Estimating terrestrial gross primary productivity in water limited ecosystems across Africa using the Southampton Carbon Flux (SCARF) Model

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Abstract

The amount of carbon uptake by vegetation is an important component to understand the functioning of ecosystem processes and their response/feedback to climate. Recently, a new diagnostic model called the Southampton Carbon Flux (SCARF) Model driven by remote sensing data was developed to predict terrestrial gross primary productivity (GPP) and successfully applied in temperate regions. The model is based on the concept of quantum yield of plants and improves on the previous diagnostic models by (i) using the fraction of photosynthetic active radiation absorbed by the photosynthetic pigment ($FAPAR_{ps}$) and (ii) using direct quantum yield by classifying the vegetation into C_3 or C_4 classes. In this paper, we calibrated and applied the model to evaluate GPP across various ecosystems in Africa. The performance of the model was evaluated using data from seven eddy covariance flux tower sites. Overall, the modelled GPP values showed good correlation (R > 0.59, $p < 0.0001$) with estimated flux tower GPP at most sites (except at a tropical rainforest site, R= 0.38, $p = 0.02$) in terms of their seasonality and absolute values. Mean daily GPP across the investigated period varied significantly across sites depending on the vegetation types from a minimum of 0.44 gC m^{-2} day^{-1} at the semi-arid and sub-humid savanna grassland sites to a maximum of 9.86 gC m^{-2} day^{-1} at the woodland and tropical rain forest sites. Generally, strong correlation is observed in savanna woodlands and grasslands where vegetation follows a prescribed seasonal cycle as determined by changes in canopy chlorophyll content and leaf area index. Finally, the mean annual GPP value for Africa predicted by the model was 35.25 Pg C yr^{-1}. The good performance of the SCARF model in water-limited ecosystems across Africa extends its potential for global application.

Key words: Gross primary productivity, remote sensing, diagnostic model, carbon exchange, photosynthetic quantum yield, C3/C4 photosynthesis

1. Introduction

Gross primary productivity (GPP) plays a critical role in the functioning of terrestrial ecosystems particularly through the regulation of water, energy and nutrient cycles (Gitelson et al., 2012; Verma et al., 2005). While there has been significant improvements in reliability of the estimates of terrestrial GPP in other regions of the world, particularly North America and Europe, estimates remain highly uncertain across the African continent (Ardo et al., 2008; Merbold et al., 2009; Papale et al., 2006; Sjöström et al., 2011). This is despite wide acknowledgement about the critical contributions made by the continent's ecosystems in global carbon dynamics (e.g. Ciais et al., 2011; Sjöström et al., 2011). For example, estimates by Williams et al. (2007) indicated that ecosystems across Africa account for as much as one-fifth of global GPP which is mainly attributed to vastness of the tropical rainforests and the savanna ecosystems. Although recent estimates place Africa as carbon neutral (e.g. Williams et al., 2007), rapid population growth and urbanization (Birch & Wachter, 2011) and general improvement in standards of living (Potts, 2012) are likely to worsen the continent's heavy dependency on natural resources causing uncertainties to its future carbon balance. The uniqueness of African ecosystems is also marked by the heterogeneous nature of the savanna ecosystems which poses challenges in allocating light conversion efficiencies in global GPP models (Suyker & Verma, 2010, 2012).

The uncertain nature of current CO_2 fluxes demands that efforts are directed towards improving data and knowledge availability if we are to improve on future predictions for this region. Several projects have been established as part of initiatives to improve data availability on greenhouse gas (GHG) fluxes for Africa, for example the CARBOAFRICA Project which set up the first flux network for Africa in 2006 (Baldochi et al., 2012; Papale et al., 2006; Sjöström et al., 2011). Although the EC technique remains an efficient source of consistent estimation of ecosystem GPP at local scale (Falge et al., 2002; McCallum et al., 2013; Wu et al., 2010, Ran et al., 2016), the reliability of the estimates are limited only to the extent of the tower footprint in operation. This renders it impractical for estimating carbon fluxes at regional scale especially given the limited spatial coverage of flux sites across the continent (Ardo et al., 2008).

Many models with varying assumptions on how ecosystems respond to environmental factors have been developed for scaling up EC measurements and provide a detailed spatial temporal variation of GPP at a regional to global scale (Coops et al., 2009). In particular, the production efficiency group of models (PEM) (e.g. Ruimy et al, 1999; Turner et al., 2003; Veroustraete et al, 2002) which are based on the light use efficiency concept (LUE) (Monteith, 1972) has been widely adopted. The LUE concept suggests that ecosystem GPP is a function of the amount of photosynthetically active radiation (PAR) intercepted by a canopy, fraction of PAR that is actually absorbed by the canopy (FAPAR) and interacting environmental stress factors that tend to limit potential maximum efficiency (Monteith, 1972). The growth in the use of this family of models is largely due to the ever-increasing available knowledge, data and techniques to derive its key driving variables from Earth Observation (EO) data (Verma et al., 2005, Hilker et al., 2008).

Even though the inception of EO has significantly contributed to advancements in carbon flux modelling, results are still uncertain. An inter-comparison of global models (including both diagnostic and prognostic models) by Cramer et al. (1999)

indicate considerable uncertainty in estimated GPP (a range of 44.4 $PgCyr^{-1}$ to 66.3 $PgCyr^{-1}$) across seventeen participating models. A recent review of GPP spatial-temporal patterns by Anav et al (2015) also found large variations in global mean GPP estimates from various models. In a separate study, Williams et al. (2007) documented that although the level of error from many global models is varied, most seem to concur that as much as 50% of the uncertainty is attributed to the African ecosystems. Such variations could arise since different models adopt different assumptions to simulate ecosystem structure and vegetation responses to complex interactions of environmental factors (Gitelson et al., 2012). For example, most PEMs (e.g. MOD17 Product) use a constant maximum LUE to represent a given biome. This results in reduced ability of the models to capture species-specific LUE variations between plant functional types (PFTs), across seasons, as well as across plant development stages.

The ability to infer vegetation condition and structure from space-borne measurements makes it possible to derive FAPAR from satellite based indices like the normalised difference vegetation index (NDVI) (Asrar et al., 1992; Fensholt et al., 2004; Ogutu and Dash, 2013) and leaf area index (LAI) (Jarvis & Leverenz, 1983, Li et al., 2015). The accurate estimation of FAPAR is important for reliable GPP estimates since FAPAR indicates the level of light absorption in the integrated canopy and consequently controls plant physiological processes represented in productivity models (Myneni & Williams, 1994; Ruimy et al., 1999). Recent studies have also indicated that the use of whole canopy FAPAR ($FAPAR_{ca}$) to estimate GPP, as it is often the case with PEM models, tends to propagate uncertainty as $FAPAR_{ca}$ includes light absorbed by non-photosynthesizing components of the canopy e.g. stem, tree branches and dead foliage (Ogutu & Dash, 2013; Zhang et al., 2014; Zhang et al., 2012; Zhang et al., 2009; Zhang et al., 2016). Ogutu & Dash (2013) gave a clear distinction between FAPAR for the whole canopy and the actual photosynthetic FAPAR ($FAPAR_{ps}$) based on an inverted relationship between net ecosystem exchange (NEE) and incoming PAR. Their results concluded that the FAPAR for whole canopy is consistently higher than that actually used for photosynthesis suggesting that the use of the former may result in an overestimation of GPP and the amount of this overestimation may vary across the growing season. Additional errors in the PEMs may emanate from the use of coarse resolution land cover maps and meteorological data and thus lead to inconsistencies in the estimates of the LUE term (Harris & Dash, 2010; Sims et al., 2006; Wu et al., 2009, Ran et al., 2016).

Recently, a new model called Southampton Carbon Flux Model (SCARF, Ogutu et al., 2013) was developed with the aim of mitigating some of the above shortcomings. For example, it uses the fraction of PAR absorbed only by the photosynthetic components of the canopy ($FAPAR_{ps}$) derived from a spectral index that is sensitive to canopy chlorophyll content for a wide range of vegetation canopies (i.e. the MERIS terrestrial chlorophyll index - MTCI, Dash & Curran, 2004). In addition, the model exploits the intrinsic quantum yield of the two main photosynthetic pathways of plants (C3 and C4 photosynthesis) and does not primarily depend on a detailed land cover map to determine the ability of different vegetation species to convert light energy into biomass. The initial evaluation of the model in ecosystems where vegetation development is mainly controlled by temperature (e.g. Northern higher latitudes) showed good agreement with *in-situ* measurements (Ogutu et al., 2013).

In this study, we calibrated this model and used it to estimate GPP in ecosystems across Africa, where moisture is the main determinant of ecosystem GPP (Scholes et al., 2004; Svoray & Karnieli, 2011; Weber et al., 2009). Apart from evaluating the models performance in relation to *in-situ* GPP measurements and MOD17 GPP product, the study also investigated the sensitivity and uncertainty of the SCARF model to determine the relative importance of the main biophysical and meteorological input parameters to the model's output.

2. Data and methods

2.1. The SCARF model

The SCARF Model follows the general form of PEM models but it has extended capability by separating $FAPAR_{ps}$ from $FAPAR_{ca}$. The LUE term is also replaced by an intrinsic quantum yield term that specifies the capacity of plants in the C3 and C4 photosynthetic pathways to convert incident light energy and other resources into biomass (Ogutu et al., 2013). The use of $FAPAR_{ps}$ accounts for APAR that is absorbed by photosynthesising parts of the vegetation canopy while a quantum yield term in this case reduces uncertainties due to land cover misclassification since plants are treated only based on their photosynthetic pathways. In its basic form, the GPP from the model (GPP_{SCARF} g C m^{-2} day^{-1}) can be estimated following Ogutu et al. (2013):

$$GPP_{SCARF} = PAR * FAPAR_{ps} * (a * k) \quad (1)$$

Where PAR (µmol m^{-2} s^{-1}) is the incoming photosynthetically active radiation, $FAPAR_{ps}$ (µmol m^{-2} s^{-1}) is time averaged absorbed active radiation (APAR) derived as a product of fraction of APAR absorbed only by photosynthesising tissue in the canopy, a (µmol µmol^{-1}) is the maximum quantum yield for either C3 or C4 plants and k represents modifying conditions affecting maximum quantum yield. Parameters a and k in above equation can be expanded to:

$$a = P_{C3}\, a_{C3}\, f_{C3}^{vpd}\, \Psi_e \qquad (2)$$

$$k = (1 - P_{C3}) a_{C4}\, f_{C4}^{vpd} \qquad (3)$$

Where P_{C3} represents the proportion (%) of C3 plants, $(1\text{-}P_{C3})$ represents the proportion of C4 plants within a study site, a_{C3} and a_{C4} represent the maximum quantum yields for C3 and C4 plants, respectively, ψ_e (unitless) is the influence of temperature and leaf CO_2 concentration on the maximum quantum yield of C3 plants. f_{C3}^{vpd} and f_{C4}^{vpd} represent the influence of vapour pressure deficit (VPD) on C3 and C4 photosynthesis, respectively.

C3 and C4 plants are essentially separated by their distinct photosynthetic responses to temperature and CO_2 partial pressure at the leaf surface. CO_2 partial pressure in the chloroplast is 5-10 times higher in C4 than in C3 photosynthesis and this efficiently prevents photorespiration due to suppression of oxygen competition and saturation of Rubisco carboxylase activity (Ehleringer & Björkman, 1977). Since the process of photorespiration is both temperature and CO_2 dependent, photosynthesis is generally higher in C4 than C3 plants at high temperature and low CO_2 partial pressure (Brooks & Farquhar, 1985). The values adopted in the SCARF Model to parameterise a_{C3} and a_{C4} (0.08 mol mol^{-1} and 0.06 mol mol^{-1} respectively) concur with both laboratory and field based measurements (Collatz et al., 1991; Collatz et al., 1992; Ehleringer & Björkman, 1977).

2.1.1. Sub-models

A number of sub-models were incorporated in the SCARF Model and these included Vapour Pressure Deficit (VPD), $FAPAR_{ps}$ and ψ_e which estimate the influence of temperature and leaf CO_2 concentration on the maximum quantum yield of C3 plants.

2.1.1.1. The Vapour pressure deficit sub model

Vapour Pressure Deficit (VPD) is a key physiological variable used in ecosystem productivity models as it is directly related to environmental stress. It can be defined as the difference (deficit) between the amount of moisture in the air and how much moisture the air can hold when it is saturated. It brings together the effects caused by both relative humidity and temperature as a single indicator of plant health. High VPD causes plant leaves to reduce stomatal aperture to regulate excessive water losses through transpiration (T) which in turn reduce CO_2 assimilation for photosynthesis. To incorporate the effect of VPD on the quantum yield, a sigmoid function was adopted since high VPD causes moisture stress in the plant, and therefore inhibits photosynthesis, while low VPD will generally result in an increase in photosynthesis but tends to flatten out with continued decrease. In the original SCARF model the VPD function was parameterised using the equation below (Ogutu et al., 2013; Tu, 2000):

$$f_D(Dk) = \frac{1}{1 + \exp[1.3(VPD - 3)]} \qquad (4)$$

Where *VPD* (Pa)is the instantaneous moisture condition

For site level evaluation of the model, in-situ VPD observations were used. However, for application at the regional scale, VPD values used were estimated following Unwin (1980) whereby VPD is expressed as the difference between saturation vapour pressure (SVP) and actual vapour pressure (AVP). SVP (Pa) is calculated as follows:

$$SVP = 6.11 * \exp((L./Rv) * (1./273 - 1/(273.15 + T))) \quad (5)$$

Where L is latent heat of vaporisation ($2.5 * 10^6$ Jkg^{-1}), Rv is a gas constant for water vapour (461 JK^{-1} kg^{-1}) and T is air temperature (ºC). AVP (Pa) is calculated as:

$$AVP = (RH/100) * SVP \quad (6)$$

Where RH is relative humidity (%), calculated as follows:

$$RH = 100 * (\exp((17.625 * DPT)/(243.04 + DPT))/\exp((17.625 * T)/(243.04 + T))) \quad (7)$$

Where DPT is dew point temperature (ºC)

Evaluation of estimated VPD against those derived from the measurements at the flux tower was performed for seven sites and the agreement was considered as modest to very good (R^2=0.61 to 0.96).

2.1.1.2. FAPARps sub-model

$FAPAR_{ps}$ for a canopy has a strong linear relationship with the total quantities of chlorophyll present in that canopy (Ogutu et al., 2013). The MTCI has been used as a surrogate for GPP and chlorophyll content (e.g. Dash et al., 2010; Harris & Dash, 2010, 2011) and $FAPAR_{ps}$ (e.g. Ogutu et al., 2013) yielding strong positive relationship. The current study assumes MTCI to be a proxy for $FAPAR_{ps.}$ A full description of how $FAPAR_{ps}$ was derived through the inversion of EC NEE data and related to MTCI can be found in Ogutu et al. (2013). The relationship between $FAPAR_{ps}$ and MTCI derived in Ogutu et al (2013) as shown below was used in the current study.

$$fAPAR_{ps} = 0.76 * MTCI + 0.07 \quad (8)$$

Influence of temperature on C3 photosynthesis

To estimate the influence of temperature and CO_2 partial pressure on the maximum quantum yield of C3 photosynthesis, the term ψ_e was incorporated following (Hanan et al., 1998)

$$\psi_e = -0.0043049\,T - 0.0002077\,T^2 + 0.8973228 \quad (9)$$

Where *T* is the atmospheric air temperature. The model was implemented at the site level by using *in-situ* temperature measurements, while at continent scale by using European Centre for Medium-Range Weather Forecasts (ECMWF) reanalysed air temperature measured at 2m above the ground surface.

2.2. Eddy covariance flux data

Seven EC flux sites (with data covering a total of 15 years) within the CARBOAFRICA flux network were used in the analyses (Table 1). These sites measure fluxes in some of the dominant and typical representative ecosystems across Africa. The study was primarily depended upon coincident data available for flux data and the MERIS MTCI data which is a dominant variable from which GPP is computed. The Tchizalamou (CG-Tch) in the Republic of Congo represents tropical grassland ecosystems in central-west Africa while the Bontioli site in Burkina Faso (BF-Bon) and Demokeya in Sudan (SD-Dem) take measurements in sub-humid and semi-arid Sahel climates, respectively. Mongu in Zambia (ZM-Mon), Malopeni (ZA-Map) and Skukuza (ZA-Kru), both in South Africa, represent sub-humid and semi-arid savannas of southern Africa while Ankasa site in Ghana (GH-Ank) represents tropical rain forest ecosystems. Due to the scarcity of flux tower sites in Africa, no data was available for the tropical dryland forests in Africa. Therefore, the model was not calibrated and validated for this biome and due to this, the SCARF model results for this biome my contain uncertainties.

The selected EC data are gap-filled CARBOAFRICA Level 4 datasets which are available at different temporal scales including 30 minutes, daily, weekly as well as monthly scales. GPP is calculated from NEE values computed either using the one-point or profile approach in the storage term computation (standardized and original NEE respectively) (Papale et al., 2006). Gap filling of the NEE measurements is then achieved through Marginal Distribution Sampling (MDS) and Artificial Neural Network (ANN). This study used GPP values estimated from standardized NEE and then gap-filled using the MDS method. A detailed description of the level 4 CARBOAFRICA dataset and its original processing is given in Papale et al. (2006).

Daily estimates of flux GPP were chosen for this study and values were then aggregated by calculating the mean value to 10-day (dekadal) time steps to coincide with the MERIS MTCI data. Flux GPP values were also aggregated by calculating the mean to 8-day time steps to match MOD17 GPP product since it was also used to evaluate the performance of the SCARF model. However, for PAR values, level 2 dataset was used (i.e. the 30 minute averages of photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1})) after being aggregated to daily and decadal averages. Table 1 gives the main characteristics while Figure 1 shows the distribution and locations of the participating sites.

Table 1: Main characteristics of the seven evaluation flux tower sites

Site	Country	Lat	Lon	Ecosystem	C3/C4 cover	MAP (mm)	MAT (ºC)	Years	References
Tchizalamou	Dem Rep Of Congo	-4.2892	11.6564	Tropical-humid grassland	0/100	1150	26	2006-2010	(Merbold et al., 2009)
Bontioli	Burkina Faso	10.1822	-3.6727	Sub-humid Savanna	70/30	926	26.1	2008	(Brummer et al., 2008; Papale et al., 2006)
Demokeya	Sudan	13.2829	30.4783	Semi-arid savanna	30/70	320	26	2005-2008	(Ardö et al., 2008)
Skukuza	South Africa	-25.0197	31.4969	Sub-humid wooded savanna	30/70	545	22	2006-2008	(Papale et al., 2006)
Malopeni	South Africa	-23.8325	31.2145	Sub-humid savanna	30/70	458	22.2	2009	(Papale et al., 2006)
Mongu	Zambia	-15.4377	23.2527	Sub-humid woodland	95/5	945	24.5	2006-2008	(Papale et al., 2006)
Ankasa	Ghana	5.2697	-2.6948	Tropical evergreen forest	100/0	1900	26	2011	(Chiti et al., 2010; Fattore et al., 2014)

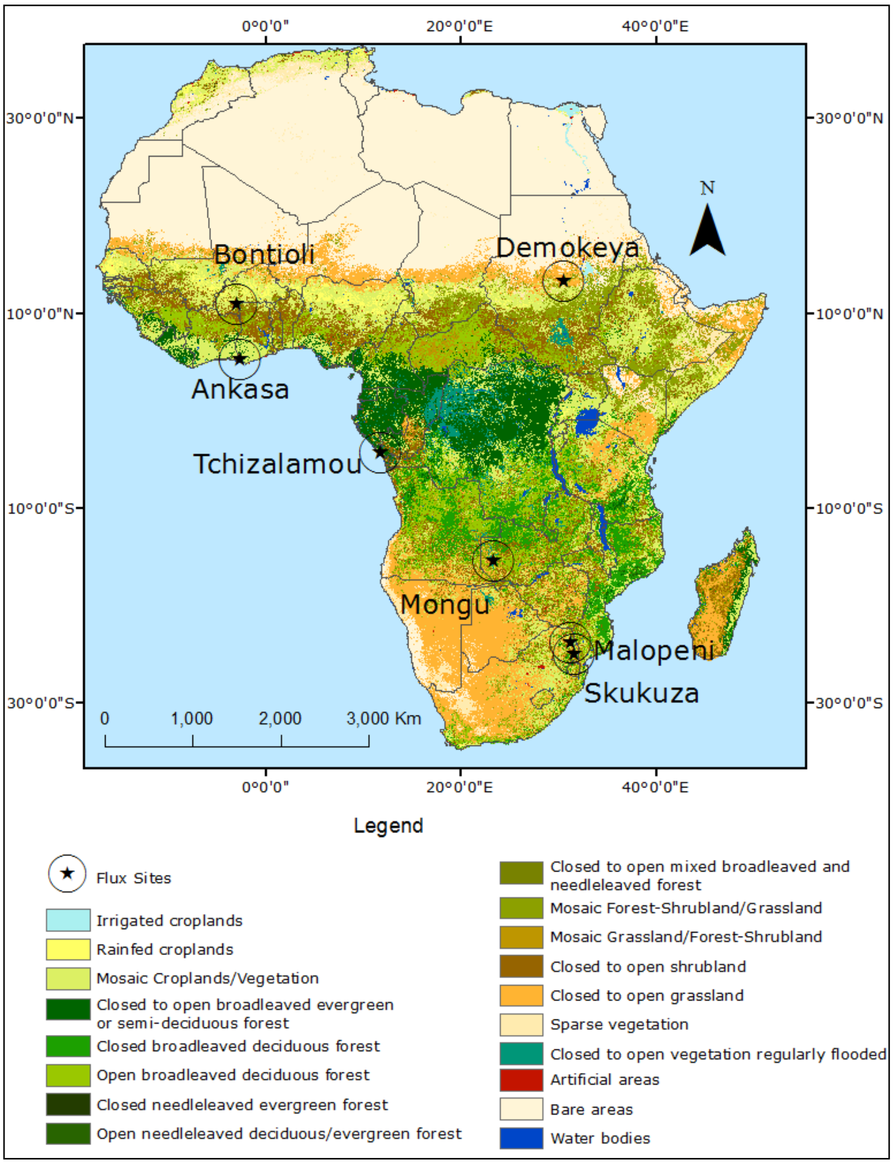

Figure 1: A GlobCover map of Africa showing generalised land cover types and the locations of flux tower sites used in evaluation exercise

2.3. Meteorological data

A number of meteorological measurements including daily mean of atmospheric temperature (T_a, ºC), PAR (µmol m^{-2} s^{-1}), VPD (hPa) and dew point temperature (DPT, ºC) were used for this study. *In-situ* measurements of T_a, VPD and PAR recorded at the flux site were direct input variables in the SCARF model for site level evaluation. However, for modelling GPP across coterminous Africa, T_a and VPD were obtained from ECMWF website (http://data-portal.ecmwf.int/data/d/interim_full_daily/) at full resolution (0.75º x 0.75º grids). DPT data was used in a sub-model to estimate VPD since there was no readily available product for VPD. A GLASS PAR product (Liang & Zhang, 2012), which is freely available at ftp://ftp.glcf.umd.edu/glcf/GLASS/PAR/, with a 5km spatial and 3 hours temporal resolution was also used to control rate of photosynthetic conversion in the model at continent scale. Daily images acquired at 12 noon and aggregated to monthly averages were used. Pixels with zero/missing values were omitted in the statistics. Further details about the GLASS PAR product can be found in (Liang & Zhang, 2012; Liang et al., 2006).

All raster grids were resampled to match the 1km x 1km ground resolution of the MTCI data.

2.4. Land cover data and determination of C3/C4 proportions

Land cover information was derived from a 2009 GlobCover map obtained from the European Space Agency (ESA) GlobCover Portal Website (http://due.esrin.esa.int/globcover/). The data has a ground pixel size of 300m and was used for two purposes. Firstly, to derive maps of C3 and C4 distribution and their relative proportions in each 1km grid cell, and secondly to define pixel-based maximum quantum yields for C3 and C4 photosynthesis. The C3/C4 proportions used for site level implementation of the model (Table 1) were based on figures published in Merbold et al. (2009). To estimate the relative proportions of C3/C4 plants in each 1km^2 pixel, first the land cover map was reclassified into C3, C4 and C3/C4 maps. The C3 map contained all pixels dominated by forests and woodlands, while the C4 map contained all pixels dominated by grasslands. The C3/C4 map contained all pixels with mixed savannas and all cropland. Since the land cover map does not specify vegetation composition in areas where mosaics of grasslands, shrublands and forests, a 50-50 ratio between C3/C4 was assumed in these pixels. The same assumption was also made for cropland because both C3 and C4 crops are widely grown across Africa but their distribution is not specified in the land cover map.

2.5. Data Processing

2.5.1. Processing of MTCI time series data

The 1km dekadal original MTCI data were provided by the Natural Environmental Research Council Earth Observation Data Centre (NERC NEODC) - ftp://l3-server.infoterra.co.uk/pub/) of the European Space agency (ESA) and processed by Astrium GEO-Information Service. The MTCI Level 2 product was calculated using three red/near infra-red bands of the ENVISAT MERIS data to produce an image indicating the amount of chlorophyll content per unit area (Curran & Dash, 2005).

A considerable amount of error is usually expected in any efforts of up-scaling point measurements obtained from a flux tower to the spatial scale of the satellite pixel e.g. the 1km x 1km extent of the MTCI images. Since it is difficult to identify the exact pixel from which the flux tower measurements are made, a 3x3 km sample, whose centre is at the respective tower location, was extracted and averaged (zero values were excluded) to get a representative value to correspond with the tower GPP. Visual inspection of each flux site on Google Earth also confirmed that all the sites were homogeneous for at least 1km in any direction from each respective site. A separate assessment based on 2005 MODIS land cover product also confirmed that at least 88% of the pixels in the 3x3km grid had the same land cover value as the centre (flux tower) pixel.

2.5.2. Processing MODIS GPP time series data

The MOD17 GPP Version 6 Product was obtained from both the NASA Earthdata Search portal (https://search.earthdata.nasa.gov/search?q= MOD17A2H+V006) and Oak Ridge National Laboratory Distributed Active Archive Centre's (ORNL DAAC, MODIS Land Subsets (https://modis.ornl.gov/cgi-bin/MODIS/global/subset.pl). The Version 6 product is at 500m resolution, therefore a 1.5 x 1.5 km sample, centred at each respective flux site, was used to extract time series GPP values for these sites. The MOD17 GPP values were available in kg C m^{-2} in 8 days and were converted to g C m^{-2} day^{-1} to be consistent with the GPP measured by the EC technique.

2.5.3. Sensitivity and uncertainty analyses

The overall importance of an input parameter in a model can be assessed based on its impact on the model output. One way of achieving this is to test how much of the model output is explained by a parameter through regression analysis of the input parameter with the model output. The other method is to allow one parameter to vary at a time while others are held constant (e.g. Hamby, 1993). In this study, the regression method was employed. Modelled GPP values were regressed against T_a, PAR, VPD and MTCI and the statistics on goodness of fit were determined.

The Monte Carlo technique was also used to assess the degree of sensitivity and uncertainty of GPP due to the quantum yield parameters for C3 and C4 plants (a_3 and $a4$, respectively) at all seven study sites. The maximum quantum yields (a_3 =0.08 and a_4 =0.06µmol µmol^{-1}) used in the initial evaluation of the SCARF model (Ogutu et al., 2013) are based on laboratory and field experiments carried out for different vegetation types from different ecosystems, mostly outside the African environments. The main concern for the current work is related to the stochasticity associated with these parameters since they are not fixed but may vary with time and space. Given the diversity and heterogeneity of the ecosystems considered in this study, an attempt was made to estimate the biases associated with the inaccuracies and unavoidable random variation in the use of the two maximum quantum yields.

According to published literature, values of a_3 vary from a minimum of 0.0525 to a maximum of 0.08 while a_4 varies from 0.0535 to 0.065 (Ehleringer & Björkman, 1977; Ehleringer & Pearcy, 1983;Singsaas et al., 2001). To determine the variability in output that result from the two parameters, 500 random samples were generated for each parameter based on ranges of the documented values and 500 model runs were performed based on the randomly generated samples. Mean, standard deviation, root mean square error (RMSE) and range were computed for the modelled GPP and compared to *in-situ* GPP for each site. The 'best guess' for each random parameter and site was determined based on the model run with the smallest RMSE calculated between observed and modelled GPP for each participating flux site. The implementation of the model at both site and regional scale was thus based on the 'best guesses' of a_3 and a_4 for different ecosystems.

3. Results

3.1. Model sensitivity and uncertainty analyses

3.1.1. Importance of different parameters to model output

The sensitivity of GPP_{SCARF} to the main environmental drivers changes substantially through time and among ecosystems. A fundamental distinction can be noted between moisture stressed and water sufficient ecosystems particularly in relation to their response to VPD, PAR and T_a. VPD has weak to very strong negative relationships ($-0.17>R^2>-0.99$) against GPP_{SCARF} in sub-humid and semi-arid ecosystems (i.e. Mongu, Demokeya, Skukuza, Bontioli, and Malopeni) while it exhibits modest positive correlations in tropical humid grassland (Tchizalamou) and rain forest (Ankasa) ecosystems ($R^2=0.61$ and 0.40, respectively) (Table 2). The difference between the responses of these ecosystems can be explained by how the vegetation attempts to optimise CO_2 uptake and water loss in response to changing moisture conditions. In water sufficient areas, increasing VPD would increase stomatal conductance (g_s) (and ET) but since plants do not initiate stomatal resistance owing to sufficient soil moisture, rate of CO_2 assimilation increases. VPD is particularly important in the sub-humid and semi-arid savanna ecosystems of Bontioli and Demokeya ($R^2=-0.99$ and -0.94, respectively) (Table 2) where T_a and PAR are constantly high throughout the year.

The response of GPP_{SCARF} to T_a almost always mirror that of PAR even though the correlation coefficients differ in absolute values. Both PAR and temperature have strongest positive correlation in tropical humid and rainforest ecosystems (i.e. Chizalamou and Ankasa - Table 2). These two sites have a relatively wet and cloudy climate compared to the other study sites. These conditions result in increased relative humidity, cloudiness and precipitation incidences which in turn reduce temperature and available PAR. Therefore, temperature and PAR are important in determining the levels of primary productivity in these sites. As expected, both T_a and PAR had a negative correlation with GPP_{SCARF} in the sub-humid and semi-arid ecosystems (i.e. Mongu, Demokeya, Skukuza, Bontioli, and Malopeni) as high PAR and T_a may cause photoinhibition and high ET/VPD, respectively in these water limited ecosystems.

The model's sensitivity to MTCI is highest in savanna woodland ecosystems, moderate in tropical grassland and weak in tropical rain forests. However, of importance is the fact that while response of GPP to MTCI is both strong and positive in all other ecosystems, it is negative in tropical rainforests (Table 2). As the vegetation in tropical evergreen forests has high chlorophyll concentration and multi-layered canopies, most of the incident light energy is absorbed by chloroplasts at the top of the canopy while deep layers are deprived of light energy. This may suggest that photosynthesis could be quite high at the top most layers of the canopy but overall productivity is reduced due to decreased photosynthetic rates within the deep and under storey owing to light deprivation.

Table 2. Importance of the various input parameters as determined by the coefficient of determination (R^2 values) between time series of GPP_{SCARF} and main meteorological and vegetation biophysical parameters

Flux Site	n (10-day time step)	Coefficient of determination (R^2 values) between GPP_{SCARF} and			
		PAR	VPD	MTCI	Temperature
Mongu	68	-0.18	-0.77	0.89	-0.22
Tchizalamou	85	0.91	0.61	0.65	0.86
Demokeya	78	-0.07	-0.94	0.75	-0.03
Skukuza	59	-0.65	-0.22	0.92	-0.59
Bontioli	22	-0.42	-0.99	0.94	-0.52
Malopeni	31	-0.60	-0.17	0.57	-0.51
Ankasa	33	0.86	0.40	- 0.25	0.61

3.1.2. Uncertainties resulting from the quantum yield terms

The model variability due to the uncertain quantum yield terms was achieved based on 500 random samples generated between acceptable ranges for a_3 and a_4 from which 500 model runs were subsequently performed for each site (Figure 2). The importance of the two parameters was both site and season dependent. For example, both parameters were more important at Mongu, Bontioli, Tchizalamou and Demokeya during the main growing season when the estimated

GPP was within one standard deviation of the modelled GPP (Figure 2). During the senescence stages, observed GPP was outside the model range indicating that, as expected, maximum quantum yields of both C3 and C4 were no longer main determinants of GPP. Other parameters closely linked to seasonality especially $FAPAR_{ps}$ (chlorophyll content) and VPD make it impossible to achieve maximum photosynthetic rates during the senescence stages of plant development. VPD was identified as the main cause of overestimation of GPP during the dry season in European and North American ecosystems during the initial evaluation of the SCARF model (Ogutu et al., 2013). The same trend is observed for ecosystems represented in the current study. The only difference, though, is that the model range is larger especially in ecosystems dominated by C3 species. This could be expected given the range of uncertainty for a_3 (0.053 to 0.08 mol mol^{-1}) compared to a_4 (0.053 to 0.065 mol mol^{-1}).

'Best guesses' of maximum quantum yields for C3 and C4 photosynthesis, as represented by model runs with smallest RMSE, indicate a consistent a_3 of 0.0543 and a_4 of 0.0532 across all mixed savanna sites while an a_3 of 0.08 and a_4 of 0.056 were observed for the woodland sites of Mongu and Bontioli. Tropical sites of Tchizalamou and Ankasa with 100% proportions of C3 and C4 plants, respectively, returned near-maximum values for both a_3 and a_4 owing to little influence resulting from heterogeneity in vegetation composition and structure as in the savannas.

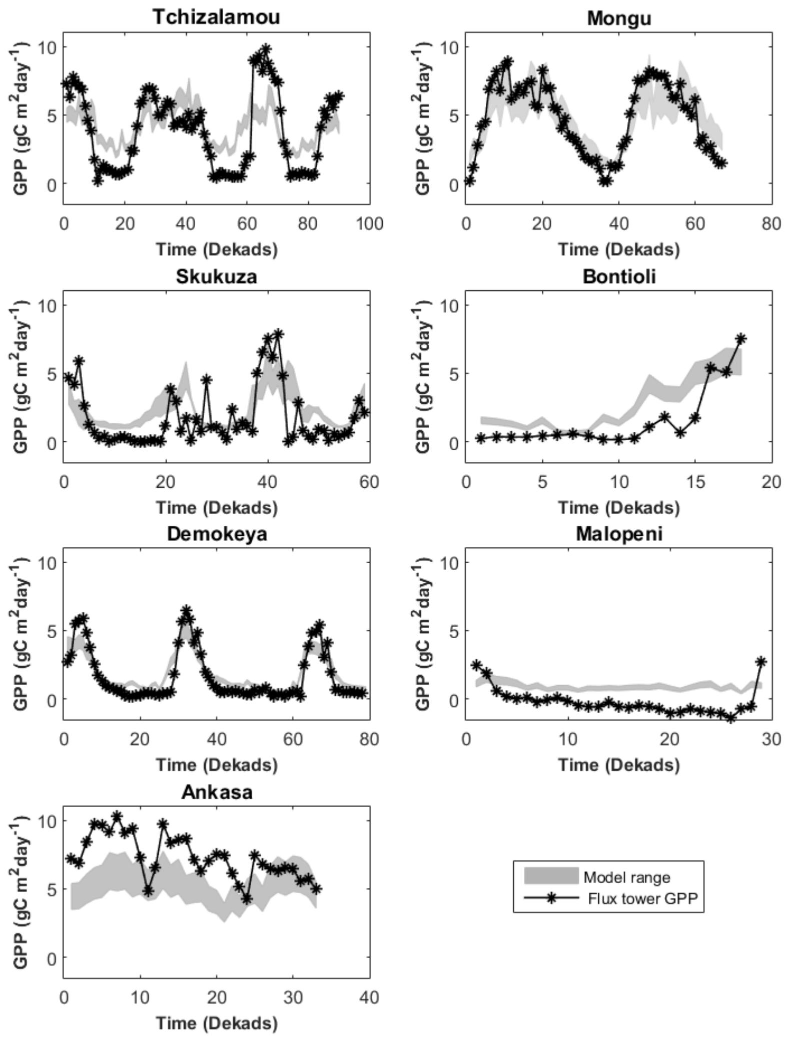

Figure 2. Simulated and observed GPP for flux tower sites. The grey area marks the range of GPP from two hundred model runs.

3.2. Seasonal and annual variability of model GPP across Africa

SCARF model GPP was evaluated against *in-situ* flux measurements at seven flux sites. Overall, GPP_{SCARF} values show good agreement with observed GPP at most sites (except tropical rainforest site) in terms of seasonality (Figure 3) and absolute values (Figure 4). There is good coincidence between predicted GPP peaks and growth season as well as troughs within low growth seasons (Figure 3). Mean daily GPP across the investigated period varied significantly across sites from a minimum of 0.44 gC m^{-2} day^{-1} at the semi-arid and sub-humid savanna grassland sites to a maximum of 9.86 gC m^{-2} day^{-1} at the woodland and tropical rain forest sites. The highest seasonal at-site variability was observed at Tchizalamou and least variability was observed at Malopeni (Figure 3).

The SCARF model output have modest to very strong positive correlation with observed GPP at most sites (R 0.59 to 0.91, $p < 0.0001$) apart from the tropical rainforest site (R = 0.38, $p=0.02$). The comparison between MOD17 product and *in-situ* flux tower GPP estimates resulted in slightly lower R^2 and higher RMSE values in most of the sites (Figure 4). Overall, the MOD17 product tended to underestimate GPP in most of the evaluated sites (Figure 4). For the SCARF model, the coefficient of correlation between the model data and the flux tower estimates were strongest ($R>0.83$, $p<0.0001$) in savanna biomes dominated by woody species (i.e. Mongu and Bontioli), moderate ($R> 0.5$, $p<0.0001$) in more heterogeneous grassland and savanna ecosystems (i.e. Skukuza, Demokeya, and Tchizalamou) and low (R = 0.38, p = 0.02) in the evergreen rainforest site (i.e. Ankasa) (Figure 4). For the MOD17 product strong correlation ($R> 0.76$, $p<0.0001$) was observed in the savanna site of Demokaya and wooded savanna site of Bontioli, moderate correlation ($R> 0.55$, $p<0.0001$) at Tchizalamou, Mongu and

Skukuza and weak correlation (R = 0.08, p = 0.698) at the evergreen tropical forest site (i.e. Ankasa) (Figure 4). Overall, the correlation coefficients were strongest in ecosystems where vegetation follows a prescribed seasonal cycle as determined by canopy chlorophyll content and leaf area index.

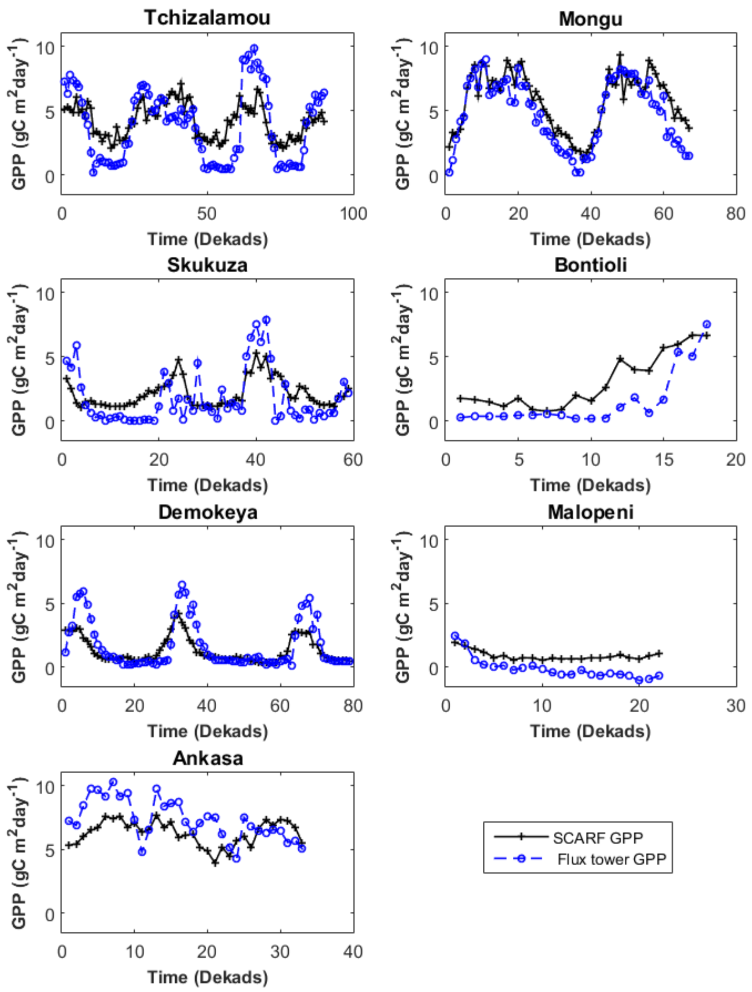

Figure 3: Seasonal and spatial trends of *in-situ* and SCARF model GPP for flux tower sites.

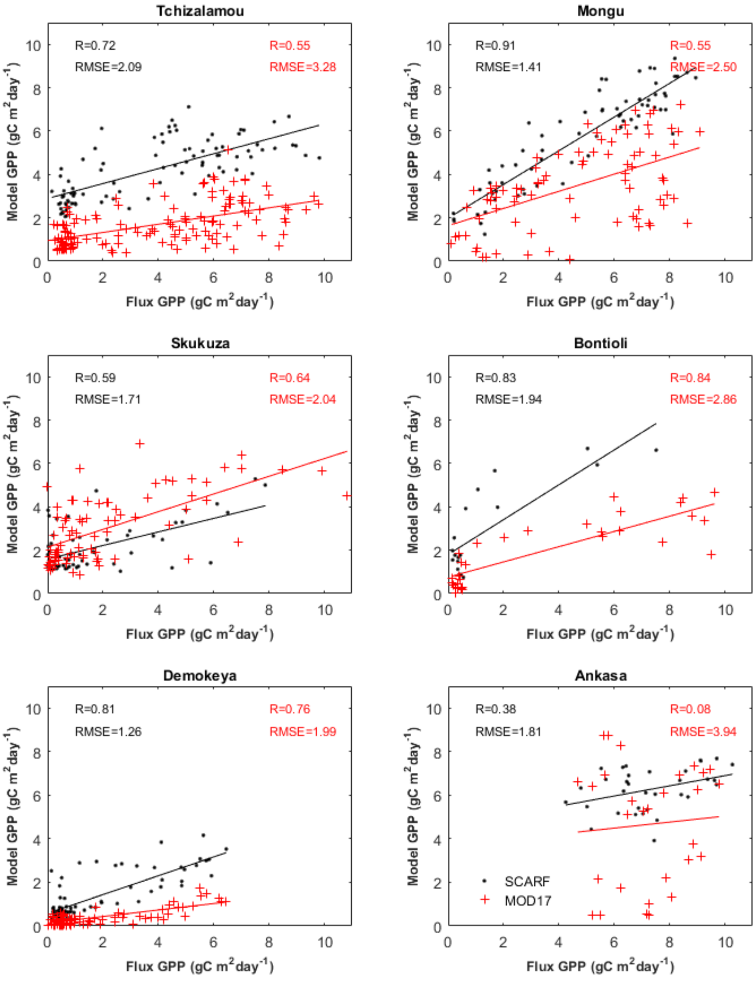

Figure 4: Relationship between SCARF model output (black dots), MOD17 (red asterisks) and *in-situ* flux tower GPP measurements at various sites.

3.3. Spatial distribution of GPP across Africa

Figure 5 (*a* and *b*) show the distribution of GPP predicted by the SCARF model and MOD17 product, respectively. The distribution of GPP_{SCARF} across the coterminous Africa concur with the findings from the site level analysis where highest GPP values are concentrated in the central tropical rain forests, moderate values within pixels dominated by woody species and lower productivity in grasslands and sparsely vegetated areas. SCARF model has higher absolute values in most of the sub-humid and semi-arid savanna ecosystems and parts of the tropical rain forests while MOD17 GPP depicts higher values in isolated regions for example on the island of Madagascar. Overall, GPP_{SCARF} has a minimum GPP of 100 g Cm^{-2} yr^{-1} and maximum of 4,500 g Cm^{-2} yr^{-1} compared to 60 and 3,900 g C m^{-2} yr^{-1} from the MOD17 product. The total annual GPP predicted by the SCARF model for the year 2010 was 35.25 Pg C yr^{-1} and that from MOD17 was 21.39 Pg C yr^{-1}, showing that SCARF model prediction was higher than that from MOD17 product.

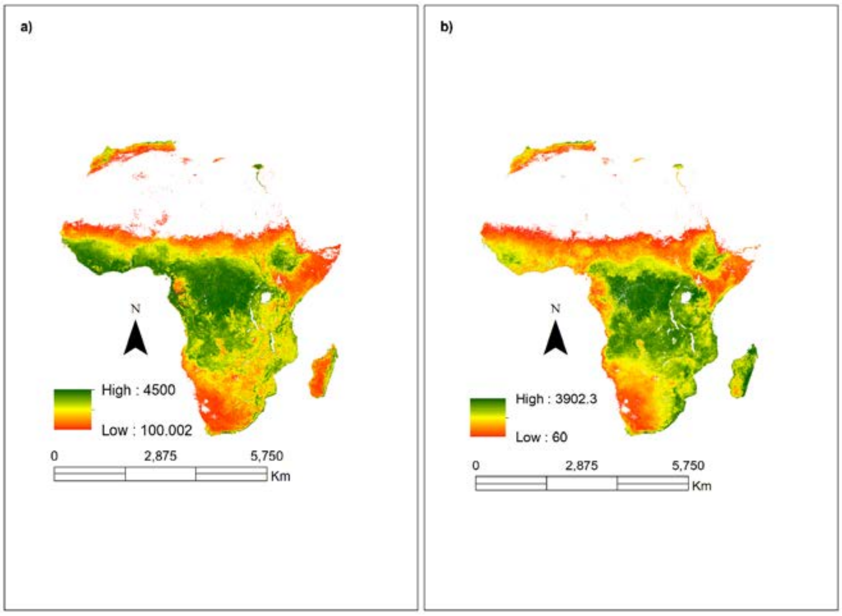

Figure 5: Spatial distribution of annual sum GPP (g C m^{-2} yr^{-1}) from (a) SCARF model and (b) MOD17 product for period January to December 2010

4. Discussion

4.1. Model sensitivity and uncertainty

Analyses of the importance of different biophysical and meteorological input parameters on GPP_{SCARF} show that VPD has negative influence at most of the sub-humid and semi-arid ecosystems (R^2=-0.17 to -0.99) which is consistent with other studies, for example, Sjöström et al. (2013). The relationship was expected since moisture availability is the main controller of vegetation seasonality and development in these ecosystems (e.g. Ibrahim et al., 2015; Merbold et al., 2009; Scholes et al., 2004). A negative relationship between GPP and T_a, was observed in the semi- arid and sub-humid ecosystems. Similar relationships were also observed between GPP and PAR at these sites. In these ecosystems, high temperature coupled with low moisture availability will act to reduce GPP. However, there was a positive relationship between T_a and GPP at two sites (i.e. Ankasa and Tchizalamou). In these sites, the wet and cloudy climate tends to reduce temperature and PAR, hence the observed positive relationship between GPP and the two variables.

The model output had modest to very strong positive correlations with MTCI (R^2=0.57 to 0.94, MTCI is used as a $FAPAR_{ps}$ surrogate in the model). A weak negative relationship (R^2=-0.25) between MTCI and model GPP observed at a tropical rainforest site (Ankasa) suggests that chlorophyll content ceases to be the dominant determinant of GPP in this biome. The initial validation of the SCARF Model (Ogutu et al., 2013) also documented weaker correlations (R^2=0.60)of model results with flux measurements for evergreen needle leaf forests. Given the minimal fluctuations of chlorophyll content in evergreen forests, the model may predict high GPP even during periods of low productivity resulting in poor correlations. This theory may explain the increase in model GPP_{SCARF} around dekad 25 to 33 at Ankasa (Figure 3) while observed GPP shows a gradual decline.

A stronger correlation of PAR with GPP_{SCARF} at the evergreen ecosystem (R^2=0.86) may suggest that while MTCI may cease to be the most important parameter in tropical rainforest productivity, light availability plays a more important role. Tropical rainforest ecosystems show indications that light could be a major limiting factor to photosynthesis during the wet season. Reduced incident light energy at the canopy may result due to both high incidences of cloudiness and/or high chlorophyll concentrations that will deprive light to understorey vegetation. Light available to individual leaves in a canopy decreases according to the Beer's law of light extinction and given the high leaf area index reported in tropical rain forests (e.g. LAI>6; Clark et al., 2008), the under storey may be completely deprived of light energy. While high chlorophyll content may increase photosynthesis at the top most canopy layers, total productivity may decline as a result of very low photosynthetic activity in the deeply buried understorey (DeLucia and Thomas, 2000; Kim et al., 2016). The high GPP values occurring from decade 5 to 15 coincide with the low rainfall season at Ankasa. This suggests that the vegetation canopy intercepts more radiation owing to reduced cloud condition resulting in increased vegetative growth.

The initial evaluation of the SCARF model undertaken by Ogutu et al., (2013) assumed a uniform distribution of the maximum quantum yields for C3 and C4 without accounting for regions/pixels with considerable heterogeneity for example mixed savannas or croplands. In the current study, efforts to differentiate quantum yields for different ecosystems were made for two main reasons; first the maximum quantum yields can vary based on random occurrences of environmental and climatological factors (Collatz et al., 1991, 1992; Ehleringer & Bjorkman, 1977) and, second, African ecosystems depict huge variations and heterogeneity through space. The results showed that the influence of quantum yield on modelled GPP was both site and season dependent. The heterogeneous sites (i.e. mixed savanna and woodland sites) did not achieve their maximum quantum yield value during the model simulations. The homogenous sites (i.e. the tropical humid grassland and the evergreen forest sites) returned near-maximum values for both a_3 and a_4. Even though C4 photosynthesis is thought to reach maximum values in hotter environments like the ones investigated in this study, maximum a_4 was not achieved at any of the savanna sites. This can be explained by the fact that savanna ecosystems depict considerable heterogeneity occurring over short spatial scales, sometimes in the order of a few metres (Desanker et al., 1997; Scholes et al., 2004; Walker, 1987). Under such conditions tree canopies often shade and control water and light availability for grasses and shrubs. Overall, the findings show the importance of varying the quantum yield value proportionally to the heterogeneity of the site when running the SCARF model.

4.2. Seasonal and inter-annual variability of model GPP across Africa

An analysis of seasonal and inter-annual variability of GPP_{SCARF} shows that the model has capability to track seasonal changes in productivity across various biomes in Africa (Figure 3). Even though the dynamics of modelled GPP at each evaluated site depicted notable seasonal and ecosystem dependent trends, the model generally tended to overestimate dry season GPP across all seasonally dry ecosystems. This trend supports observations by Ogutu et al. (2013) over temperate regions. An explanation for this overestimation is that the use of VPD alone may not be adequate to control GPP in dry environments or during the dry season (Ogutu et al., 2013).

The comparison of absolute values of GPP predicted by the SCARF model and GPP estimated at flux tower sites showed a strong positive relationship ($R > 0.59$, $p<0.0001$) in all but one study site(i.e. Ankasa tropical forest, $R = 0.38$, $p= 0.02$). The absolute GPP values predicted by the SCARF model ranged from 0.44 gCm^{-2}

in low productivity sites (e.g. Malopeni svanna ecosystem) to 9.86 gCm^{-2} in high productivity sites (e.g. Ankasa rain forest). The correlation coefficients and error margins for the SCARF in the current study are also similar (or even better in other instances) as those reported in the initial evaluation of the model in North America and European ecosystems (Ogutu et al., 2013). However, the GPP absolute values predicted by the SCARF model for the northern latitudes (Ogutu et al., 2013) were considerably higher than those predicted by the SCARF model for African tropical regions in the present study. Similar trends have also been reported by Kicklighter et al.,(1999) and can be partially explained by the longer day length in the northern latitudes during summer. Evaluation of the SCARF model and the MOD17 GPP product in their capability to represent GPP estimated at the studied flux tower sites showed that, in most cases, the output from the SCARF model was closer to the *in-situ* GPP (lower RMSE values) compared to the MOD 17 product (Figure 4). The MOD17 product tended to underestimate growing season GPP in most of the evaluated sites. Similar findings were reported in a comparison between SCARF model and MOD17 GPP model over Europe and USA (Ogutu et al., 2013). The main differences may be partly explained by the fact that the two models are premised on different assumptions regarding the interactions between input parameters as well as the sources of data used. For example, the MOD17 product uses $fAPAR_{ca}$ while GPP_{SCARF} is based on $fAPAR_{ps}$ and also the different techniques used to define the conversion of intercepted light (i.e. the LUE term).

Overall, the fact that the SCARF model shows a good capability to track the variability of GPP in the highly heterogeneous ecosystems in Africa, including the savannas which have been associated with high uncertainties in global estimates of carbon fluxes (Ciais et al., 2011; Merbold et al., 2009; Williams & Jackson, 2007), presents an opportunity to use the model improve GPP estimation across Africa.

4.3. Global and regional application of the SCARF Model

The spatial variability of GPP predicted by the SCARF model in Africa (Figure 5) agrees with other maps from global models (e.g. Cramer et al., 1999; Huston & Wolverton, 2009) and the general pattern from the MOD17 model. The total annual GPP predicted by the SCARF model for Africa in 2010 was 35.25 Pg C yr^{-1}, which was higher than annual GPP from MOD17 (21.39 Pg C yr^{-1}). However, this values fall within those reported in previous studies. For example, a study by Valentini *et al* (2014) using a number of models reported that the mean annual GPP for Africa ranged from 20.61 to 40.91 Pg C yr^{-1} with a mean of 28.16 Pg C yr^{-1} for the year 1990-2009.

Even though the flux tower sites used in the current study were few, solid conclusions can be reached on the applicability of the SCARF model in African environments based on these sites as they represent the typical ecosystems of the continent. The scarcity of *in-situ* data available on African carbon fluxes remains a stumbling block in the quest to fully understand and improve GPP estimates for the continent. Therefore using models such as the SCARF model can help bridge this gap. The good performance of SCARF model in Europe and USA (Ogutu et al., 2013) and in Africa (this study) demonstrates its potential as a reliable diagnostic model that can be used to generate GPP estimates globally. The SCARF model has three advantages compared to existing PEMs. Firstly, it prescribes only two quantum yield terms (i.e. maximum quantum yield for C3 and C4 plants) to represent the rate of conversion of absorbed PAR into dry matter, thereby eliminating the need for species specific LUE term. Secondly, it explicitly uses only the fraction of absorbed photosynthetic radiation absorbed by photosynthetic elements in the canopy (which is the actual PAR used in photosynthesis) as opposed to that of the total canopy. The use of FAPAR by photosynthetic elements in the canopy improves the accuracy of the model. Finally, the SCARF model does not require a detailed land cover map thereby limiting error propagation from inaccuracies in land cover classification. The recently launched SENTINEL satellites (i.e. SENTINEL 2 and 3) by the European Space Agency have spectral bands that can be used to derive key components of the SCARF model globally. This provides a unique opportunity to operationally produce global and regional GPP using the SCARF model at relatively high spatial resolution.

5. Conclusion

The study calibrated and applied the SCARF model to predict seasonal and spatial variability of GPP across African ecosystems. The SCARF model showed strong and positive correlation with *in situ* GPP measurements across most of the sites except at tropical rainforest ecosystem where a weak correlation was found. The seasonal variability of GPP was strongly connected to variability of main input parameters namely temperature, PAR, VPD and MTCI. The GPP from the model was negatively related to Temperature and PAR in water limited ecosystems. The influence of VPD on the SCARF model was varied across the ecosystem. Positive influence on GPP was observed in moisture sufficient ecosystems while negative influence in ecosystems that experience moisture deficit during part or most of the season. Monte Carlo analysis of the uncertainty in the model due to the choice of quantum yield parameters showed that these parameters varied more in heterogeneous ecosystems compared to homogenous ecosystems. The SCARF Model shows great potential to improve GPP predictions across a wide range of natural ecosystems occurring in Africa as shown by a strong positive coefficient of correlation ($R > 0.59$, $p<0.0001$) in most ecosystems evaluated in this study. The annual GPP for Africa derived from the SCARF model (i.e. 35.25 C yr^{-1}) was within the range of those reported in previous studies. This study has demonstrated the potential of an innovative approach to estimating carbon flux in understudied ecosystems of global importance. It comes at a timely moment, when relevant remotely sensed data (e.g. data from the Sentinel satellites by the European Space Agency) which can be used to parameterise such a model are becoming available and when the uncertainty associated with carbon flux measurement across the African continent is recognised as a major research challenge.

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References

Anav, A., Friedlingstein, P., Beer, C., Ciais, P., Harper, A., Jones, C., Murray-Tortarolo, G., Papale, D., Parazoo, N.C., Peylin, P., Piao, S., Sitch, S., Viovy, N., Wiltshire, A., & Zhao, M. (2015). Spatiotemporal patterns of terrestrial gross primary production: A review. *Reviews of Geophysics, 53*, 785-818

Ardö, J., Mölder, M., El-Tahir, B.A., & Elkhidir, H.A.M. (2008). Seasonal variation of carbon fluxes in a sparse savanna in semi arid Sudan. *Carbon Balance and Management, 3*, 7

Asrar, G., Myneni, R.B., & Choudhury, B.J. (1992). Spatial heterogeneity in vegetation canopies and remote sensing of absorbed photosynthetically active radiation: A modeling study. *Remote Sensing of Environment, 41*, 85-103

Baldocchi, D., Reichstein, M., Papale, D., Koteen, L., Vargas, R., Agarwal, D., & Cook, R. (2012). The role of trace gas flux networks in the biogeosciences. *Eos, Transactions American Geophysical Union, 93*, 217-218

Baldocchi, D., Reichstein, M., Papale, D., Koteen, L., Vargas, R., Agarwal, D., & Cook, R. (2012). The role of trace gas flux networks in the biogeosciences. *Eos, Transactions American Geophysical Union, 93*, 217-218

Birch, E., & Wachter, S. (2011). World Urbanization: The Critical Issue of the Twenty-First Century. *Global Urbanization*, 3-23

Brooks, A., & Farquhar, G.D. (1985). Effect of temperature on the CO2/O2 specificity of ribulose-1, 5-bisphosphate carboxylase/oxygenase and the rate of respiration in the light. *Planta, 165*, 397-406

Brümmer, C., Falk, U., Papen, H., Szarzynski, J., Wassmann, R., & Brüggemann, N. (2008). Diurnal, seasonal, and interannual variation in carbon dioxide and energy exchange in shrub savanna in Burkina Faso (West Africa). *Journal of Geophysical Research: Biogeosciences, 113*, n/a-n/a

Chiti, T., Certini, G., Grieco, E., & Valentini, R. (2010). The role of soil in storing carbon in tropical rainforests: the case of Ankasa Park, Ghana. *Plant and Soil, 331*, 453-461

Ciais, P., Bombelli, A., Williams, M., Piao, S.L., Chave, J., Ryan, C.M., Henry, M., Brender, P., & Valentini, R. (2011). The carbon balance of Africa: synthesis of recent research studies. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 369*, 2038

Clark, D.B., Olivas, P.C., Oberbauer, S.F., Clark, D.A., & Ryan, M.G. (2008). First direct landscape-scale measurement of tropical rain forest Leaf Area Index, a key driver of global primary productivity. *Ecology Letters, 11*, 163-172

Collatz, G.J., Ball, J.T., Grivet, C., & Berry, J.A. (1991). Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology, 54*, 107-136

Collatz, G.J., Ribas-Carbo, M., & Berry, J.A. (1992). Coupled Photosynthesis-Stomatal Conductance Model for Leaves of C₄ Plants. *Functional Plant Biology, 19*, 519-538

Coops, N.C., Ferster, C.J., Waring, R.H., & Nightingale, J. (2009). Comparison of three models for predicting gross primary production across and within forested ecoregions in the contiguous United States. *Remote Sensing of Environment, 113*, 680-690

Cramer, W., Kicklighter, D.W., Bondeau, A., Iii, B.M., Churkina, G., Nemry, B., Ruimy, A., Schloss, A.L., & Intercomparison, T.P.O.F.T.P.N.M. (1999). Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology, 5*, 1-15

Curran, P.J., & Dash, J. (2005). ALGORITHM THEORETICAL BASIS DOCUMENT ATBD 2.22 CHLOROPHYLL INDEX. *University of Southampton, Southampton-UK*

Dash, J., & Curran, P.J. (2004). The MERIS terrestrial chlorophyll index. *International Journal of Remote Sensing, 25*, 5403-5413

Dash, J., Curran, P.J., Tallis, M.J., Llewellyn, G.M., Taylor, G., & Snoeij, P. (2010). Validating the MERIS Terrestrial Chlorophyll Index (MTCI) with ground chlorophyll content data at MERIS spatial resolution. *International Journal of Remote Sensing, 31*, 5513-5532

DeLucia, E.H., & Thomas, R.B. (2000). Photosynthetic Responses to CO_2 Enrichment of Four Hardwood Species in a Forest Understory. *Oecologia, 122*, 11-19

Desanker, P.V., Frost, P.G.H., Justice, C.O., & Scholes, R.J. (1997). The Miombo Network: Framework for a terrestrial transect study of land-use and land-cover change in the miombo ecosystems of Central Africa. In, *IGBP Global change report*: International Geosphere-Biosphere Programme

Ehleringer, J., & Björkman, O. (1977). Quantum Yields for CO_2 Uptake in C_3 and C_4 Plants Dependence on temperature, CO_2, and O_2 concentration. *Plant Physiology, 59*, 86-90

Ehleringer, J., & Pearcy, R.W. (1983). Variation in Quantum Yield for CO_2 Uptake among C_3 and C_4 Plants. *Plant Physiology, 73*, 555

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K.J., Elbers, J.A., Goldstein, A.H., Grelle, A., Granier, A., Guðmundsson, J., Hollinger, D., Kowalski, A.S., Katul, G., Law, B.E., Malhi, Y., Meyers, T., Monson, R.K., Munger, J.W., Oechel, W., Paw U, K.T., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Valentini, R., Wilson, K., & Wofsy, S. (2002). Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology, 113*, 53-74

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K.J., Elbers, J.A., Goldstein, A.H., Grelle, A., Granier, A., Guðmundsson, J., Hollinger, D., Kowalski, A.S., Katul, G., Law, B.E., Malhi, Y., Meyers, T., Monson, R.K., Munger, J.W., Oechel, W., Paw U, K.T., Pilegaard, K., Rannik, Ü., Rebmann, C., Suyker, A., Valentini, R., Wilson, K., & Wofsy, S. (2002). Seasonality of ecosystem respiration and gross primary production as derived from FLUXNET measurements. *Agricultural and Forest Meteorology, 113*, 53-74

Fattore, F., Bertolini, T., Materia, S., Gualdi, S., Thongo M'Bou, A., Nicolini, G., Valentini, R., De Grandcourt, A., Tedesco, D., & Castaldi, S. (2014). Seasonal trends of dry and bulk concentration of nitrogen compounds over a rain forest in Ghana. *Biogeosciences, 11*, 3069-3081

Fensholt, R., Sandholt, I., & Rasmussen, M.S. (2004). Evaluation of MODIS LAI, fAPAR and the relation between fAPAR and NDVI in a semi-arid environment using in situ measurements. *Remote Sensing of Environment, 91*, 490-507

Gitelson, A.A., Peng, Y., Masek, J.G., Rundquist, D.C., Verma, S., Suyker, A., Baker, J.M., Hatfield, J.L., & Meyers, T. (2012). Remote estimation of crop gross primary production with Landsat data. *Remote Sensing of Environment, 121*, 404-414

Hamby, D.M. (1993). A numerical comparison of sensitivity analysis techniques. In. Westinghouse Savannah River Co., Aiken, SC (United States).

Hanan, N.P., Kabat, P., Dolman, A.J., & Elbers, J.A. (1998). Photosynthesis and carbon balance of a Sahelian fallow savanna. *Global Change Biology, 4*, 523-538

Harris, A., & Dash, J. (2010). The potential of the MERIS Terrestrial Chlorophyll Index for carbon flux estimation. *Remote Sensing of Environment, 114*, 1856-1862

Harris, A., & Dash, J. (2011). A new approach for estimating northern peatland gross primary productivity using a satellite-sensor-derived chlorophyll index. *Journal of Geophysical Research: Biogeosciences, 116*, n/a-n/a

Hilker, T., Coops, N.C., Wulder, M.A., Black, T.A., & Guy, R.D. (2008). The use of remote sensing in light use efficiency based models of gross primary production: A review of current status and future requirements. *Science of The Total Environment, 404*, 411-423

Huston, M.A., & Wolverton, S. (2009). The global distribution of net primary production: resolving the paradox. *Ecological Monographs, 79*, 343-377

Ibrahim, Z.Y., Balzter, H., Kaduk, J., & Tucker, J.C. (2015). Land Degradation Assessment Using Residual Trend Analysis of GIMMS NDVI3g, Soil Moisture and Rainfall in Sub-Saharan West Africa from 1982 to 2012. *Remote Sensing, 7*

Jarvis, P.G., & Leverenz, J.W. (1983). Productivity of Temperate, Deciduous and Evergreen Forests. In O.L. Lange, P.S. Nobel, C.B. Osmond, & H. Ziegler (Eds.), *Physiological Plant Ecology IV: Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence* (pp. 233-280). Berlin, Heidelberg: Springer Berlin Heidelberg

Kicklighter, D.W., Bondeau, A., Schloss, A.L., Kaduk, J., McGuire, A.D., & Intercomparison, T.P.O.F.T.P.N.M. (1999). Comparing global models of terrestrial net primary productivity (NPP): global pattern and differentiation by major biomes. *Global Change Biology, 5*, 16-24

Kim, D., Oren, R., & Qian, S.S. (2016). Response to CO2 enrichment of understory vegetation in the shade of forests. *Global Change Biology, 22*, 944-956

Li, W., Weiss, M., Waldner, F., Defourny, P., Demarez, V., Morin, D., Hagolle, O., & Baret, F. (2015). A Generic Algorithm to Estimate LAI, FAPAR and FCOVER Variables from SPOT4_HRVIR and Landsat Sensors: Evaluation of the Consistency and Comparison with Ground Measurements. *Remote Sensing, 7*

Liang, S., & Zhang, X. (2012). Global Land Surface Products: Photosynthetically Active Radiation Data Collection(2008-2010). In: Beijing Normal University.

Liang, S., Zheng, T., Liu, R., Fang, H., Tsay, S.-C., & Running, S. (2006). Estimation of incident photosynthetically active radiation from Moderate Resolution Imaging Spectrometer data. *Journal of Geophysical Research: Atmospheres, 111*, n/a-n/a

Formatted: German (Germany)

McCallum, I., Franklin, O., Moltchanova, E., Merbold, L., Schmullius, C., Shvidenko, A., Schepaschenko, D., & Fritz, S. (2013). Improved light and temperature responses for light-use-efficiency-based GPP models. *Biogeosciences, 10*, 6577-6590

Merbold, L., Ardö, J., Arneth, A., Scholes, R.J., Nouvellon, Y., de Grandcourt, A., Archibald, S., Bonnefond, J.M., Boulain, N., Brueggemann, N., Bruemmer, C., Cappelaere, B., Ceschia, E., El-Khidir, H.A.M., El-Tahir, B.A., Falk, U., Lloyd, J., Kergoat, L., Le Dantec, V., Mougin, E., Muchinda, M., Mukelabai, M.M., Ramier, D., Roupsard, O., Timouk, F., Veenendaal, E.M., & Kutsch, W.L. (2009). Precipitation as driver of carbon fluxes in 11 African ecosystems. *Biogeosciences, 6*, 1027-1041

Monteith, J.L. (1972). Solar radiation and productivity in tropical ecosystems. *Journal of applied ecology, 9*, 747-766

Myneni, R.B., & Williams, D.L. (1994). On the relationship between FAPAR and NDVI. *Remote Sensing of Environment, 49*, 200-211

Ogutu, B.O., & Dash, J. (2013). An algorithm to derive the fraction of photosynthetically active radiation absorbed by photosynthetic elements of the canopy (FAPARps) from eddy covariance flux tower data. *New Phytologist, 197*, 511-523

Ogutu, B.O., Dash, J., & Dawson, T.P. (2013). Developing a diagnostic model for estimating terrestrial vegetation gross primary productivity using the photosynthetic quantum yield and Earth Observation data. *Global Change Biology, 19*, 2878-2892

Papale, D., Reichstein, M., Aubinet, M., Canfora, E., Bernhofer, C., Kutsch, W., Longdoz, B., Rambal, S., Valentini, R., Vesala, T., & Yakir, D. (2006). Towards a standardized processing of Net Ecosystem Exchange measured with eddy covariance technique: algorithms and uncertainty estimation. *Biogeosciences, 3*, 571-583

Ran, Y., Li, X., Sun, R., Kljun, N., Zhang, L., Wang, X., & Zhu, G. (2016). Spatial representativeness and uncertainty of eddy covariance carbon flux measurements for upscaling net ecosystem productivity to the grid scale. *Agricultural and Forest Meteorology, 230*, 114-127

Ruimy, A., Kergoat, L., Bondeau, A., & Intercomparison, T.P.O.F.T.P.N.M. (1999). Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. *Global Change Biology, 5*, 56-64

Scholes, R.J., Frost, P.G.H., & Tian, Y. (2004). Canopy structure in savannas along a moisture gradient on Kalahari sands. *Global Change Biology, 10*, 292-302

Sims, D.A., Rahman, A.F., Cordova, V.D., El-Masri, B.Z., Baldocchi, D.D., Flanagan, L.B., Goldstein, A.H., Hollinger, D.Y., Misson, L., Monson, R.K., Oechel, W.C., Schmid, H.P., Wofsy, S.C., & Xu, L. (2006). On the use of MODIS EVI to assess gross primary productivity of North American ecosystems. *Journal of Geophysical Research: Biogeosciences, 111*, n/a-n/a

Singsaas, E.L., Ort, D.R., & DeLucia, E.H. (2001). Variation in measured values of photosynthetic quantum yield in ecophysiological studies. *Oecologia, 128*, 15-23

Sjöström, M., Ardö, J., Arneth, A., Boulain, N., Cappelaere, B., Eklundh, L., de Grandcourt, A., Kutsch, W.L., Merbold, L., Nouvellon, Y., Scholes, R.J., Schubert, P., Seaquist, J., & Veenendaal, E.M. (2011). Exploring the potential of MODIS EVI for modeling gross primary production across African ecosystems. *Remote Sensing of Environment, 115*, 1081-1089

Sjöström, M., Zhao, M., Archibald, S., Arneth, A., Cappelaere, B., Falk, U., de Grandcourt, A., Hanan, N., Kergoat, L., Kutsch, W., Merbold, L., Mougin, E., Nickless, A., Nouvellon, Y., Scholes, R.J., Veenendaal, E.M., & Ardö, J. (2013). Evaluation of MODIS gross primary productivity for Africa using eddy covariance data. *Remote Sensing of Environment, 131*, 275-286

Suyker, A.E., & Verma, S.B. (2010). Coupling of carbon dioxide and water vapor exchanges of irrigated and rainfed maize–soybean cropping systems and water productivity. *Agricultural and Forest Meteorology, 150*, 553-563

Suyker, A.E., & Verma, S.B. (2012). Gross primary production and ecosystem respiration of irrigated and rainfed maize–soybean cropping systems over 8 years. *Agricultural and Forest Meteorology, 165*, 12-24

Svoray, T., & Karnieli, A. (2011). Rainfall, topography and primary production relationships in a semiarid ecosystem. *Ecohydrology, 4*, 56-66

Tu, K. (2000). Modeling plant-soil-atmosphere carbon dioxide exchange using optimality principles. PhD Thesis; University of New Hampshire

Turner, D.P., Ritts, W.D., Cohen, W.B., Gower, S.T., Zhao, M., Running, S.W., Wofsy, S.C., Urbanski, S., Dunn, A.L., & Munger, J.W. (2003). Scaling Gross Primary Production (GPP) over boreal and deciduous forest landscapes in support of MODIS GPP product validation. *Remote Sensing of Environment, 88*, 256-270

Unwin, D.M. (1980). *Microclimate measurement for ecologists*. Academic Press Inc.

Valentini, R., Arneth, A., Bombelli, A., Castaldi, S., Cazzolla Gatti, R., Chevallier, F., Ciais, P., Grieco, E., Hartmann, J., Henry, M., Houghton, R.A., Jung, M., Kutsch, W.L., Malhi, Y., Mayorga, E., Merbold, L., Murray-Tortarolo, G., Papale, D., Peylin, P., Poulter, B., Raymond, P.A., Santini, M., Sitch, S., Vaglio Laurin, G., van der Werf, G.R., Williams, C.A., & Scholes, R.J. (2014). A full greenhouse gases budget of Africa: synthesis, uncertainties, and vulnerabilities. *Biogeosciences,* 11, 381-407

Verma, S.B., Dobermann, A., Cassman, K.G., Walters, D.T., Knops, J.M., Arkebauer, T.J., Suyker, A.E., Burba, G.G., Amos, B., Yang, H., Ginting, D., Hubbard, K.G., Gitelson, A.A., & Walter-Shea, E.A. (2005). Annual carbon dioxide exchange in irrigated and rainfed maize-based agroecosystems. *Agricultural and Forest Meteorology, 131*, 77-96

Veroustraete, F., Sabbe, H., & Eerens, H. (2002). Estimation of carbon mass fluxes over Europe using the C-Fix model and Euroflux data. *Remote Sensing of Environment, 83*, 376-399

Walker, B.H. (1987). *Determinants of tropical savannas.* Published by IRL Press on behalf of the ICSU Press for the International Union of Biological Sciences

Weber, U., Jung, M., Reichstein, M., Beer, C., Braakhekke, M.C., Lehsten, V., Ghent, D., Kaduk, J., Viovy, N., Ciais, P., Gobron, N., & Rödenbeck, C. (2009).

The interannual variability of Africa's ecosystem productivity: a multi-model analysis. *Biogeosciences, 6*, 285-295

Williams, C.A., Hanan, N.P., Neff, J.C., Scholes, R.J., Berry, J.A., Denning, A.S., & Baker, D.F. (2007). Africa and the global carbon cycle. *Carbon Balance and Management, 2*, 3

Williams, J.W., & Jackson, S.T. (2007). Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment, 5*, 475-482

Wu, C., Munger, J.W., Niu, Z., & Kuang, D. (2010). Comparison of multiple models for estimating gross primary production using MODIS and eddy covariance data in Harvard Forest. *Remote Sensing of Environment, 114*, 2925-2939

Wu, C., Niu, Z., Tang, Q., Huang, W., Rivard, B., & Feng, J. (2009). Remote estimation of gross primary production in wheat using chlorophyll-related vegetation indices. *Agricultural and Forest Meteorology, 149*, 1015-1021

Zhang, Q., Cheng, Y.-B., Lyapustin, A.I., Wang, Y., Gao, F., Suyker, A., Verma, S., & Middleton, E.M. (2014). Estimation of crop gross primary production (GPP): fAPARchl versus MOD15A2 FPAR. *Remote Sensing of Environment, 153*, 1-6

Zhang, Q., Middleton, E.M., Cheng, Y.-B., Huemmrich, K.F., Cook, B.D., Corp, L.A., Kustas, W.P., Russ, A.L., Prueger, J.H., & Yao, T. (2016). Integrating chlorophyll fAPAR and nadir photochemical reflectance index from EO-1/Hyperion to predict cornfield daily gross primary production. *Remote Sensing of Environment, 186*, 311-321

Zhang, Q., Middleton, E.M., Gao, B.C., & Cheng, Y.B. (2012). Using EO-1 Hyperion to Simulate HyspIRI Products for a Coniferous Forest: The Fraction of PAR

Absorbed by Chlorophyll ($FAPAR_{chl}$) and Leaf Water Content (LWC). *IEEE Transactions on Geoscience and Remote Sensing, 50*, 1844-1852

Zhang, Y., Xu, M., Chen, H., & Adams, J. (2009). Global pattern of NPP to GPP ratio derived from MODIS data: effects of ecosystem type, geographical location and climate. *Global Ecology and Biogeography, 18*, 280-290