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ORIGINAL PAPER

How can crop modeling and plant physiology help to understand the plant responses to climate change? A case study with sugarcane

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Abstract Global climate changes are now well accepted to happen and can likely impact agriculture. Process-based dynamic crop models are able to estimate a range of crop responses to the environment and to assess the biophysical effects of future climate scenarios on crop growth and yield. They are hence scientifically accepted as a predictor of future agricultural scenarios, and the multi-model approach has shown the best performance in such prediction activities. The need of several models for such studies is mainly a consequence of the different physiological and physical approaches applied by model developers. Physiological processes are in fact essential elements for improving plant modeling, and most of the model weakness would be overcome by better understanding of the main physiological aspects related to plant growth and development. Sugarcane (*Saccharum* spp.) is an important crop for coping with climate change mitigation as a source of bioenergy and food. In this paper we aim to demonstrate how important is plant physiology for advancing the process-based crop models by briefly reviewing the history of the modeling along the last five decades and presenting the key physiological process considered in crop models. The paper was based in the DSSAT/CANEGRO sugarcane model and a set of field experiments for exemplifying some model responses to key climatic variables expected to vary in the following decades. Those responses were discussed under the light of plant physiology knowledge. We selected two sites in the State of Sao Paulo for an exercise of local sensitivity analysis. As air CO_2 concentration is the most likely environmental variable expected to change, we stressed the CO_2 effects on plant photosynthesis and water use to highlight the model strengths and opportunities for model improvements based on plant physiology findings.

Keywords Simulation · Global warming · Carbon dioxide · *Saccharum* spp.

1 Introduction

Global climate changes are now well accepted to happen and likely impact several sectors of the World economy. Among them, the agricultural activities face the significant challenge of increasing crop production (CP) to provide food security for a population

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projected to reach 9 billion by mid-century while protecting the environment and the functioning of ecosystems (Rosenzweig et al. 2013). To examine the full range of climate change impacts on agriculture, the best methodologies for assessing the biophysical effects of climate on crop growth and yield are the process-based dynamic crop growth models (e.g., Keating et al. 1999; Brisson et al. 2003; Jones et al. 2003; Palosuo et al. 2011). This approach has been scientifically accepted as a predictor of future impact of climate changes because their algorithms are supposed to rely on the state of the art of the physiological and physical principles for a given species (Rosenzweig et al. 2013). In addition, previous studies with maize and wheat have shown how prediction uncertainty can be reduced by using model ensemble (Palosuo et al. 2011; Rötter et al. 2011; Asseng et al. 2013). The uncertainty reduction is a consequence of the differences among approaches used in those models, and the complimentary benefits of having several models as estimators of biophysical processes.

Physiological processes are in fact essential elements for improving plant modeling, and most of the model weakness would be overcome by better understanding of the main physiological aspects related to plant growth and development. Besides being genotype-dependent, photosynthesis, respiration, carbon partitioning and water relations are differentially affected by the agricultural environment. Long-term climate projections have shown that the air temperature, rainfall, air CO_2 concentration and solar radiation are the most likely climate variables to be changed in the future (Trenberth et al. 2007). These are also important variables driving plant physiology and hence process-based crop models. In fact, most of crop modeling has been developed to understand the effects of agricultural practices and environmental factors on CP, emphasizing food and energy supply (Keating et al. 2003; Jones et al. 2003).

Sugarcane (*Saccharum* spp.) is an important crop for coping with climate change mitigation as ethanol and biomass for energy are produced from it (Goldemberg 2007). It is also important for food security, as near 75 % of world′s sugar comes from sugarcane plantations. As Brazil is the biggest sugarcane producer and this crop has social and economic importance, sugarcane is used in this mini-review as a case study for understanding how plant physiology and process-based crop models are currently integrated. In this paper we aim to demonstrate how important is plant physiology for advancing the process-based crop models quality by briefly reviewing the history of the modeling along the last five decades and presenting the key physiological process considered in crop models. In addition, the sugarcane production is simulated in some climate scenarios and some biophysical processes representing important uncertainty sources for crop models are discussed.

2 Main crop models: a brief review

A model is a characterization of a real system and it may take the form of a drawing, a simple written verbal description or may be a complicated set of equations to be used in the simulation of a giving system. Crop modeling can be defined as a dynamic simulation of crop growth by numerical integration of constituent processes with the aid of computers, being a technology used to construct a relatively transparent surrogate for a real crop (Sinclair and Seligman 1996).

A basic understanding and appreciation of the key plant physiological processes and the interactions with other processes in the farming system are the foundation to crop modeling and then many of the decision support systems made right along the value chain of any cropping industry; from genotype and site selection, to strategic crop management, infrastructure investment and marketing decisions (Lisson et al. 2005). The need for such decision support system emerged mainly in the early 90s as a consequence of system analysis approach applied to the agricultural research. This, in turn, was motivated by increasing information needs for agricultural decision making at all levels due to increased demands for agricultural products and increased pressures on land, water, and other natural resources (Jones et al. 2003). So, the generation of new data through traditional agronomic research methods and their publication are not sufficient to meet these increasing needs. Traditional agronomic experiments are conducted at particular points in time and space, making results site- and season-specific, time consuming and expensive. On this regard, McCown et al. (1996) stated that among the many changes taking place in the culture of Western agricultural research, there is an increased recognition that a ‘system approach’ is needed to meet the challenges presented by the complexities, uncertainties and conflicts in modern agricultural production systems.

In general, crop models are classified according to how they describe the observed data in terms of biophysical laws or only using a mathematical relationship unconstrained by physical laws, such as that of energy conservation (thermodynamics), by biological information and by any knowledge about the system structure. The latters are called empirical models, while those in which the modeler tries to construct a description of the system behavior based on component processes and if possible at lower hierarchical level of organization are called mechanistic models. Mechanistic modeling is ‘hard science’ and follows the traditional reductionist method used in the physical sciences, plant biology and biochemistry (Thornley and Johnson 1990). In agricultural sciences, the mechanistic models are also known as process-based crop models because the modeler takes into account the physiological and physical process controlling the species development and its relationship with the environment. Decisions support systems are composed by several software tools having as a central component a crop model describing the relationships between plant, atmosphere, soil and biotic components. Most of the available crop models around the world were developed under this view, and they were pushed by the system analysis approach spread on the agricultural research during the 70s and 80s.

By using models, one can analyze and manipulate a giving system with far greater ease than the complex and cumbersome original one. During the twentieth century an unprecedented science development occurred by a blend of induction and deduction, with induction leading from specific observations to general laws and deduction from general principles to specific predictions. Models are developed and refined step by step guided by experimental results filling small knowledge gaps rather than grand design experiments (Overman and Scholtz III 2002). This phenomenon has occurred with sugarcane crop models, which have been mostly based on some few seminal papers adapting the models from maize and other crops to sugarcane. Nowadays, there are some models dedicated to crop simulation worldwide: AUSCANE (Jones et al. 1989), DSSAT/CANEGRO (DC) (Inman-Bamber 1991; Singels et al. 2008), QCANE (Liu and Kingston 1995), APSIM-Sugar (Keating et al. 1999; Thorburn et al. 2005), MOSICAS (Martiné 2003), StoCrop-Cane (Marin and Jones 2014) and CASUPRO (Villegas et al. 2005). However, this is a small number of models for such an important crop as compared to the 27 models available for wheat (Asseng et al. 2013). Among the sugarcane models, only two are widely available and supported: APSIM-Sugar and DC. In this paper we used DC model for predicting sugarcane yield in some climate scenarios and discuss how plant physiology is important for advancing the process-based crop models quality.

3 Crop models and physiological variables

The DC model was originally developed using a detailed dataset collected in experiments carried out in South Africa with the cultivar NCo376 (Inman-Bamber 1991). So, this cultivar is assumed as a standard for DC model, and it comes with a set of default values for the physiological and biophysical parameters. The complete list of model parameters was described by Singels et al. (2008) and is shown in Tables 1, 2, and 3. These tables were organized under the philosophy of DSSAT crop models, i.e. only cultivar parameters (Table 1) are supposed to vary among cultivars, while species and ecotype parameters are supposed to be constant (Tables 2, 3). It is interesting to emphasize that the way these tables were organized reveals how the modeling groups understand such cropping system, and how it differs from other modeling groups (e.g. APSIM-Sugar).

In general, the variables are organized in groups dealing with photosynthesis, biomass partitioning, sucrose accumulation, root growth, canopy characteristics, water balance and uptake, lodging, phenology (Tables 1, 2, 3). Regarding the environmental regulation, the effects of temperature and water availability are considered on photosynthesis, respiration, sucrose accumulation, water balance and growth, which are supposed to be similar among cultivars (Table 2).

In DC model, the radiation use efficiency (RUE or εc) is cultivar-dependent (Table 1), which does not happen in the APSIM-Sugar model (Keating et al. 1999). In fact, significant differences in photosynthesis were found among sugarcane cultivars, with this key physiological process being 30 % higher ($n = 248$, $p < 0.05$) in IACSP96-2042 as compared to IACSP94-2094 (Ribeiro et al. unpublished data). As photosynthesis is a component of εc, the DC model

Table 1 Cultivar parameters, description and units for the DSSAT/CANEGRO model

Category	Parameter	Description	Units	RB867515	NCo376
Photosynthesis	PARCEMAX	Radiation use conversion efficiency	g MJ^{-1}	11.1	9.9
Biomass partitioning	APFMX	Aboveground biomass partitioning of a mature crop	Fraction	0.88	0.88
	STKPFMAX	Stalk partition fraction of aboveground biomass	Fraction	0.65	0.65
Canopy	LFMAX	Maximum number of green leaves per stalk	Units	10	12
	MXLFAREA	Area of the biggest leaf	cm^2	546	360
	MXLFARNO	Leaf no. of the biggest leaf		18	14
	PI1	Phyllochron for leaves younger than Pswitch	°C d	89	69
	PI2	Phyllochron for leaves older than Pswitch	°C d	107	169
	PSWITCH	Leaf no. where switch in phyllochron occurs		18	18
	TTPLNTEM	Thermal time requirement for crop emergence	°C d	408	428
	TTRATNEM	Thermal time requirement for ratton emergence	°C d	203	203
	CHUPIBASE	Thermal time requirement for start of stalk elongation	°C d	547	1,050
	TT_POPGROWTH	Thermal time requirement to peak tiller population	°C d	628	600
	MAX_POP	Peak tiller population	m^{-2}	15	30
	POPTT16	Final tiller population	m^{-2}	10	13.3

Parameter values for cultivar NCo376, the default cultivar in DSSAT/CANEGRO, and RB867515 are shown

seems to represent such variability of εc among sugarcane cultivars more properly (Marin et al. 2011).

4 Sugarcane response to climate changes

The relations between plant physiology and crop modeling were exemplified through a targeted sensitivity analysis to air CO_2 concentration, rainfall and air temperature. Several levels for each variable were simulated using baseline results as reference. Piracicaba (22°52′S, 47°30′W, 560 m above sea level) and Ilha Solteira (20°24′S, 51°24′W, 335 m above sea level) were chosen to represent different climates of the State of São Paulo, Brazil, with the time-series of rainfall, solar radiation and air temperature being available from 1992 to 2007.

The sensitivities were studied by simulating environmental modifications for 15 years and analyzing mean and standard deviation responses: variation in rainfall of ±30 %, in air CO_2 concentration (350–750 μmol mol^{-1}) and in air temperature (−3 to +9 °C). Before these set of simulations, we previously calibrated the model using a set of experimental data from an important sugarcane cultivar (RB867515), which is extensively grown in Brazil. These dataset are the same used by Marin et al. (2012), where all experimental details are described.

Rates of photosynthesis, respiration, expansive growth and evapotranspiration are influenced by air temperature and the DC model takes them into account. Increased temperatures caused large increase in potential evapotranspiration, with increases of 7.8 % in Piracicaba and 10.5 % in Ilha Solteira for +3 °C rise (Figs. 1, 2). The actual crop transpiration was also increased about 6.6 % in Piracicaba and 6.1 % in Ilha Solteira for +3 °C (Figs. 1, 2). However, the increased evapotranspiration led to an increase in the water stress severity. Considering the DC model, water stress is quantified using a soil water deficit factor (SWDF1) that ranges from 1 (no stress) to zero (fully stressed). In Piracicaba, the average SWDF1 increased by 6.7 and 26.7 % for the +3 and +6 °C scenarios, respectively (Fig. 1). In Ilha Solteira, the corresponding increases were 3.7 and 11.1 %, respectively (Fig. 2). A possible cause for the lower SWDF1 response in Ilha Solteira as compared to Piracicaba is that the water stress levels of the baseline scenario are much higher in Ilha Solteira than in Piracicaba. Both places have a dry period during the winter, but it is remarkably drier in Ilha Solteira than in Piracicaba. In fact, there is a reduction in the ratio between winter and summer cumulative actual evapotranspiration as temperature increases. For the baseline, winter evapotranspiration represented 61 % of summer

Table 2 Species parameters, description, units and default values for the DSSAT/CANEGRO model

Category	Parameter	Description	Units	Value
Photosynthesis	Tbasephotos	Base temperature for photosynthesis	°C	7.0
	Critsw	Water stress threshold for prolonged impact from severe water stress on photosynthesis	Fraction	0.2
	HuRecover	Thermal time required for full recovery of photosynthesis after a severe water stress event	°C d	150
	RespQ10	Fractional increase in respiration rate per 10 °C rise in temperature (Q_{10} coefficient)	Fraction	1.68
	RespGcf	Fraction of gross photosynthesis lost due to growth respiration	Fraction	0.242
Biomass partitioning	PCB	Fraction of total dry mass allocated to above ground biomass	Fraction	0.6
	Max_rootpf	Maximum partitioning of daily mass increments to roots	Fraction	0.95
Sucrose accumulation	FTCON	Temperature response shape parameter	Fraction	0.32
	SURCON	Sucrose partitioning: gives the response time of shifts in carbon partitioning between sucrose and fiber in the stalk due to environmental changes (varies between 0 and 1)	Fraction	0.99
Root growth	RTcmpg	Root length per root mass	cm g^{-1}	500
	Wrk	Extinction coefficient of root length density by depth	Fraction	−0.01
	RLVmin	Minimum root length density in soil layers	cm cm^{-3}	0.02
Canopy	SenesF	Number of senesced leaves per shoot per 100 stress days	Units	5
	Reset	Rainfall required to reset stress day counter	Mm	5
	Percoeff	Fraction of plant elongation attributable to stalk elongation	Fraction	0.16
	CHTCoeff	Coefficient determining canopy height as a function of stalk height and number of leaves	cm cm^{-1}	0.864
	Hillpar1	Empirical function shape parameter	Fraction	2.453
Water balance and uptake	EORATIO	Ratio of potential ET in unstressed sugarcane canopy to grass reference ET (Kc from FAO-56)	Fraction	1.15
	RWUEP1	Soil water supply: potential ET ratio threshold below which photosynthesis is limited	Fraction	1
	RWUEP2	Soil water supply: potential ET ratio threshold below which expansive growth is limited	Fraction	2
	RWUMX	Maximum root water uptake per unit root length	cm^3 cm^{-1}	0.07
Lodging	LG_RATING	Lodging score when crop is fully lodged	Fraction	8
	LG_CRIT_WIND	Wind run threshold for lodging	km d^{-1}	200

transpiration for both locations, but when temperature was increased by 3 °C, that ratio dropped to 52 and 58 % in Piracicaba and in Ilha Solteira, respectively. In addition, high temperatures accelerated canopy development, with plants reaching 80 % canopy cover 15 days sooner for +3 °C at both sites, which can be inferred from the fraction of intercepted light (Figs. 1, 2). In fact, light fractional interception (FI) was increased mainly in Piracicaba, which in turn has led to an increase in canopy photosynthesis (data not shown). The stalk fresh mass (SFM) in Piracicaba responded positively to an increase in air temperature up to +6 °C (11 % higher than the baseline), decreasing thereafter (Fig. 1). In Ilha Solteira, the SFM response was flatter (3 % higher than the baseline at +3 °C), and negative (5 % lower than the baseline) for an increase of +9 °C (Fig. 2).

Increases in rainfall caused a positive response of SFM, with increases of 7.4 % in Piracicaba and 6.4 % in Ilha Solteira (Figs. 1, 2). When considering the rainfall range of 60 % (−30 to +30 %), SFM varied in 21.2 % in Piracicaba and 18.2 % in Ilha Solteira. In addition, the temporal SFM variability was reduced as rainfall was increased in Ilha Solteira, as indicated by the CV % reduction from 24.5 to 18.7 %. Water-dependent processes, such as canopy growth and development and leaf gas exchange, mediate the effects of rainfall on crop yield. In this way, genotypic

Table 3 Ecotype parameters, description, units and default values for the DSSAT/CANEGRO model

Category	Parameter	Description	Units	Value
Sucrose accumulation	DELTTMAX	Max. change in sucrose content per unit change in stalk mass in the unripen section of the stalk	t^{-1}	0.07
	SWDF2AMP	Sensitivity of sucrose partitioning to water stress	Fraction	0.5
Canopy height	dPERdT	Change in plant extension rate per unit change in effective temperature	mm h^{-1} $°C^{-1}$	0.176
Canopy light extinction	EXTCFN	Maximum canopy light extinction coefficient	Fraction	0.84
	EXTCFST	Minimum canopy light extinction coefficient	Fraction	0.58
	LFNMXEXT	Leaf no. (all leaves attached) at which maximum light extinction occurs		20
Canopy leaves	AREAMX_CF (1) (2) (3)	Cultivar parameters for quadratic equation defining maximum leaf area		0 27.2 −20.8
	WIDCOR	Parameter affecting the width of leaves		1
	WMAX_CF (1) (2) (3)	Cultivar parameters for quadratic equation defining max leaf width per leaf number		−0.0345 2.243 7.75
	LMAX_CF (1) (2) (3)	Cultivar parameters for quadratic equation defining max leaf length per leaf number		−0.376 12.2 21.8
	MAXLFLENGTH	Absolute max leaf length (overrides LMAX_CF calculated values)		100
	MAXLFWIDTH	Absolute max leaf width (overrides LMAX_Cf calculated values)		3.5
Tiller population	POPCF (1)	Stalk population coefficient, in ideal conditions (no stress), as function of thermal time	Stalks	1.826
	POPCF (2)	Stalk population coefficient, in ideal conditions (no stress), as function of thermal time	Fraction	−0.00201
	POPDECAY	Fraction of tillers above the future mature tiller population (at a thermal time of 1,600 °C d), that senesce per unit thermal time	Fraction	0.004
Phenology	TTBASEEM	Base temperature for emergence and start of stalk elongation	°C	10
	TTBASELFEX	Base temperature for leaf phenology	°C	10
	TTBASEPOP	Base temperature for leaf phenology	°C	16
	TBASEPER	Base temperature for leaf phenology	°C	10.57
Lodging	LG_AMRANGE	Range in aerial mass from the start to the end of lodging	Mg ha^{-1}	30
	LG_GP_REDUC	Reduction in gross photosynthesis due to full lodging	Fraction	0.28
	LG_FI_REDUC	Reduction in canopy light interception due to full lodging	Fraction	0.1

differences in water stress sensitivity may affect the predicted response by changing the SWDF1 parameter. By evaluating SWDF1, it is clear that sugarcane yield is more responsive to rainfall reduction as compared to rainfall increase, mainly in Piracicaba (Figs. 1, 2).

A direct relationship between SFM and $[CO_2]$ was found in Piracicaba and Ilha Solteira (Figs. 1, 2), despite the climate differences between these sites. The lower sugarcane yield in Ilha Solteira was due to the drier climate and higher water deficit as compared to Piracicaba. Interestingly, there was a decrease in the variability of SFM under high $[CO_2]$ in both locations, as suggested by the error bars. In the DC model increased $[CO_2]$ caused a large reduction in crop transpiration, reaching −11.0 % in Piracicaba (Fig. 1) and −10.5 % in Ilha Solteira (Fig. 2) under 750 µmol mol^{-1}. As consequence,

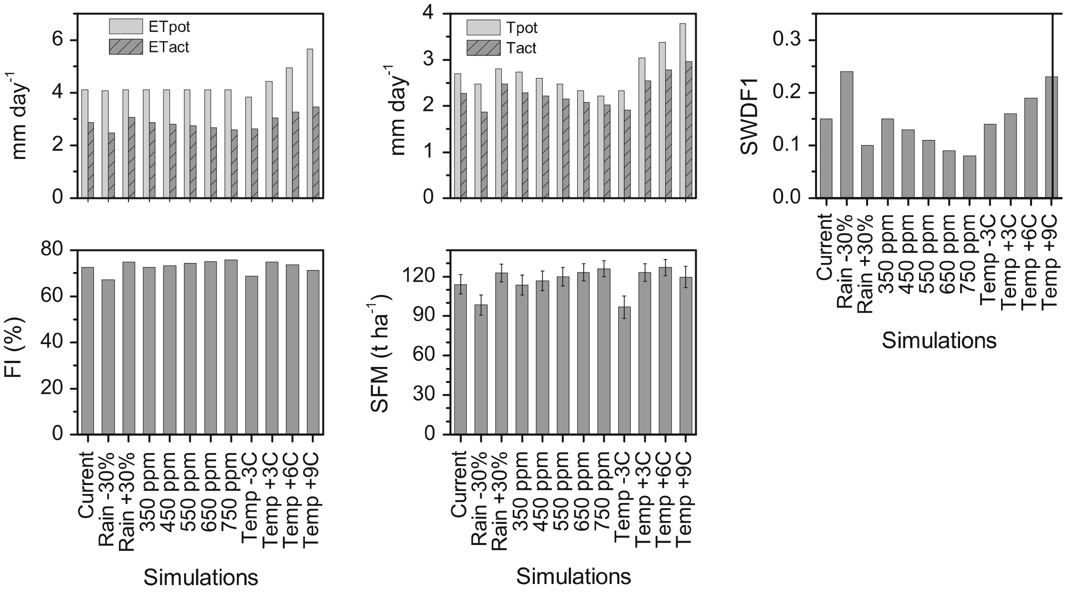

Fig. 1 Sensitive analyses of potential (ETpot), actual evapotranspiration (ETact), potential (Tpot), actual transpiration (Tact), soil water deficit factor (SWDF1), light fractional interception (FI), and stalk fresh mass at harvest (SFM) for the different climate scenarios in Piracicaba SP Brazil

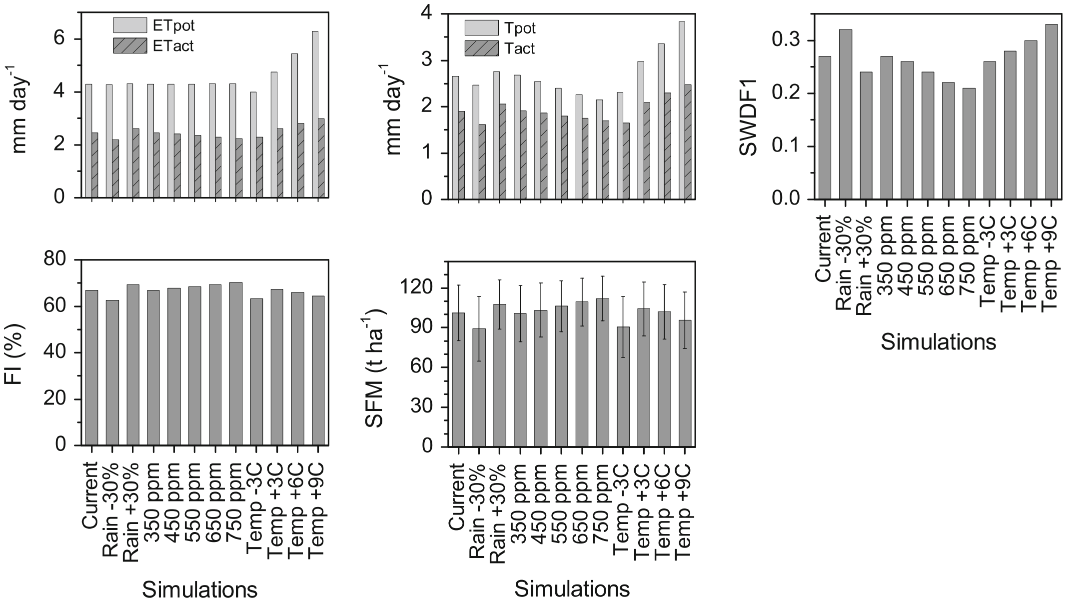

Fig. 2 Sensitive analyses of potential (ETpot), actual evapotranspiration (ETact), potential (Tpot), actual transpiration (Tact), soil water deficit factor (SWDF1), light fractional interception (FI), and stalk fresh mass at harvest (SFM) for the different climate scenarios in Ilha Solteira SP Brazil

crop evapotranspiration was also reduced by −9.1 and −8.9 %, respectively. This caused a large reduction in water stress severity (SWDF1) of −46.7 % in Piracicaba and −22.2 % in Ilha Solteira at 750 ppm (Figs. 1, 2). As shown, the effects of increasing [CO_2] in SFM are quite clear in Piracicaba, where a linear increase is revealed from 350 to 750 μmol mol^{-1} (Fig. 1). Such response is a consequence of changes in transpiration and photosynthesis in the DC model.

5 On the physiological bases of sugarcane response to climate changes

Before addressing the specific effects of environmental variables on biomass production, it would be helpful for guiding the discussion to take a simple representation of the main factors controlling CP. According to Zhu et al. (2010), the CP is defined by the Eq. 1:

$$\mathrm{CP} = 0.487 \cdot \mathrm{Qg} \cdot \varepsilon \mathrm{i} \cdot \varepsilon \mathrm{c} \cdot \varepsilon \mathrm{p} \qquad (1)$$

where 0.487 represents the PAR fraction of Qg, Qg is the total solar radiation during a given time, εi is the light interception efficiency and εc is the conversion efficiency. While εi is regulated by canopy development, structure, and longevity, εc is driven by the carbon balance of the entire plant canopy, which in turn is based on photosynthetic and respiratory rates. The partitioning efficiency (εp) represents the biomass partition to the crop portion of economic interest, such as grains in maize or stalks in sugarcane.

It is easy to understand that keeping constant the potential production driven factors (CO_2, solar radiation, air temperature), the option for increasing crop yield would be improving such efficiencies. Conventional crop breeding programs have improved the yield through increases in εi and εp, searching for crops with canopy structure able to increase the radiation interception, rapid cover the soil surface and preferential partition of carbon to harvestable plant portions (Zhu et al. 2010). As alternative, crop yield may be improved through increases in εc by improving canopy photosynthesis and reducing respiratory losses. In a C4 plant with a theoretical maximal εc of 0.06 (on Qg basis), around 20 % of energy loss occurs in processes related to carbohydrate biosynthesis (17.5 %) and respiration (2.5 %). This loss was estimated without the occurrence of photorespiratory losses in C4 plants, which are three times higher than the respiratory ones in C3 plants (Zhu et al. 2010).

Our simulation has shown that increases in temperature have increased FI (Figs. 1, 2), which is in turn related to the εi. On the other hand, the high temperature increased the sensitivity to water stress due to increased evapotranspiration, transpiration and SWDF1 (Figs. 1, 2). This latter response limits crop yield in a scenario where the increasing temperature happens in parallel to decreasing rainfall. In our case, rainfall was not changed and crop yield increased, mainly in Piracicaba (Fig. 1). In general, C4 species are well adapted to hot environments, showing optimum temperature range for photosynthesis between 30 and 40 °C (Long 1999; Ghannoum et al. 2000). However, respiration is a key physiological process related to plant growth that exponentially responds to air temperature (Connor et al. 2011). Therefore, our simulations suggest that canopy photosynthesis is increased rather than respiration, causing improvement of SFM in climate scenarios with +3 and +6 °C (Figs. 1, 2).

Regarding SFM, an increase of 30 % in rainfall seems to be a similar effect of increasing temperature in 3–6 °C (Fig. 1). The SWDF1 indicates that sugarcane crops are more water stressed in Ilha Solteira than in Piracicaba, which is caused by an imbalance between rainfall and atmospheric demand. Therefore, the effect of changing 30 % of rainfall in Ilha Solteira is lower than in Piracicaba (Figs. 1, 2). A well-hydrated crop is able to maintain canopy structure and growth due to turgor maintenance, which has positive impact in εi and crop yield. On the other hand, the water deficit scenario due to reduction of 30 % in rainfall may reduce SFM through changes in all efficiencies. While water stress causes variation in canopy architecture and size (reducing εi), it may also affect εc by reducing photosynthesis (Inman-Bamber and Smith 2005). Regarding sugarcane photosynthesis, the water deficit induces biochemical and stomatal limitations that are reversible after plant rehydration (Inman-Bamber and Smith 2005; Machado et al. 2009; Ribeiro et al. 2013; Sales et al. 2013). One would argue that even εp might be changed as plants are able to improve root growth to explore soil profile. However, Smith et al. (2005) have reported that sugarcane plants maintain a functional equilibrium between shoots and roots, with small and transient changes in the shoot:root ratio.

The effect of high [CO_2] on transpiration response is related to the partial stomatal closure under high air CO_2 concentration. Low stomatal conductance is able to reduce water loss through transpiration and improve plant water status (Owensby et al. 1997). The responses of different C4 species vary, but a survey from Drake et al. (1997) considering 41 samplings covering 28 species suggests an average decrease in

Table 4 Responses of growth (G) and photosynthesis (P_N) in some plant species exposed to increasing air CO_2 concentration

Species	CO_2 exposure		G	P_N	References
	Time	ppm			
Bothriochloa ischaemum	2 years	550	n.a.	+	Anderson et al. (2001)
Paspalum conjugatum	90 days	710	–	–	Ziska et al. (1991)
Flaveria trinervia	31–40 days	700	+	+	Ziska et al. (1999)
Panicum miliaceum			=	+	
Panicum maximum			=	+	
Sorghum bicolor	60 days	700	n.a.	–	Watling et al. (2000)
	60 days	570	=	+	Cousins (2001)
	79 days	570	–	n.a.	Derner et al. (2003)
Saccharum spp.	1 year	720	+	+	De Souza et al. (2008)
Saccharum officinarum	70 days	720	+	=	Vu et al. (2006)
	120 days	720	n.a.	+	Vu and Allen (2009a)
	90 days	720	+	=	Vu and Allen (2009b)
Zea mays	30 days	1,100	+	+	Maroco et al. (1999)
	56 days	720	–	–	Prins et al. (2011)
Seven C4 grasses	180 days	660	+	+	Wand et al. (1999)

+ means increase, – means reduction, = means no response, *n.a.* not available

stomatal conductance of nearly 20 %. Based on anatomical and physiological differences between C3 and C4 plants, these latter are assumed to respond to high [CO_2] by closing their stomata to a greater extent than C3 plants (Tolbert and Zelitch 1983).

Not long time ago, there was a general belief that C4 plants would not respond to increases in [CO_2], which were in accordance with results of Ottman et al. (2001) for sorghum, Leakey et al. (2006) for maize and Maherali et al. (2002) for a Texas native C4 grassland. However, the DC algorithm seems to reflect the response of sugarcane growth under modified environments reported by Ziska and Bunce (1997), Vu et al. (2006), De Souza et al. (2008) and Vu and Allen (2009a). These four papers reported increases in photosynthesis and biomass production even under well-watered and fertilized conditions under different experimental designs and climate conditions. For instance, De Souza et al. (2008) and Vu and Allen (2009a) reported an increase of 30 % in photosynthesis and 40 % in biomass production for plants growing under 720 ppm [CO_2] inside open top chambers. They also reported a reduction in stomatal conductance and transpiration of more than 30 %. In addition, Vu and Allen (2009b) included treatments with increased air temperature and [CO_2] and observed even higher increments of stalk dry mass (84 %) and stem juice (124 %) when compared to those in which [CO_2] was elevated at a constant temperature. Regardless plants are facing or not limiting conditions in those studies (Table 4), one must consider the significant response of photosynthesis to increasing [CO_2], with impacts in εc. As consequence, biomass production may be increased.

The positive and significant photosynthetic responses to CO_2 suggest that the carboxylation site of Rubisco is not CO_2-saturated, which would be related to low CO_2 availability and transport failure of four-carbon molecules from mesophyll to bundle sheath cells. Some published results support the response to CO_2 in C4 species either under favorable or stressful conditions (Table 4). Marchiori (2010) found significant short-term response of photosynthesis to increasing air CO_2 concentration in three sugarcane cultivars under field conditions, with the ratio between the photosynthetic rates measured at 600 and 380 $\mu mol\ mol^{-1}$ of CO_2 varying from 1.22 to 1.37.

6 Sensitivity to high [CO_2]: a 'hot' topic for climate change

Among climate variables expected to change in the following decades, [CO_2] shows little uncertainty regarding its rise in the future, and our sensitivity simulation (Figs. 1, 2) has pointed the [CO_2] role for climate change studies. Crop simulation models can provide the capability for predicting the effects of this environmental change on physiology and yield across a wide range of species and day-to-day conditions. Yet, much more is now known about Rubisco kinetics, photosynthetic responses to CO_2, stomatal function and leaf-level feedback mechanisms than 20–30 years ago (Allen et al. 1997). Despite these advances, few crop models have incorporated such advances in a detailed algorithm for computing photosynthetic rate, photosynthesis sensitivity to CO_2 and CO_2-induced decreases in transpiration.

On the other hand, the importance of species-dependent differences in photosynthetic acclimation to high CO_2 is still under intense discussion on the scientific community and might be an interesting issue for plant physiology studies in order to better support the modeling efforts. For instance, we could consider the approached used in the main two sugarcane models effectively supported by their respective institutions. In the APSIM-Sugar model, high atmospheric CO_2 concentration is considered by multiplying the default transpiration efficiency (TUE) and RUE coefficients by modifiers (TUE and RUE CO_2 modifiers), as follows (Howden et al. 2007; Webster et al. 2009; Biggs et al. 2013):

$$\text{TUE } CO_2 \text{ modifier} = 0.0008 \cdot [CO_2] \quad (2)$$

$$\text{RUE } CO_2 \text{ modifier} = \left(\frac{1}{350} \cdot 0.05\right) \cdot [CO_2] + 0.95 \quad (3)$$

The DC model has little direct response simulated to photosynthesis (Fig. 3) and only the transpiration responds to high [CO_2] by increasing the leaf resistance to water vapor loss, leading to higher water use efficiency and reducing water stress. The DC photosynthesis algorithm calculates daily total biomass increments using a RUE approach (Singels and Bezuidenhout 2002) and a [CO_2] fertilization effect algorithm (Singels et al. 2013), which accounts for the photosynthesis (P_G) and hence yields:

$$P_G = FI \times PAR \times \varepsilon c \times R_{PG} \quad (4)$$

where FI is fractional interception of PAR, PAR is the photosynthetically active solar radiation (MJ m^{-2}) and εc is the RUE (g MJ^{-1}). The standard P_G at [CO_2] of 330 μmol mol^{-1} is adjusted using an adjustment factor (R_{PG}) that depends on [CO_2].

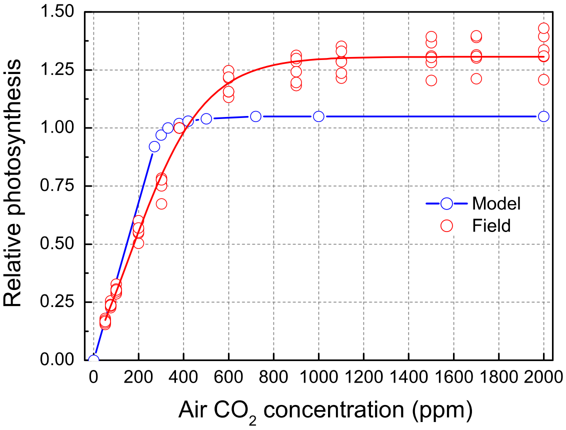

Fig. 3 Relative variation of photosynthetic rate as function of atmospheric CO_2 concentration considered in the DSSAT/CERES-Maize model (*blue circles*) and measured in sugarcane cultivars under field conditions (*red circles*). *Blue circles* represent the data points that define the function (Gerrit Hoogenboom, 2011, p. comm.). Each *red circle* represents the mean value of nine measurements taken in three sugarcane cultivars (redrawn from Marchiori 2010). The reference (unit) is the photosynthetic rate measured at air CO_2 concentration of 330 ppm in the model and 380 ppm in field measurements. (Color figure online)

Rather than defining this relationship mathematically, the DC model provides a mechanism for interpolating R_{GP} from a set of coordinate pairs (Gerrit Hoogenboom, pers. comm., 2011). Each of these data points is defined in the species file and the function for maize (taken from the 2011 DSSAT v.4.5 source code) was used for sugarcane, as shown in Fig. 3 (blue line). As the response of sugarcane photosynthesis to [CO_2] under field conditions may differ significantly from maize response (Fig. 3, open symbols), there is still enough room for improving sugarcane models. On this regard, we would highlight the need for field experiments to reveal the underlying acclimation mechanisms and the real impact of climate change in crop growth and yield. According to Ghannoum et al. (2000), the two possible alternatives to explain the improved growth performance of C4 plants under high [CO_2] are: (i) increased photosynthetic rates due to high intercellular CO_2 concentration; and (ii) improved shoot water relations and increased temperature due to reductions in stomatal conductance. In fact, some data obtained in field-grown sugarcane plants have confirmed a reduction of

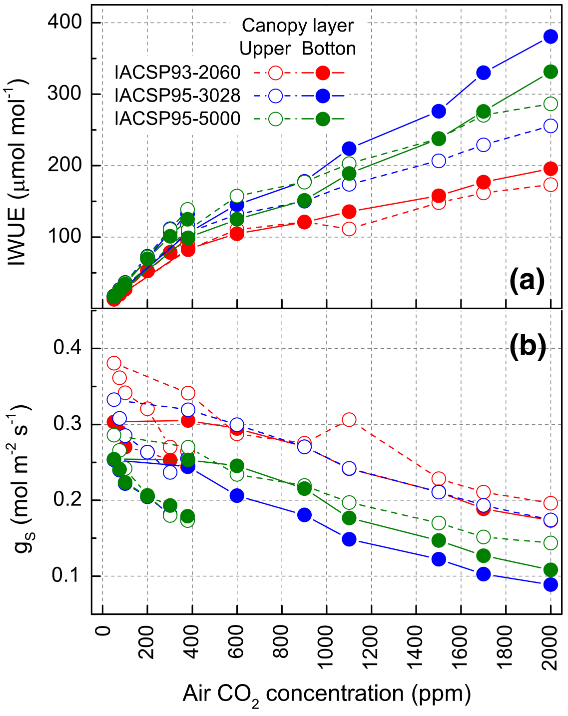

Fig. 4 Short-term responses of intrinsic water use efficiency (**a**) and stomatal conductance (**b**) to increasing air CO_2 concentration in three sugarcane cultivars grown under field conditions. Measurements were taken at two canopy layers (*upper* and *bottom*). Each *symbol* represents the mean value of nine measurements (redrawn from Marchiori 2010). (Color figure online)

stomatal conductance and a large increase of the intrinsic water use efficiency when increasing air CO_2 concentration (Fig. 4).

Besides the effect of $[CO_2]$ on photosynthesis, the DC model also simulates the impact of $[CO_2]$ on stomatal resistance and transpiration (e.g. Long et al. 2004), following the method proposed by Allen et al. (1985):

$$r_s = \frac{\left(3.28 \cdot 10^{-2} - 5.49 \cdot 10^{-5} \cdot [CO_2] + 2.96 \cdot 10^{-8} \cdot [CO_2]^2\right)^{-1} + r_{lb}}{LAI} \quad (5)$$

where r_s is the canopy resistance to water vapor diffusion ($s\ m^{-1}$), $[CO_2]$ is the $[CO_2]$ expressed in ppm, r_{lb} is leaf boundary resistance (assumed as 10 $s\ m^{-1}$) and LAI is the leaf area index ($m^2\ m^{-2}$).

The Eq. 5 predicts stomatal resistances of 62 and 135 $s\ m^{-1}$ at $[CO_2]$ of 380 and 880 µmol mol^{-1}, respectively. Although derived for sweet corn, these values compare well with sugarcane stomatal diffusion resistances measured under current atmospheric $[CO_2]$ by Venkataramana et al. (1986), Grantz and Meinzer (1990), De Souza et al. (2008), and Vu and Allen (2009a). The DC model uses an adjustment factor for potential transpiration derived from the theoretical ratio of grass reference evapotranspiration. This is calculated using the Penman–Monteith equation with canopy resistance calculated for the additional $[CO_2]$ to that calculated using the reference $[CO_2]$ of 330 µmol mol^{-1} (Marin et al. 2012). This, in turn, was derived from the fact that C4 plants have a CO_2 concentrating mechanism in the leaf mesophyll cells which binds CO_2 and transports it as a four-carbon molecule to vascular bundle sheath cells for decarboxylation (Sage and Monson 1999).

Assuming the plant physiology knowledge on processes and responses to environmental changes as fundamental for crop modeling improvements, we have shown simulation uncertainties of photosynthetic responses to $[CO_2]$ (Fig. 3) and differential stomatal sensitivities to $[CO_2]$ increase, leading to the water productivity increase (Fig. 4). Another issue that could be addressed by models is the differential sensitivity to drought stress among sugarcane cultivars. Sales et al. (2013) have reported a rapid recovery of photosynthesis after the stressful event in a cultivar with high constitutive activity of antioxidant enzymes. In addition, early stomatal closure with consequent maintenance of shoot water status and reasonable photosynthetic rates under water deficit are other interesting responses to prevent or alleviate the negative impact of drought in biomass production (Machado 2009; Ribeiro et al. 2013). As there is variation in photosynthetic sensitivity to constraining conditions, one may argue that εc varies among sugarcane genotypes. In this way, a variation of ±10 % of εc leads to large changes in simulated crop yield (Fig. 5).

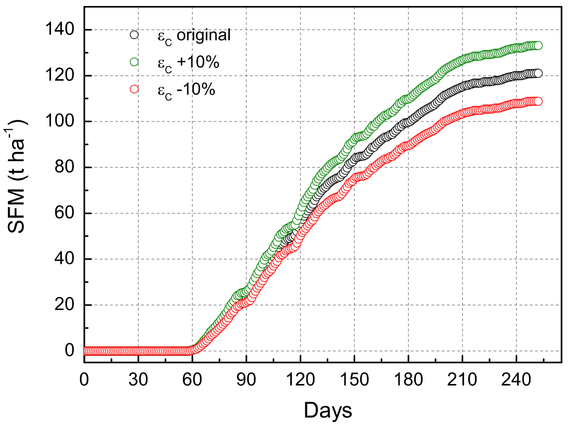

Fig. 5 DSSAT/Canegro sensitivity for stalk fresh mass yield (SFM) output due to radiation conversion efficiency (εc) changes for cultivar RB867515 after model calibration using seven Brazilian experimental datasets. (Color figure online)

7 Concluding remarks

Global climate changes are now well accepted to happen and likely impact agricultural sector. Long-term impact projections can be done using process-based dynamic crop growth models, with differences between models resulting of different ways to understand the real crop. Simulation uncertainty is a measure of the lack of physical and physiological knowledge on the real system, and/or a result of the difficult to turn it into computer codes the physiological knowledge already achieved. So, prediction uncertainty can be reduced by using model ensemble, as a consequence of the differences among models approaches and the complimentary benefits of having several models estimating physical and physiological processes. Stochastic simulation can then be indicated as a way of computing the input data and biophysical process uncertainties.

The essential role of plant physiology for modeling is well known (Lisson et al. 2005); however, genotype-dependent differences in response to environmental changes have not been well addressed so far. We have shown that responses to increasing air CO_2 concentration vary among sugarcane genotypes as well as the sensitivity and recovery of sugarcane photosynthesis under water deficit. Knowledge gaps on crop ageing and εc, sucrose accumulation and water content in stalks were reported by Lisson et al. (2005). Data on ageing, εc, εi, photosynthesis, respiration, and canopy development are poorly reported in field-grown sugarcane plants through the entire plant cycle. For sucrose accumulation, data on the dynamic of sugars (sucrose vs. reducing sugars) is still required even almost a decade after Liu and Bull (2001) and Lisson et al. (2005) have pointed this gap. Besides the importance of stalk water for commercial yield simulation, stalk water content is also physiologically important as a water source for surrounding tissues under water stress and for alleviating the impact of water stress on leaf gas exchange.

The lack of field data on sugarcane response to water stress is still leaving room for some disagreement. While Lisson et al. (2005) reported the low sensitivity to water deficit, our sensitivity analysis revealed a significant reduction of SFM due to rainfall decrease. Regarding photosynthetic responses to increasing air CO_2 concentration, one should take into account that plants are facing multiple stresses under field conditions, where there is a considerable deviation from the optimum condition. This may be a possible reason of increased SFM and photosynthesis under high CO_2, responses non-expected in C4 plants under non-limiting conditions. Anyway, research on photosynthetic responses to increasing CO_2 in field-grown sugarcane plants is needed to reveal the underlying acclimation mechanisms and the real impact of this climate change in crop growth and yield.

Finally, a close interaction between plant physiology and modeling is essential to improving the existing models, for creating new models, and for improving predictions on crop responses to climate changes and variability.

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