CO₂-response function of radiation use efficiency in rice for climate change scenarios

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Abstract – The objective of this work was to evaluate a generalized response function to the atmospheric CO_2 concentration [f(CO_2)] by the radiation use efficiency (RUE) in rice. Experimental data on RUE at different CO_2 concentrations were collected from rice trials performed in several locations around the world. RUE data were then normalized, so that all RUE at current CO_2 concentration were equal to 1. The response function was obtained by fitting normalized RUE versus CO_2 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 CO_2 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 CO_2 emissions for the next generation of climate scenarios for the 21st century.

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

Função de resposta a CO₂ na eficiência de uso da radiação em arroz para cenários de mudanças climáticas

Resumo – O objetivo deste trabalho foi avaliar uma função de resposta generalizada à concentração de CO_2 atmosférico [f (CO_2)] pela eficiência de uso de radiação (RUE) em arroz. Os dados experimentais de RUE, em diferentes concentrações de CO_2, foram coletados de ensaios sobre o arroz realizados em diferentes locais do mundo. Os dados de RUE foram normalizados de modo que todos os valores de RUE, na atual concentração de CO_2, foram iguais a 1. A função de resposta foi obtida pelos valores de RUE normalizados versus a concentração de CO_2, ajustados à função de Morgan-Mercer-Flodin (MMF), com uso do método de Marquardt para estimar os coeficientes do modelo. O ajuste da função foi medido pelo desvio-padrão dos coeficientes estimados, o coeficiente de determinação (R^2) e a raiz do quadrado médio do erro (RQME). A f(CO_2) descreve uma resposta não linear sigmoidal da RUE em arroz, em função da concentração do CO_2 atmosférico, o que tem significado ecofisiológico e, portanto, é uma função robusta que pode ser facilmente acoplada a modelos de simulação de arroz, além de abranger as emissões de CO_2 para a próxima geração de cenários climáticos para o século 21.

Termos para indexação: *Oryza sativa*, aquecimento global, modelagem, fotossíntese.

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 CO_2 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 CO_2 emission scenarios, named "representative concentration pathways" – RCP, selected by a new Integrated Assessment Modeling Consortium, with radiative forcing pathways based on possible trajectories of CO_2 concentration over the 21st century, as follows: RCP2.6, increase up to 490 ppmv CO_2 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 CO_2, radiative forcing of 4.5 W m^{-2} until 2100, and stabilizing afterwards; RCP6.0, increase up to 850 ppmv CO_2 radiative forcing of 6.0 W m^{-2} until 2100, and stabilizing afterwards; RCP8.5, increase superior to 1,370 ppmv CO_2, 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 CO_2 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 hectars grown annually (United States Department of Agriculture, 2011). Traditionally, the effect of CO_2 on agricultural crops, including rice, has been simulated in climate change studies using the "current/elevated CO_2" approach, i.e., crop models are run at current CO_2 (usually 350-360 ppmv) and, then, run again at an elevated CO_2 concentration scenario (usually doubled CO_2 – 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 CO_2 effects on crops by using a CO_2 – 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 photosyntheticaly active radiation (PAR) (Weerakoon et al., 2000; Mall & Aggarwal, 2002).

There is a lack of a response function to atmospheric CO_2 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 CO_2 concentration [f(CO_2)] 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(CO_2).

Literature data on the response of RUE to CO_2 in rice are usually from Open Top Chambers (OTC) and from Free-Air CO_2 Enrichment (FACE) experiments, in which a current and an elevated CO_2 levels are set. These approaches make it difficult to hypothesize upon the general shape of a f(CO_2). From a biochemical perspective, however, CO_2 is the substrate for photosynthesis, and leaf photosynthesis rate is expected to increase steadily in the range from 350–400 to 800–1000 ppmv CO_2 in C_3 plants, like rice, because the current CO_2 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 CO_2 suppresses photorespiration in C_3 plants because it increases carboxylation and decreases the oxygenase activity of Rubisco (Streck, 2005). But at the canopy level, the response to CO_2 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 CO_2 in rice. The general form of the MMF function is:

$$Y = (ab + c X^n)/(b + X^n) \quad (1)$$

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 = infinite and sigmoidal curves for 1<n<infinite, only by changing the shape coefficient (Streck et al., 2003).

For the f(CO_2), X is the atmospheric CO_2 concentration, and Y is the normalized RUE response. By normalized RUE, we mean that the RUE values 1 at current atmospheric CO_2 concentration. Therefore, the lower limit of the range of RUE response is 1 at current 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 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 CO_2 concentration on RUE in rice and which were published in international main stream journals. The source and some details of these trials are presented in Table 1. RUE data were normalized by dividing RUE at elevated CO_2 concentration treatments by RUE at the current CO_2 concentration treatment, and assuming that all current CO_2 treatments were 1. The CO_2 concentration from the whole data sets varied from 330 ppmv to 990 ppmv (Table 1), which covers the 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 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 1. Source and some details of the rice trials used to develop the CO_2 response function of radiation use efficiency (RUE).

Cultivar	Experimental protocol	Location	Levels of CO_2 (ppmv)	Units of RUE	Reference
IR72	Open Top Chambers experiment – dry/wet season and high nitrogen (200 kg ha⁻¹)	Los Baños, Philippines (15°N, 121°E)	350, 600 and 700	g MJ⁻¹	Weerakoon et al. (2000)
Nonspecified	Numerical experiment	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)	350 and 700	g MJ⁻¹	Soltani et al. (2001)
IR36, IR50, Ratna, Rasi, Akashi, Jaya and Cauvery	Numerical experiment	Several locations in India varying from Kapurthala (31°N) to Aduthurai (11°N) and from Ludhiana (75.8°E) to Cuttack (86°E)	330, 660 and 990	g MJ⁻¹	Mall & Aggarwal (2002)
BG300	Open Top Chambers experiment – average of pre-heading, post-heading and total crop duration and two growing seasons	Batalagoda, Sri Lanka (7°50'N, 80°50'E)	370 and 570	g MJ⁻¹	De Costa et al. (2006)
Kirara397 Kakehashi Akitakomachi Hitomebore	Free-air CO_2 enrichment experiment – average of four cultivars; pre-head, post-head and two years	Shizukuishi, Iwate, Japan (39°38'N, 140°57'E)	365, 548 and 570	g mol⁻¹	Shimono et al. (2009)

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 = 3.096×10^{23}, standard error = 1.188×10^{24}; 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:

$$Y = (3.096 \times 10^{23} + 1.4382 \times [CO_2]^{8.378})/(3.096 \times 10^{23} + [CO_2]^{8.378}) \quad (2).$$

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
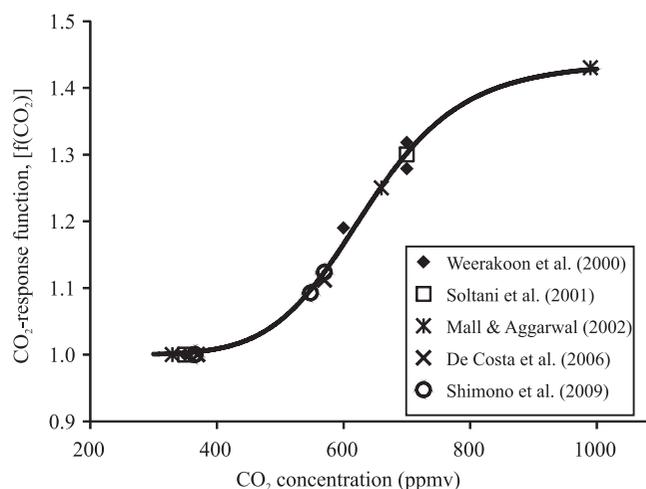

Figure 1. The CO_2-response function for radiation use efficiency in rice. Points are from published data listed in Table 1; the curve is the fitted MMF function with coefficients given in the equation $Y = (3.096 \times 10^{23} + 1.4382 \times [CO_2]^{8.378})/(3.096 \times 10^{23} + [CO_2]^{8.378})$.

is a more robust ecophysiological parameter than photosynthesis rate of individual leaves, our approach to develop a $f(CO_2)$ response function is more appropriate for assessing the response of crop canopies to increased atmospheric CO_2.

The saturation of RUE response to CO_2 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 CO_2 concentrations, photosynthesis is limited by the carboxylation capacity of Rubisco, while at high CO_2 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, to respond positively to elevated atmospheric CO_2 concentration that has been extensively claimed as the probable acclimation of leaf photosynthesis to CO_2 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 CO_2 concentrations (Chen et al., 2005). In addition, in rice plants exposed to high CO_2 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 $f(CO_2)$ in the present study (Table 1), are from long-term experiments (plants were grown under elevated CO_2 throughout their entire growing period), which indicates that the acclimation of photosynthesis to elevated CO_2 at leaf level did not offset the fertilization effect at canopy level, and that there was an overall positive effect of elevated CO_2 on crop growth.

The photosynthesis acclimation to elevated CO_2 is the basis for a second hypothesis to explain the small increase of RUE in the range 500-600 ppmv of CO_2 of the $f(CO_2)$ (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 CO_2, i.e. under CO_2-saturated conditions. Under CO_2-nonsaturation conditions, such as in the study by Chen et al. (2005), in which rice plants were exposed to 580 ppmv CO_2, the acclimation of leaf photosynthesis had a greater impact on plant biomass, with a lower increase of crop biomass than at higher CO_2 (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 CO_2 concentration (Figure 1) has important implications for its use in the upcoming CO_2 emission scenarios which will guide the IPCC 2014 AR5 (Moss et al., 2010). For the most optimist scenario (RCP2.6), which assumes a maximum CO_2 concentration of about 490 ppmv, little benefits from CO_2 fertilization is expected for rice. For the RCP4.5 scenario, which assumes a maximum CO_2 concentration of about 650 ppmv, the final CO_2 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 CO_2 fertilization in rice are not expected after the year 2070.

The $f(CO_2)$ proposed in this paper (equation 2) takes into account the effect of CO_2 on RUE and can be easily coupled to a process-based rice simulation model such as InfoCrop. Because the data used for developing the $f(CO_2)$ 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 CO_2 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-CO_2 emission scenarios are also different from the AR4 ones and introduce new challenges for simulation studies, as CO_2 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(CO_2) response function in rice, which covers all CO_2 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 CO_2 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 CO_2 emission scenarios during the 21st century.

Acknowledgments

References

AGGARWAL, P.K.; KALRA, N.; CHANDER, S.; PATHAK, H. InfoCrop: a dynamic simulation model for the assessment of crop yields, losses due to pests, and environmental impact of agro-ecosystems in tropical environments. I. Model description. **Agricultural Systems**, v.89, p.1-25, 2006.

BOUMAN, B.A.M.; LAAR, H.H. van. Description and evaluation of the rice growth model ORYZA2000 under nitrogen-limited conditions. **Agricultural Systems**, v.87, p.249-273, 2006.

BOWES, G. Growth at elevated CO_2: photosynthetic responses mediated through Rubisco. **Plant, Cell and Environment**, v.14, p.795-806, 1991.

CHEN, G.-Y.; YONG, Z.-H.; LIAO, Y.; ZHANG, D.-Y.; CHEN, Y.; ZHANG, H.-B.; CHEN, J.; ZHU, J.-G.; XU, D.-Q. Photosynthetic acclimation in rice leaves to free-air CO_2 enrichment related to both ribulose-1,5-bisphosphate carboxylation limitation and ribulose-1,5-bisphosphate regeneration limitation. **Plant and Cell Physiology**, v.46, p.1036-1045, 2005.

CONFALONIERI, R.; ACUTIS, M.; BELLOCCHI, G.; DONATELLI, M. Multi-metric evaluation of the models WARM, CropSyst, and WOFOST for rice. **Ecological Modelling**, v.220, p.1395-1410, 2009.

DE COSTA, W.A.J.M.; WEERAKOON, W.M.W.; HERATH, H.M.L.K.; AMARATUNGA, K.S.P.; ABEYWARDENA, R.M.I. Physiology of yield determination of rice under elevated carbon dioxide at high temperatures in a subhumid tropical climate. **Field Crops Research**, v.96, p.336-347, 2006.

HASEGAWA, T.; HORIE, T. Leaf nitrogen, plant age and crop dry matter production in rice. **Field Crops Research**, v.47, p.107-116, 1996.

KITAGIMA, K.; MULKEY, S.S.; SAMANIEGO, M.; WRIGHT, S.J.P. Decline of photosynthetic capacity with leaf age and position in two tropical pioneer tree species. **American Journal of Botany**, v.89, p.1925-1932, 2002.

KLERING, E.V.; FONTANA, D.C.; BERLATO, M.A.; CARGNELUTTI FILHO, A. Modelagem agrometeorológica do rendimento de arroz irrigado no Rio Grande do Sul. **Pesquisa Agropecuária Brasileira**, v.43, p.549-558, 2008.

KRISHNAN, P.; SWAIN, D.K.; BHASKAR, B.C.; NAYAK, S.K.; DASH, R.N. Impact of elevated CO_2 and temperature on rice yield and methods of adaptation as evaluated by crop simulation studies. **Agriculture, Ecosystems and Environment**, v.122, p.233-242, 2007.

MAKINO, A.; HARADA, M.; KANEKO, K.; MAE, T.; SHIMADA, T.; YAMAMOTO, N. Whole-plant growth and N allocation in transgenic rice plants with decreased content of ribulose-1,5-bisphosphate carboxylase under different CO_2 partial pressures. **Australian Journal of Plant Physiology**, v.27, p.1-12, 2000.

MALL, R.K.; AGGARWAL, P.K. Climate change and rice yields in diverse agro-environments of India. I. Evaluation of impact assessment models. **Climatic Change**, v.52, p.315-330, 2002.

MATTHEWS, R.B.; KROPFF, M.J.; HORIE T.; BACHELET, D. Simulating the impact of climate change on rice production in Asia and evaluating options for adaptation. **Agricultural Systems**, v.54, p.399-425, 1997.

MORGAN, P.H.; MERCER, L.P.; FLODIN, N.W. General model for nutritional responses of higher organisms. **Proceedings of the National Academy of Sciences of the United States of America**, v.72, p.4327-4331, 1975.

MOSS, R.H.; EDMONDS, J.A.; HIBBARD, K.A.; MANNING, M.R.; ROSE, S.K.; VUUREN, D.P. van; CARTER, T.R.; EMORI, S.; KAINUMA, M.; KRAM, T.; MEEHL, G.A.; MITCHELL, J.F.B.; NAKICENOVIC, N.; RIAHI, K.; SMITH, S.J.; STOUFFER, R.J.; THOMSON, A.M.; WEYANT J.P.; WILBANKS T.J. The next generation of scenarios for climate change research and assessment. **Nature**, v.463, p.747-756, 2010.

O'NEILL, B.C.; SCHWEIZER, V. Mapping the road ahead. **Nature Climate Change**, v.1, p.352-353, 2011.

PEDRO JÚNIOR, M.J.; SENTELHAS, P.C.; MORAES, A.V.C.; VILLELA, O.V. Estimativa da produtividade de arroz irrigado por inundação em função da temperatura do ar e da radiação solar. **Scientia Agricola**, v.52, p.96-100, 1995.

SAGE, R.F.; SHARKEY, T.D.; SEEMANN, J.R. Acclimation of photosynthesis to elevated CO$_2$ in five C$_3$ species. **Plant Physiology**, v.89, p.590-596, 1989.

SAS INSTITUTE. **SAS/STAT user's guide statistics**. Version 8. Cary: SAS Institute, 2001.

SETIYONO, T.D.; CASSMAN, K.G.; SPECHT, J.E.; DOBERMANN, A.; WEISS, A.; YANG, H.; CONLEY, S.P.; ROBINSON, A.P.; PEDERSEN, P.; DE BRUIN, J.L. Simulation of soybean growth and yield in near-optimal growth conditions. **Field Crops Research**, v.119, p.161-174, 2010.

SETIYONO, T.D.; WEISS, A.; SPECHT, J.; BASTIDAS, A.M.; CASSMAN, K.G.; DOBERMANN, A. Understanding and modeling the effect of temperature and daylength on soybean phenology under high-yield conditions. **Field Crops Research**, v.100, p.257-271, 2007.

SHIMONO, H.; OKADA, M.; YAMAKAWA, Y.; NAKAMURA, H.; KOBAYASHI, K.; HASEGAWA, T. Genotypic variation in rice yield enhancement by elevated CO$_2$ relates to growth before heading, and not to maturity group. **Journal of Experimental Botany**, v.60, p.523-532, 2009.

SINCLAIR, T.R.; MUCHOW, R.C. Occam's razor, radiation-use efficiency, and vapor pressure deficit. **Field Crops Research**, v.62, p.239-243, 1999.

SOLTANI, A.; ZEINALI, E.; GALESHI, S.; NIARI, N. Simulating G F D L predicted climate change impacts on rice cropping in Iran. **Journal of Agricultural Science and Technology**, v.3, p.81-90, 2001.

STRECK, N.A. Climate change and agroecosystems: the effect of elevated CO$_2$ and temperature on crop growth, development and yield. **Ciência Rural**, v.35, p.730-740, 2005.

STRECK, N.A.; ALBERTO, C.M. Estudo numérico do impacto da mudança climática sobre o rendimento de trigo, soja e milho. **Pesquisa Agropecuária Brasileira**, v.41, p.1351-1359, 2006.

STRECK, N.A.; PAULA, F.L.M. de; BISOGNIN, D.A.; HELDWEIN, A.B.; DELLAI, J. Simulating the development of field grown potato (*Solanum tuberosum* L.). **Agricultural and Forest Meteorology**, v.142, p.1-11, 2007.

STRECK, N.A.; WEISS, A.; BAENZIGER, P.S. A generalized vernalization response function for winter wheat. **Agronomy Journal**, v.95, p.155-159, 2003.

UNITED STATES DEPARTMENT OF AGRICULTURE. Foreign Agricultural Service. Production, Supply and Distribution Online. **Custom query**. Washington: USDA, 2011. Available at: <http://www.fas.usda.gov/psdonline/psdquery.aspx>. Accessed on: 17 June 2011.

WALTER, L.C.; ROSA, H.T.; STRECK, N.A. Simulação do rendimento de grãos de arroz irrigado em cenários de mudanças climáticas. **Pesquisa Agropecuária Brasileira**, v.45, p.1237-1245, 2010.

WEERAKOON, W.M.W.; INGRAM, K.T.; MOSS, D.N. Atmospheric carbon dioxide and fertilizer nitrogen effects on radiation interception by rice. **Plant and Soil**, v.220, p.99-106, 2000.