Abstract – The objective of this work was to evaluate a generalized response function to the atmospheric CO2 concentration \([f(CO_2)]\) by the radiation use efficiency (RUE) in rice. Experimental data on RUE at different CO2 concentrations were collected from rice trials performed in several locations around the world. RUE data were then normalized, so that all RUE at current CO2 concentration were equal to 1. The response function was obtained by fitting normalized RUE versus CO2 concentration to a Morgan-Mercer-Flodin (MMF) function, and by using Marquardt's method to estimate the model coefficients. Goodness of fit was measured by the standard deviation of the estimated coefficients, the coefficient of determination \((R^2)\), and the root mean square error \((RMSE)\). The \(f(CO_2)\) describes a nonlinear sigmoidal response of RUE in rice, in function of the atmospheric CO2 concentration, which has an ecophysiological background, and, therefore, renders a robust function that can be easily coupled to rice simulation models, besides covering the range of CO2 emissions for the next generation of climate scenarios for the 21st century.

Index terms: *Oryza sativa*, global warming, modeling, photosynthesis.

Introduction

After the 2009 Copenhagen Summit, which included the 15th Conference of the Parts (COP 15) to the United Nations Framework Convention on Climate Change and the 5th Meeting of the Parts (MOP 5) to the Kyoto Protocol, little or no progress has been achieved for the reduction of global CO2 emissions in the coming decades, therefore, a new generation of climate scenarios has been proposed to guide the projections of temperature increase for the Fifth Assessment Report (AR5) of the Intergovernmental Panel on Climate Change (IPCC), scheduled to be released in 2014 (Moss et al., 2010; O’Neill & Schweizer, 2011). The new climate projections will be based on four CO2 emission scenarios, named “representative concentration pathways” – RCP, selected by a new Integrated Assessment Modeling Consortium, with radiative forcing pathways based on possible trajectories of CO2 concentration over the 21st century, as follows: RCP2.6, increase up to 490 ppmv CO2 until 2020-2030 and, then, declines, so that the radiative
forcing is 2.6 W m⁻² at 2100; RCP4.5, increase up to 650 ppmv CO₂, radiative forcing of 4.5 W m⁻² until 2100, and stabilizing afterwards; RCP6.0, increase up to 850 ppmv CO₂, radiative forcing of 6.0 W m⁻² until 2100, and stabilizing afterwards; RCP8.5, increase superior to 1,370 ppmv CO₂, radiative forcing higher than 8.5 W m⁻² up to 2100, and continuing to rise after 2100 (Moss et al., 2010).

Plants respond to atmospheric CO₂ mostly by increasing photosynthesis rate, which has the potential to increase agricultural crops growth and yield (Streck, 2005). Rice (Oryza sativa L.) is the staple food of about half of the world population, and Brazil is the largest rice producer outside Asia, with about 2.8 million hectares grown annually (United States Department of Agriculture, 2011). Traditionally, the effect of CO₂ on agricultural crops, including rice, has been simulated in climate change studies using the “current/elevated CO₂” approach, i.e., crop models are run at current CO₂ (usually 350-360 ppmv) and, then, run again at an elevated CO₂ concentration scenario (usually doubled CO₂ – 700 ppmv) (Matthews et al., 1997; Streck & Alberto, 2006; Walter et al., 2010). The four new RCP-based groups of climate scenarios demand a redesign of this traditional approach, for simulating the CO₂ effects on crops by using a CO₂ – response function in simulation models.

Crop simulation models vary in complexity from simple empirical statistic-based models (Pedro Júnior et al., 1995; Klering et al., 2008) to very complex process-based models (Hasegawa & Horie, 1996; Mall & Aggarwal, 2002; Bouman & Laar, 2006; Confalonieri et al., 2009). Models with intermediate levels of complexity combine advantages from the former (simplicity) and from the latter (mechanisms) by using general and robust response functions for describing plant processes on a canopy level, which requires less and more easily-measured coefficients and inputs. For rice, the InfoCrop is a recent process-based model with intermediate complexity (Aggarwal et al., 2006), which gave similar or better simulations of rice yield in India than Oryza, a more complex process-based model (Krishnan et al., 2007).

A robust canopy-based approach is the radiation use efficiency (RUE), which is widely used in crop simulation models, including InfoCrop, as a surrogate for biochemical and leaf-based approaches to describe the complex photosynthesis process. RUE is defined as the amount of crop dry matter produced per unit of solar radiation intercepted or absorbed by the crop canopy (Sinclair & Muchow, 1999). Common values of RUE in rice vary from 1.32 to 2.95 g MJ⁻¹ of intercepted photosynthetically active radiation (PAR) (Weerakoon et al., 2000; Mall & Aggarwal, 2002).

There is a lack of a response function to atmospheric CO₂ concentration, when RUE is used as the driving variable for increasing crop dry matter production in rice simulation models, which constituted the rationale for this study. Anticipating the upcoming IPCC 2014 AR5, the objective of this work was to evaluate a generalized response function to the atmospheric CO₂ concentration [f(CO₂)] by the RUE in rice, which can easily be coupled to process-based rice simulation models.

Materials and Methods

A widely used approach in crop simulation models is to describe the effects of environmental variables such as solar radiation, temperature and photoperiod, on crop growth and development with adimensional response functions which vary from zero to one (Streck et al., 2003, 2007; Setiyono et al., 2007, 2010). The underlying hypothesis in the present study was that a similar approach can be used for developing a f(CO₂).

Literature data on the response of RUE to CO₂ in rice are usually from Open Top Chambers (OTC) and from Free-Air CO₂ Enrichment (FACE) experiments, in which a current and an elevated CO₂ levels are set. These approaches make it difficult to hypothesize upon the general shape of a f(CO₂). From a biochemical perspective, however, CO₂ is the substrate for photosynthesis, and leaf photosynthesis rate is expected to increase steadily in the range from 350–400 to 800–1000 ppmv CO₂ in C₃ plants, like rice, because the current CO₂ concentration (390 ppmv) in the atmosphere is insufficient to saturate the ribulose 1.5-bisphosphate carboxylase/oxygenase (Rubisco), the enzyme responsible for primary carboxylation in the metabolic process that drives photosynthesis (Bowes, 1991; Streck, 2005). An increase in the availability of CO₂ suppresses photorespiration in C₃ plants because it increases carboxylation and decreases the oxygenase activity of Rubisco (Streck, 2005). But at the canopy level, the response to CO₂ may not follow the same shape mainly because some leaves (those located within and in the lower portion of the canopy) are in
the shade and may be senescent. Shaded and senescent leaves have very low photosynthesis efficiency because of high respiration rates and low leaf nitrogen content (Kitagima et al., 2002). Therefore, we selected a flexible response function – the Morgan-Mercer-Flodin (MMF) function (Morgan et al., 1975) –, for describing the response of RUE to CO₂ in rice. The general form of the MMF function is:

\[ Y = \frac{ab + c X^n}{b + X^n} \]  

(1)

in which: \( Y \) is the response (dependent) variable; \( X \) is the explanatory (independent) variable; \( a \) is the intercept when \( X = 0 \); \( c \) is the asymptote, as \( X \) approaches infinity; \( n \) is a shape coefficient; and \( b \) is interpreted as \( b = (X_{0.5})^n \), with \( X_{0.5} \) being the value of \( X \), when \( Y \) is half of the maximum response. The MMF is a very flexible function because users can set the intercept and the asymptote – two coefficients which define the range of the response variable –, and because it can take several shapes, varying from a rectangular hyperbole for \( n = 1 \) to a step-function for \( n = \infty \) and sigmoidal curves for \( 1 < n < \infty \), only by changing the shape coefficient (Streck et al., 2003).

For the \( f(\text{CO}_2) \), \( X \) is the atmospheric \( \text{CO}_2 \) concentration, and \( Y \) is the normalized RUE response. By normalized RUE, we mean that the RUE values 1 at current atmospheric \( \text{CO}_2 \) concentration. Therefore, the lower limit of the range of RUE response is 1 at current \( \text{CO}_2 \) concentrations and, thus, the coefficient \( a \) in equation (1) was set to be equal to 1. The other three coefficients \( (b, c, n) \) of the equation (1) were estimated as follows.

Published data on RUE at several atmospheric \( \text{CO}_2 \) concentrations, from different rice trials conducted in OTC, FACE, and numerical experiments conducted with different cultivars under different conditions and in distinct locations were used. These data were collected from a thorough literature search on trials which tested the effect of \( \text{CO}_2 \) concentration on RUE in rice and which were published in international mainstream journals. The source and some details of these trials are presented in Table 1. RUE data were normalized by dividing RUE at elevated \( \text{CO}_2 \) concentration treatments by RUE at the current \( \text{CO}_2 \) concentration treatment, and assuming that all current \( \text{CO}_2 \) treatments were 1. The \( \text{CO}_2 \) concentration from the whole data sets varied from 330 ppmv to 990 ppmv (Table 1), which covers the \( \text{CO}_2 \) concentrations of the RCP2.6, RCP4.5 and RCP6.0 emission scenarios by the year 2100 and the RCP8.5 emission scenario up to about the year 2070, which should guide the AR5 of the 2014 IPCC (Moss et al., 2010).

Normalized RUE versus \( \text{CO}_2 \) concentrations were then fitted to equation (1), by setting \( a = 1 \), and coefficients \( b, c \) and \( n \) were estimated with the PROC NLIN procedure (SAS Institute, 2001), with the

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Experimental protocol</th>
<th>Location</th>
<th>Levels of ( \text{CO}_2 ) (ppmv)</th>
<th>Units of RUE</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>IR72</td>
<td>Open Top Chambers experiment – dry/wet season and high nitrogen (200 kg ha⁻¹)</td>
<td>Los Baños, Philippines (15°N, 121°E)</td>
<td>350, 600 and 700</td>
<td>g MJ⁻¹</td>
<td>Weerakoon et al. (2000)</td>
</tr>
<tr>
<td>Nonspecified</td>
<td>Numerical experiment</td>
<td>Two locations in Iran (Rasht: 37.25°N, 49.6°E, 7 m below sea level; Ahwaz: 31.03°N, 48.07°E, 23 m above sea level)</td>
<td>350 and 700</td>
<td>g MJ⁻¹</td>
<td>Soltani et al. (2001)</td>
</tr>
<tr>
<td>IR36, IR50, Ratna, Rasi, Akashi, Jaya and Cauvery</td>
<td>Numerical experiment</td>
<td>Several locations in India varying from Kapurthala (31°N) to Adathurai (11°N) and from Ludhiana (75.8°E) to Cuttack (86°E)</td>
<td>330, 660 and 990</td>
<td>g MJ⁻¹</td>
<td>Mall &amp; Aggarwal (2002)</td>
</tr>
<tr>
<td>BG300</td>
<td>Open Top Chambers experiment – average of pre-heading, post-heading and total crop duration and two growing seasons</td>
<td>Batalagoda, Sri Lanka (7°50'N, 80°50'E)</td>
<td>370 and 570</td>
<td>g MJ⁻¹</td>
<td>De Costa et al. (2006)</td>
</tr>
<tr>
<td>Kirara397 Kakehashi Akitakomachi Hitomebore</td>
<td>Free-air ( \text{CO}_2 ) enrichment experiment – average of four cultivars; pre-head, post-head and two years</td>
<td>Shizukuishi, Iwate, Japan (39°38'N, 140°57'E)</td>
<td>365, 548 and 570</td>
<td>g mol⁻¹</td>
<td>Shimono et al. (2009)</td>
</tr>
</tbody>
</table>
Marquardt’s method for minimizing the square error of the fit. Goodness of fit was measured by the standard deviation of the estimates of the coefficients b, c and n, the coefficient of determination ($R^2$), and the root mean square error (RMSE) (Streck et al., 2003).

Results and Discussion

Normalized RUE, published in the literature, varied from 1 at 330–370 ppmv to 1.44 at 990 ppmv, i.e., RUE increase as CO$_2$ increase. This feature is consistent with the response of increase in photosynthesis with CO$_2$ fertilization in C$_3$ plants (Streck, 2005). The estimates of the coefficients of the MMF function (equation 1) with the fitting procedure were: $a = 1; b = 3.096 \times 10^{23}$, standard error = 1.188 $\times 10^{23}; c = 1.4382$; standard error = 0.0147; and $n = 8.378$, standard error = 0.6017. The probability (p-value) of all three coefficients were highly significant ($p<0.01$), the coefficient of determination was high ($R^2 = 0.999$), and the root mean square error was low (RMSE = 0.012). The MMF function was appropriate to describe the response of RUE to the atmospheric CO$_2$ concentration in rice. Therefore, the $f(CO_2)$ response function of RUE in rice is:

$$Y = \frac{(3.096 \times 10^{23} + 1.4382 \times [CO_2]^{8.378})}{(3.096 \times 10^{23} + [CO_2]^{8.378})}$$

(2).

From equation (2): the coefficient $X_{0.5}$, which represents the CO$_2$ concentration, when the response of RUE is half of the maximum response, is 637 ppmv; the coefficient c is the maximum increase in the attained, RUE due to the increase in CO$_2$ concentration; and the coefficient n = 8.378 gives a sigmoidal shape to the curve. A value of 1.4382 for the asymptote (coefficient c in equation 2) means that the maximum increase in RUE, due to elevated CO$_2$, was 44% greater than the RUE at current CO$_2$.

The sigmoidal response indicates that RUE in rice increases slowly, in the range from 350 to 500 ppmv of CO$_2$, then it has a quasi-linear (the highest rate) increase from about 500 to 750 ppmv and, again, shows a slow increase in RUE from about 750 to 950 ppmv, leveling off at CO$_2$ concentrations greater than 950 ppmv (Figure 1).

The sigmoidal response of RUE to an increase in atmospheric CO$_2$ concentration, obtained in the present study (equation 2, Figure 1), differed from the overall response of leaf photosynthesis to CO$_2$ commonly reported in C$_3$ plants, which follows a rectangular hyperbole-type shape response (Sage et al., 1989; Streck, 2005). The main difference between the sigmoidal response and rectangular hyperbole response to CO$_2$ was from about 350 to 700 ppmv. In this range, Rubisco carboxilation activity is promptly increased with the increase in atmospheric CO$_2$, resulting in a linear increase in the rate of leaf photosynthesis. This biochemical response has been used as a general background, for assuming that plant growth increases linearly from current to elevated CO$_2$ concentrations in crop simulation models (Matthews et al., 1997; Walter et al., 2010). Although by this linear approach, in the range from 350 to 700 ppmv, CO$_2$ gives the right response of RUE at the upper-end portion of the CO$_2$ response range (around 700 ppmv), it greatly overestimates the response of RUE on a crop canopy level at 500–600 ppmv (Figure 1), which is a CO$_2$ concentration range expected in the upcoming 20–40 years (Moss et al., 2010).

To explain the lower response of RUE, in comparison to leaf photosynthesis rate from 500–600 ppmv of CO$_2$, a hypothesis is that only sunlit leaves in the top of the canopy could fully take advantage of CO$_2$ fertilization. Throughout the growing season, there are many leaves which are shaded and senescent, in the half lower part of the canopy, and the photosynthetic efficiency of these leaves is lower than the photosynthesis of sunlit ones (Kitagima et al., 2002). Therefore, because RUE

![Figure 1. The CO$_2$-response function for radiation use efficiency in rice. Points are from published data listed in Table 1; the curve is the fitted MMF function with coefficients given in the equation $Y = (3.096 \times 10^{23} + 1.4382 \times [CO_2]^{8.378}) / (3.096 \times 10^{23} + [CO_2]^{8.378})$.](image-url)
is a more robust ecophysiological parameter than photosynthesis rate of individual leaves, our approach to develop a f(CO₂) response function is more appropriate for assessing the response of crop canopies to increased atmospheric CO₂.

The saturation of RUE response to CO₂ concentrations approaching 1000 ppmv (Figure 1) is consistent with the saturation of leaf photosynthesis in C₃ plants at 800-1000 ppmv (Sage et al., 1989; Streck, 2005). At low and intermediate atmospheric CO₂ concentrations, photosynthesis is limited by the carboxylation capacity of Rubisco, while at high CO₂ concentrations leaf photosynthesis is limited by the regeneration capacity of Rubisco in the Calvin cycle (Chen et al., 2005).

A further limitation for plants, including rice, is to respond positively to elevated atmospheric CO₂ concentration that has been extensively claimed as the probable acclimation of leaf photosynthesis to CO₂ fertilization (Chen et al., 2005; Streck, 2005). The acclimation of leaf photosynthesis in rice has been attributed to limitations in both Rubisco carboxylation and Rubisco regeneration (Chen et al., 2005). The reduction of Rubisco carboxylation and regeneration is related to the increase of soluble sugar contents (hexoses or nonstructural carbohydrates) in the leaves of plants grown at elevated CO₂ concentrations (Chen et al., 2005). In addition, in rice plants exposed to high CO₂ concentration for long periods (throughout the growing period), there is a lower concentration of Rubisco inside cells, which reduces the photosynthetic rate at plant level (Chen et al., 2005). However, the results of OTC and FACE, used for defining the f(CO₂) in the present study (Table 1), are from long-term experiments (plants were grown under elevated CO₂ throughout their entire growing period), which indicates that the acclimation of photosynthesis to elevated CO₂ at leaf level did not offset the fertilization effect at canopy level, and that there was an overall positive effect of elevated CO₂ on crop growth.

The photosynthesis acclimation to elevated CO₂ is the basis for a second hypothesis to explain the small increase of RUE in the range 500-600 ppmv of CO₂ of the f(CO₂) (Figure 1). Makino et al. (2000) reported decrease in Rubisco content, but a nonsignificant decrease in the biomass of rice plants grown at 1000 ppmv CO₂, i.e. under CO₂-saturated conditions. Under CO₂-nonsaturation conditions, such as in the study by Chen et al. (2005), in which rice plants were exposed to 850 ppmv CO₂, the acclimation of leaf photosynthesis had a greater impact on plant biomass, with a lower increase of crop biomass than at higher CO₂ (above 600 ppmv). These two hypotheses may act together, and the contribution of each one still needs to be elucidated by further studies.

The nonlinear response of RUE in rice to the increase of atmospheric CO₂ concentration (Figure 1) has important implications for its use in the upcoming CO₂ emission scenarios which will guide the IPCC 2014 AR5 (Moss et al., 2010). For the most optimistic scenario (RCP2.6), which assumes a maximum CO₂ concentration of about 490 ppmv, little benefits from CO₂ fertilization is expected for rice. For the RCP4.5 scenario, which assumes a maximum CO₂ concentration of about 650 ppmv, the final CO₂ concentration falls into the linear response of Figure 1, and RUE in rice may increase by 28%. The increase by 850 ppmv, suggested in the RCP6.0, is in the third range of response in Figure 1, with an increase of about 41% in RUE. For the RCP8.5 scenario, the response of RUE reaches a maximum of about 43% and levels off, which means that, under this very pessimist scenario, benefits from CO₂ fertilization in rice are not expected after the year 2070.

The f(CO₂) proposed in this paper (equation 2) takes into account the effect of CO₂ on RUE and can be easily coupled to a process-based rice simulation model such as InfoCrop. Because the data used for developing the f(CO₂) come from different trials conducted with different cultivars, under different locations and experimental setups (Table 1), the equation (2) was proposed as a robust and generalized response function to be used in models to simulate the effect of elevated CO₂ concentrations on RUE, in different rice ecosystems. This is particularly important in face of the new generation of climate change scenarios which will be the basis of the AR5 in 2014. This new redesigned scenario process uses the parallel approach for representing the socio-economic, technological, demographic, policy and institutional factors, which influence gas emissions to the atmosphere, and differs from the sequential approach used by Group I of IPCC 2007 AR4 (Moss et al., 2010). Compared to the sequential approach, the parallel one shortens the time between the development of emission scenarios and the use of the resulting climate scenarios and begins with the identification of major features for scenarios
of radiative forcing, setting the radiative forcing trajectories during the 21st century (Moss et al., 2010; O’Neill & Scheweizer, 2011). From an agriculture perspective, these new IPCC-CO2 emission scenarios are also different from the AR4 ones and introduce new challenges for simulation studies, as CO2 concentrations during the 21st century may stabilize before 2100 in some scenarios (RCP2.6), while they may increase in a nonlinear fashion up to reach the highest concentration by 2100 and stabilize afterwards in others (RCP4.5 and RCP6.0), or they may steadily increase beyond 2100 (RCP8.5). Therefore, developing a f(CO2) response function in rice, which covers all CO2 concentration scenarios in a dynamic fashion, will shorten the time between the release of the AR5 and the assessment of rice response to the new climate change scenarios for the coming decades. This is especially important for the rice chain in Brazil, the largest rice producer outside Asia.

Conclusion

1. The Morgan-Mercer-Flodin function is appropriate as a generalized RUE response to increasing atmospheric CO2 concentrations in rice, by describing this response in a nonlinear, sigmoidal way, with an ecophysiological background.

2. The Morgan-Mercer-Flodin function is a robust function which can be easily coupled to rice growth simulation models to cover the range of CO2 emission scenarios during the 21st century.

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CO₂-response function of radiation use efficiency in rice


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