10, 4369–4384.

Li, C., Cui, J., Sun, G., Trettin, C.C., 2004. Modeling impacts of management on carbon sequestration and trace gas emissions in forested wetland ecosystems. Environ. Manag. (Supplement) 33, S176–S186.

Medina-Elizalde, M., Rohling, E.J., 2012. Collapse of classic Maya civilization related to modest reduction in precipitation. Science 335, 956–959.

Met Office, 2011. Climate: observations, projections and impacts. Exeter Devon, United Kingdom, In: http://www.metoffice.gov.uk/media/pdf/c/6/Mexico.pdf.

Miao, Z., Lathrop Jr., R.G., Xu, M., La Puma, I.P., Clark, K.L., Hom, J., Skowtonski, N., Tuyl, S.V., 2011. Simulation and sensitivity analysis of carbon storage and fluxes in the New Jersey pinelands. Environ. Model. Softw. 26, 1112–1122.

Miehle, P., Livesley, S.J., Feikema, P.M., Li, C., Arndt, S.K., 2006. Assessing productivity and carbon sequestration capacity of *Eucalyptus globulus* plantation using the process model Forest-DNDC: calibration and validation. Ecol. Model. 192, 83–94.

Mo, X., Chen, J.M., Ju, W., Black, T.A., 2008. Optimization of ecosystem model parameters through assimilating eddy covariance flux data with an ensemble Kalman filter. Ecol. Model. 217, 157–173.

Moriasi, D., Arnold, J., Liew, M.W.V., Bingner, R., Harmel, R., Veith, T., 2007. Model evaluation guidelines for systematic quantification of accuracy in watershed simulations. ASABE 50, 885–899.

Nash, J.E., Sutcliffe, J.V., 1970. River flow forecasting through conceptual models-Part I: a discussion of principles. J. Hydrol. 10, 282–290.

Oren, R., Hsieh, C., Stoy, P., Albertson, J., McCarthy, H.R., Harrell, P., Katul, G.G., 2006. Estimating the uncertainty in annual net ecosystem carbon exchange: spatial variation in turbulent fluxes and sampling errors in eddy-covariance measurements. Global Change Biol. 12, 883–896.

Pacific, V.J., McGlynn, B.L., Riveros-Iregui, D.A., Epstein, H.E., Welsch, D.L., 2009. Differential soil respiration response to changing hydrologic regimes. Water Resour. Res. 45, W07201, http://dx.doi.org/10.1029/2009WR007721.

Pan, Y., Birdsey, R.A., Fang, J., Hounghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Ganadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993, http://dx.doi.org/10.1126/science.1201609.

Paz, H., Pineda-García, F., Pinzón-Pérez, L.F., 2015. Root depth and morphology in response to soil drought: comparing ecological groups along the secondary succession in a tropical dry forest. Oecologia, http://dx.doi.org/10.1007/s00442-015-3359-6 (published online 06 June 2015).

Perry, E., Velazquez-Oliman, G., Socki, R.A., 2003. Hydrogeology of the Yucatan Peninsula. In: Gomez-Pompa, A., Allen, M.F., Fedick, S.L., Jimenez-Osornio, J.J. (Eds.), The Lowland Maya Area: Three Millennia at the Human–Wildland Interface. Food Products Press, Binghamton, New York, pp. 115–138.

Pietch, S.A., Hasenauer, H., Kucera, J., Cermak, J., 2003. Modeling effects of hydrological changes on the carbon and nitrogen balance of oak in floodplains. Tree Phys. 23, 735–746.

Rico-Gray, V., Garcia-Franco, J.G., 1991. The Maya and the vegetation of the Yucatan peninsula. J. Ethnobiol. 11, 135–142.

Stange, F., Butterbachl, K., Papen, H., Zechmeister-Boltenstern, S., Li, C., Aber, J., 2000. A process-oriented model of $N_2O$ and NO emissions from forest soils. J. Geophys. Res. 105, 4385–4398.

Tatarinov, F.A., Cienciala, E., 2006. Application of Biome-BGC model to managed forests: 1. Sensitivity analysis. For. Ecol. Manag. 237, 267–279.

Thornton, P.E., Law, B.E., Gholz, H.L., Clark, K.L., Falge, E., Ellsworth, D.S., Goldstein, D.S., Monson, R.K., Hollinger, D., Falk, M., Chen, J., Sparks, J.P., 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. Agric. For. Meteorol. 113, 185–222.

Trettin, C.C., Laiho, R., Minkkinen, K., Laine, J., 2006. Influence of climate change factors on carbon dynamics in northern forested peatlands. Can. J. Soil Sci. 86, 269–280.

Turner, B.L.I.I., Cortina-Villar, S., Forester, D., Geoghegan, J., Keys, E., Klepeis, P., Lawrence, D., Macario Mendoza, P., Manson, S., Ogneva-Himmelberger, Y., Plotkin, A.B., Perez-Salicrup, D., Roy-Chowdhury, R., Savitsky, B., Schneider, L., Schmook, B., Vance, C., 2001. Deforestation in the southern Yucatan peninsula region: an integrative approach. For. Ecol. Manag. 154, 353–370.

Urquiza-Haas, T., Dolman, P.M., Peres, C.A., 2007. Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: effects of forest disturbance. For. Ecol. Manag. 247, 80–90.

Wang, Y.P., Jarvis, P.G., 1990. Description and validation of an array model—MAESTRO. Agric. For. Meteorol. 51, 257–280.

Wang, W., Ichii, K., Hashimoto, H., Michaelis, A.R., Thornton, P.E., Law, B.E., Nemani, R.R., 2009. A hierarchical analysis of terrestrial ecosystem model Biome-BGC: equilibrium analysis and model calibration. Ecol. Model. 220, 2009–2023.

Wentz, F.J., Ricciardulli, L., Hilburn, K., Mears, C., 2007. How much more rain will global warming bring? Science 317, 233–235.

Zhang, Y., Li, C., Trettin, C.C., Li, H., Sun, G., 2002. An integrated model of soil, hydrology and vegetation for carbon dynamics in wetland ecosystems. Global Biogeochem. Cycles 16 , http://dx.doi.org/10.1029/2001GB001838.

Zhang, X., Zwiers, F.W., Hegerl, G.C., Hugo Lambert, F., Gillett, N.P., Solomon, S., Stott, P.A., Nozawa, T., 2007. Detection of human influence on twentieth-century precipitation trends. Nature 448, 461–465.