



## MODELING CARBON FLUX OF THE *SUNDARBANS*: A THEORETICAL FRAMEWORK FOR PREDICTION OF THE *SUNDARBANS*' CONTRIBUTION AND VULNERABILITY TO CLIMATE CHANGE

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**Abstract:** Models of canopy gas exchange provide a theoretical framework for thorough analysis and interpretation of the scaling of physiological processes, enabling physiologists to extend their work to larger scales. They also fit the requirements of assessing effects of climate change on vegetation. Process-based models of forest canopy carbon uptake predict fluxes from individual leaves and canopies, and have been extended to provide estimates of carbon uptake at national and global scales. Fundamental to such models is the scaling of leaf photosynthesis to canopies by considering interception of solar radiation and leaf photosynthetic capacity. The net carbon gain of a tree canopy is the balance between carbon assimilated through photosynthesis and carbon lost through respiration. The within-canopy distribution of photosynthetic capacity is related to the distribution of leaf nitrogen, which can determine canopy-level carbon assimilation because of the nitrogen-rich photosynthetic enzyme Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) and electron-transport capacity. Photosynthesis of a canopy element depends, amongst other things, on the biochemical capacity for photosynthesis of that element, its temperature, its carbon dioxide at the sites of carboxylation, and its absorbed irradiance. During the last decade, process-based simulation models have been increasingly used to deepen the understanding of tree growth and development. Of the processes controlling tree growth and yield represented in these models, photosynthetic capacities are always of prime importance, because they determine (along with foliage distribution) potential tree carbon gains. Furthermore, environmental variables largely control actual photosynthetic rates. Thus, developing a process-based canopy photosynthesis model for the *Sundarbans* calls for reliable and comprehensive information on functional relationships between leaf CO<sub>2</sub> assimilation and plant and environmental variables of the ecosystem. Such models can be useful to predict the *Sundarbans* growth and carbon sequestration potential and their vulnerability to the change in climatic variables.

**Key words:** Modeling, photosynthesis, respiration, *Sundarbans*, climate change

### Introduction

Net primary productivity (NPP) of forest is on the increase because of fertilization by CO<sub>2</sub> and deposition of active nitrogen, but heterotrophic respiration which is related to temperature and therefore is also increasing, does not keep pace with NPP due to the residence time of carbon in the vegetation and soil. Model-based estimates of the global terrestrial carbon (C) sink data suggest that the sinks are predominantly in forests and savannas, which amounts 2-3 Gt C year<sup>-1</sup> (Grace, 2004). A model of the global carbon fluxes (NEE) to terrestrial vegetation developed by Lloyd (1999) is considered a realistic one, which explicitly considers both the effect of elevated CO<sub>2</sub> and nitrogen deposition on photosynthesis and respiration as a function of temperature. The model suggested a strong carbon sink in the tropical regions and a weaker sink in North America and Europe.

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DOI: <https://doi.org/10.53808/KUS.SI.SESB.2010.141-148-ls>

Rakkibu, M.G. 2010. Modeling carbon flux of the *Sundarbans*: a theoretical framework for prediction of the *Sundarbans*' contribution and vulnerability to climate change. *Khulna University Studies Special Issue* (SESB 2010): 141-148

A substantial amount of carbon is transferred from the terrestrial reservoir to the atmosphere as a result of deforestation. Worldwide, tropical rain forest is being converted to agriculture or being degraded at slightly less than 1% per year (FAO, 1997). The carbon dioxide emitted during this land conversion in the tropics accounts for almost all of the estimated 1.6 – 2.4 Gt of carbon that is transferred globally from vegetation to atmosphere each year as a result of change in land use (Fearnside, 2000). Despite the importance of tropical rain forests as a store of carbon, their role in the carbon cycle is not well understood because they are extensive, variable, and generally more difficult to study than other vegetation types. Past studies, such as the Anglo-Brazilian Amazonian Climate Observation Study (ABRACOS) at the ecosystem-atmosphere level (Gash *et al.*, 1996) have described the major environmental controls on tropical canopy gas and energy exchange. These controls are physical (e.g., temperature, irradiance, soil moisture), biochemical (e.g., photosynthetic capacity, enzyme reaction rates) and biological (e.g., leaf area, stomatal opening). But quantifying the interactions between these controls, and the links between carbon and energy exchange necessitates the use of mathematical models based on a mechanistic understanding of the coupled mechanisms of photosynthesis and transpiration. Once these models have been parameterized from leaf-level data, they can be tested against independent whole canopy process measurements. Once validated, the models can be used to generate regional and long-term predictions of gas exchange (Williams *et al.*, 1998). During the last decade, process-based simulation models have been increasingly used to deepen the understanding of tree growth and development. Of the processes controlling tree growth and yield represented in these models, photosynthetic capacities are always of prime importance, because they determine (along with foliage distribution) potential tree carbon gains. Furthermore, environmental variables largely control actual photosynthetic rates (Roux *et al.* 1999).

Farquhar *et al.* (1980) model of photosynthesis is widely used to parameterize the photosynthetic characteristics of trees in forests and can be used for the Sundarbans. Despite the increased use of this model for describing the daily and seasonal gain of carbon through CO<sub>2</sub> assimilation, it is increasingly being realized that parameterizing this rather complex model for leaves of a single species only, let alone for the many species that make up an ecosystem, is not straightforward. An important question to address, therefore, prior to implementation of this or any other process oriented model for describing CO<sub>2</sub> assimilation is to what extent species differ in their gas-exchange characteristics. Within the context of Farquhar *et al.* (1980) model these characteristics include the activity of ribulose 1,5-bisphosphate carboxylase-oxygenase, the rate of ribulose 1,5-bisphosphate regeneration via electron transport, and the rate of triose phosphate utilization. If the range of these estimates between species is small then the choice of appropriate parameter estimates for one or many species may be of only minor concern. If, however, considerable differences exist between species for these estimates then care must be taken to understand how species, or groups of species, differ in this regard. The objective of this paper is to give a guideline and a general impression on future possible ecosystem level study on the *Sundarbans* in order to predict its atmospheric carbon flux and response to climate change and its feedback to climate change.

### **The leaf photosynthesis models**

The rate of photosynthesis in a leaf is determined by the rates of carboxylation and regeneration of ribulose-1,5-bisphosphate (RuBP) catalyzed by the enzyme RUBISCO (ribulose-1,5-bisphosphate carboxylase-oxygenase). The net leaf photosynthesis ( $A_n$ ) is limited by the minimum of these two limiting processes (Farquhar *et al.*, 1980; von Caemmerer and Farquhar, 1981):

$$A_n = \min (A_c, A_j) - R_d \quad (1)$$

$A_c$  is the rate of photosynthesis when Rubisco activity is limiting and  $A_j$  is the rate when ribulose-1,5-bisphosphate (RuBP)-regeneration is limiting.  $R_d$  is the rate of mitochondrial respiration.

Rubisco-limited photosynthesis is given by:

$$A_c = \frac{V_{c\max}(C_i - \Gamma^*)}{\left[ C_i + K_c \left( 1 + \frac{O_i}{K_o} \right) \right]} \quad (2)$$

Where  $V_{c\max}$  is the maximum rate of Rubisco-catalyzed RuBP carboxylation (i.e, rubisco activity) when  $CO_2$  is at limiting and RuBP is at saturating concentrations,  $C_i$  and  $O_i$  are the intercellular concentrations of  $CO_2$  and  $O_2$ , respectively,  $K_c$  and  $K_o$ , the Michaelis-Menten coefficients of Rubisco activity for  $CO_2$  and  $O_2$ , respectively, and  $\Gamma^*$  is the  $CO_2$  compensation point (the value of  $C_i$  at which net  $CO_2$  uptake is zero due to photo respiration) in the absence of mitochondrial respiration. This formulation of the model assumes that the cell-wall conductance, the conductance between intercellular space and the site of carboxylation, is negligible.

The rate of photosynthesis when RuBP regeneration is limiting is given by:

$$A_j = \left( \frac{J}{4} \right) \frac{(C_i - \Gamma^*)}{(C_i + 2\Gamma^*)} \quad (3)$$

Where  $J$  is the rate of electron transport, which is related to absorbed photosynthetically active photon flux density ( $Q_{abs}$ ) by the following equation (de Pury and Farquhar, 1997; Medlyn et al., 2002):

$$\theta J^2 - (\alpha Q_{abs} + J_{\max})J + \alpha Q_{abs} J_{\max} = 0$$

or

$$J = \frac{\alpha Q_{abs} + J_{\max} - \sqrt{(\alpha Q_{abs} + J_{\max})^2 - 4\theta\alpha Q_{abs} J_{\max}}}{2\theta} \quad (4)$$

Where  $J_{\max}$  is the potential rate of electron transport when  $Q_{abs}$  is saturating,  $\theta$  determines the curvature of the light response curve,  $\alpha$  is the quantum yield of electron transport and  $Q_{abs}$  is the absorbed  $Q$  by the photosystem II ( $Q_{abs} = Q(1 - \text{reflectivity} - \text{transmissivity})$ ).

The key parameters of the model, which vary among species, are  $J_{\max}$ ,  $V_{c\max}$  and  $R_d$ . These parameters are temperature dependent and this dependence might vary among species. In addition, it is known that the parameters  $K_c$ ,  $K_o$  and  $\Gamma^*$  also vary with temperature. But these parameters, by contrast, are thought to be intrinsic properties of the Rubisco enzyme and are generally assumed constant among  $C_3$  species (Dungan *et al.*, 2003), thereby reducing the number of parameters to be fitted. On this basis, literature values are used to describe their temperature response when estimating photosynthetic parameters at different leaf temperature. The parameters  $K_c$ ,  $K_o$  and  $\Gamma^*$  have alternative formulations which could influence estimates of key parameters. It is found that the parameter  $J_{\max}$  is only slightly sensitive to the formulation of either  $K_m$  or  $\Gamma^*$  but the parameter  $V_{c\max}$  is highly sensitive to  $K_m$ . The ratio of  $J_{\max}$  and  $V_{c\max}$  is thus also highly sensitive to the formulation of  $K_m$  (Medlyn *et al.*, 2002).

Temperature dependence of  $\Gamma^*$  is given by:

$$\Gamma^* = 36.9 + 1.88*(T-25) + 0.036*(T-25)^2 \quad (5)$$

Where  $T$  is leaf temperature in °C (von Caemmerer *et al.*, 1994)

The temperature dependence of  $V_{c\max}$  can be modeled using the following Arrhenius function:

$$V_{c\max}(T_{leaf}) = V_{c\max25} \exp \left[ \frac{E_a(T_k - 298K)}{298RT_k} \right] \quad (6)$$

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Where  $V_{\text{cmax}25}$  is the value of  $V_{\text{cmax}}$  at 25 °C or 298 K reference leaf temperature,  $E_a$  is the activation energy (describes the exponential rate of rise of the function) of  $V_{\text{cmax}}$ ,  $R$  is the universal gas constant (8.314 J mol<sup>-1</sup>K<sup>-1</sup>),  $T_{\text{leaf}}$  is the leaf temperature in °C and  $T_k$  is leaf temperature in K. The temperature response of  $J_{\text{max}}$  can be fitted using a peaked function, which is essentially the Arrhenius equation modified by a term that describes how conformational changes in the enzyme at higher temperature start to negate the on-going benefits that would otherwise come from further increase in temperature.

$$J_{\text{max}}(T_k) = J_{\text{max}25} \exp\left[\frac{E_a(T_k - 298K)}{298RT_k}\right] \frac{1 + \exp\left(\frac{298\Delta S - E_d}{298R}\right)}{1 + \exp\left(\frac{T_k\Delta S - E_d}{T_k R}\right)} \quad (7)$$

Where  $J_{\text{max}25}$  is the value of  $J_{\text{max}}$  at 25 °C or 298 K reference temperature,  $E_a$  is the activation energy of  $J_{\text{max}}$ ,  $R$  is the universal gas constant (8.314 J mol<sup>-1</sup> K<sup>-1</sup>),  $T_k$  is leaf temperature in K,  $E_d$  is the deactivation energy (determines the rate of decrease of the function above the optimum) of  $J_{\text{max}}$  and  $\Delta S$  is known as an entropy term (700 J mol<sup>-1</sup> K<sup>-1</sup>).

Temperature response of  $R_d$  can be fitted using the following model:

$$R_d = R_{\text{ref}} Q_{10}^{\frac{(T_{\text{leaf}} - T_{\text{ref}})}{10}} \quad (8)$$

Where  $R_{\text{ref}}$  is respiration at reference leaf temperature in °C,  $Q_{10}$  is the relative increase in reaction rate at which  $R_d$  increases with an increase in temperature of 10 °C,  $T_{\text{leaf}}$  is the leaf temperature in °C and  $T_{\text{ref}}$  is reference leaf temperature.

### Scaling of photosynthesis and respiration in a forest with leaf properties and temperature dependencies

Among the most important components of global biogeo-chemical cycling are the processes that mediate the fluxes of carbon, water and energy between biosphere and atmosphere. The need for a clear understanding of the role of the terrestrial biosphere in global climate change generates a requirement for assessments of processes such as photosynthesis and respiration at large scales. A major difficulty in improving our understanding of the functioning of the biosphere-atmosphere system lies in the problem of effectively scaling measurements of the key processes, such as photosynthesis, respiration and evapotranspiration, to generate regional estimates of these fluxes. The photosynthetic capacities of leaves in canopies acclimate to the light environment in which the leaves are growing (Meir *et al.*, 2002). Most canopy trees experience diverse light conditions during their lifetime, starting as seedlings on the poorly lit forest floor but gaining access to the well-lit canopy layer at maturity. Many tree species have different maximum photosynthetic capacities, i.e. photosynthesis rates at light saturation according to growth stage or light conditions, or both, as a result of differences in leaf morphological and biochemical properties (Larcher, 2003). It is well known that sun leaves, i.e. leaves of the sun crown, have higher leaf nitrogen and leaf mass per unit area, corresponding to higher photosynthetic capacities, than shade leaves, i.e. leaves of the shade crown. Shade leaves have higher leaf chlorophyll content and are thinner and thus have a lower dark respiration rate and light compensation point than sun leaves (Lambers *et al.*, 1998). To guide development of models of carbon dioxide fixation there is a need for a detailed understanding of the changes in the photosynthetic capacities and respiration with the leaf chemical and morphological characteristics. The dark respiration of leaves plays a key role in the carbon economy of plants, but it is poorly understood in comparison to photosynthesis. Leaf respiration in forest canopies may consume 9-22% of gross primary production, and comprise 50-70% of above-ground (autotrophic) respiration (Malhi *et al.*, 1999;

Yoda, 1983). A linear relationship between dark respiration and leaf chemical (nitrogen and phosphorus) and physical (leaf mass per unit area) properties of forest trees has been shown in many studies (Meir *et al.*, 2001).

Within canopy, profiles of leaf nitrogen (or photosynthetic capacity) have been shown to be significantly non-uniform in canopies of a diverse range of species (de Pury and Farquhar, 1997). Profiles of leaf properties have led to the hypothesis that leaves adapt or acclimate to their radiation environment such that a plant's nitrogen resources may be distributed to maximize daily canopy photosynthesis (Hirose and Werger, 1987). An optimal distribution of leaf nitrogen exists when any re-allocation of nitrogen would decrease daily photosynthesis. It has been further hypothesized that the optimal distribution of nitrogen occurs when the nitrogen is distributed in proportion to the distribution of absorbed irradiance in the canopy, averaged over the previous several days to a week, the time over which leaves are able to adapt (de Pury and Farquhar, 1997). Photosynthetic capacity is closely linked to nitrogen content through the nitrogen-rich carbon-fixing enzyme Rubisco (Cao *et al.*, 2007). A general relationship between leaf nitrogen and maximum assimilation often occurs across gradients in geography (Reich *et al.*, 1997), functional types (Field and Mooney, 1986), species within functional types (Harrington *et al.*, 1989) and growth light environment (Niinemets and Tenhunen, 1997). This discovery has been useful in confirming hypotheses about plant functioning and establishing relationships over broad gradients of leaf characteristics (Reich *et al.*, 1997). A link to leaf nitrogen also provides the potential to estimate photosynthetic capacity at high temporal resolutions and large scales specially, if practical methods were developed to estimate nitrogen from remote sensing (Wessman, 1990). However, the utility of these relationships in describing all sources of variability at a single site is less certain. There is evidence indicating important variations in the relationship between leaf nitrogen and photosynthesis. Linear correlations do not always occur within species and the regression coefficients are often strongly dependent on species or treatment effects (Wilson *et al.*, 2000). Slopes between leaf nitrogen and maximum assimilation rates can vary by a factor of 10 among species (Evans, 1989). Several researches have concluded that effects of leaf age can be described only by changes in leaf nitrogen (Field and Mooney, 1983; Reich *et al.*, 1991), but others have not. For example, there is evidence that nitrogen allocated to Rubisco and chlorophyll can vary with leaf age (Poorter and Evans, 1998; Rey and Jarvis, 1998). Leaf photosynthetic capacity and respiration are dependent on leaf temperature. Incorporation of temperature response into models of photosynthesis for parameter up-scaling is thus important.

#### **Simulation of CO<sub>2</sub> exchange of the Sundarbans**

It is recognized that the world's forests contribute significantly to the global carbon (C) balance, and that changes in forest C uptake may act as an important feedback to the current increase in atmospheric carbon dioxide (Malhi *et al.*, 1999). The interannual and interdecadal variability in climate, and other changes in the environment, like rising atmospheric CO<sub>2</sub> concentration and large scale changes in land cover, have motivated several studies about the behavior of ecosystems in a changing environment. Such studies lead to the development of several numerical models to understand the effects of these changes on the carbon, water and energy fluxes between the ecosystems and the atmosphere. Models of carbon (C), water and energy fluxes play an important role in the quantitative understanding of both the functioning of forests and their impacts on the atmospheric C cycle (Jarvis, 1989; Sellers *et al.*, 1997). Gross canopy photosynthesis ( $P_g$ ) and foliage respiration ( $R_f$ ) can be simulated with canopy photosynthesis models or retrieved from turbulent CO<sub>2</sub> flux measurements above the forest canopy.  $P_g$  and  $R_f$  of the Sundarbans forest could be simulated with the forest canopy model MAESTRA. Biophysical parameters for the model simulation can be estimated from gas exchange measurements at leaf level. Meteorological data for the model simulation can be taken from a measurement tower established in the forest. The Sundarbans forest could be one of the important ecosystems in terms of regional and global carbon cycling; nevertheless, the impact of environmental factors on

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this ecosystem CO<sub>2</sub> flux remains barely understood. Three-dimensional multilayer biosphere-atmosphere models such as MAESTRA (Wang and Jarvis, 1990; Medlyn, 2004) are promising tools for understanding how interactions between environmental factors and leaf-level physiological parameters might impact canopy-level CO<sub>2</sub> exchange in the *Sundarbans* forest.

#### **Parameterization of the forest canopy model MAESTRA**

MAESTRA (Medlyn, 2004) is the latest version of the forest canopy model MAESTRO (Wang, 1988; Wang and Jarvis, 1990). The main features of MAESTRA are the 3D descriptions of canopy structure and radiative transfer in the canopy, coupled to the physiological responses of leaves at different locations, representing the intra-tree variability. Following are the descriptions of inputs (climatic variables and parameter sets) used to drive the model.

**Climate:** Half-hourly meteorological data including incident photosynthetically active radiation (PAR), air temperature, wind speed, relative humidity and vapour pressure saturation deficit can be obtained from the meteorological tower established in the forest.

**Tree dimensions and canopy structure:** Necessary data about tree dimensions and tree locations to build the original stand (tree map) for the investigated site for MAESTRA simulation can be made through detailed forest inventory.

**Photosynthetic responses to PAR and temperature:** In MAESTRA leaves are considered to be individually distributed in space, i.e., they are not attached to a shoot and shading occurs according to the cumulative leaf areas along the paths of beams of PAR to a simulated point in the crown of a target tree. Absorption of PAR and photosynthesis are calculated from incident, diffuse and beam radiation at one point considering leaf clumping and several leaf inclination angle classes (Ibrom *et al.*, 2006). Photosynthetic rates are estimated according to the model of Farquhar *et al.* (1980), for which the key parameters are the maximum rate of Rubisco activity ( $V_{\text{cmax}}$ ), the maximum rate of electron transport ( $J_{\text{max}}$ ), the initial slope ( $\alpha$ ) and curvature ( $\theta$ ) of the light response of electron transport and the dark respiration ( $R_d$ ) and the temperature dependences of  $V_{\text{cmax}}$ ,  $J_{\text{max}}$  and  $R_d$ . These parameters can be calculated from leaf gas exchange data of field measurements by nonlinear regression analysis. In the field measurements, relationships between these key biochemical parameters and leaf traits, such as leaf nitrogen concentration, leaf phosphorus concentration and leaf mass per area, are investigated with the intention of using these relationships for up-scaling leaf-level measurements to canopy level. Among the three leaf properties, leaf nitrogen per unit area ( $N_a$ ) usually found most significantly and strongly correlated with physiological parameters. Therefore, these parameters/ $N_a$  relationships are used as inputs in the simulation instead of estimated parameter values.

**Stomatal conductance:** Stomatal conductance ( $g_s$ ) are taken by Jarvis model of stomatal conductance (Jarvis, 1976), which is given by:

$$g_s = \text{GSREF} * f(T) * f(\text{VPD}) * f(\text{CO}_2) * F(\text{PAR}) + \text{GSMIN}$$

where, GSREF and GSMIN are the maximum and minimum stomatal conductance to CO<sub>2</sub> (mol m<sup>-2</sup> s<sup>-1</sup>) respectively and the  $f$ 's are functions of environmental variables which relate  $g_s$  to leaf temperature (T), vapour pressure saturation deficit (VPD), ambient carbon dioxide (CO<sub>2</sub>) concentration and incident PAR.

**Simulations:** Simulations are done on individual tree basis on an area considering the stand structure and leaf area distribution both vertical and horizontal for a whole cohort of forest. The structure of every individual crown is described by the general 1D (vertical)  $\beta$ -function calculated from the field measurement data. The simulation results at the tree scale are then used to calculate simulated stand gross photosynthesis, with stand leaf area index (LAI) as a scaling factor.

#### **Conclusion**

Gross primary productivity of the *Sundarbans* ecosystem could be simulated with the forest canopy model MAESTRA. If soil respiration and above ground respiration other than foliage

respiration are known, net biotic flux of the *Sundarbans* could be simulated. Contribution of the *Sundarbans* to the atmospheric CO<sub>2</sub> concentration can be assessed to see whether it functions as a source or as a sink. From the continuous climatic data generated from a climate tower it should be possible to assess the response of the *Sundarbans* to any change in climatic parameters and its feedback to climate change. Long term interdisciplinary and collaborative study on the biosphere atmosphere interaction at the *Sundarbans* should be done to know the nature and extent of service and threat of this very important ecosystem of global importance.

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