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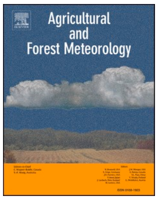

Sugarcane radiation use efficiency: varietal differences, temperature dependence, and implications for modeling biomass across environments

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ABSTRACT

Sugarcane is a major tropical C_4 crop of global economic significance, primarily used for sugar, ethanol, and bioenergy production. As climate change accelerates, with projected increases in global temperatures, understanding the temperature sensitivity of sugarcane's radiation use efficiency (RUE) is crucial for projecting yield under changing environmental conditions. In this context, this study aimed to characterize sugarcane RUE response to temperature across various environments and varieties from key producing regions worldwide. Using experimental data from six countries (Brazil, South Africa, United States of America, Zimbabwe, Argentina, and La Réunion) and 40 distinct varieties, our results indicated that maximum RUE (RUE_{MAX}) is consistent across varieties, while apparent RUE (RUE_A) showed significant variation. Based on this diverse dataset, we parameterized different RUE_{MAX} temperature response formalisms used in crop models (APSIM-Sugar, DSSAT-Canegro, MOSICAS, and emergent formalisms). We compared their ability to simulate RUE_A in various regions accurately. Our analysis revealed significant differences in formalism performance, emphasizing the need for accurate parameterization. Additionally, we demonstrated that predictions of biomass production under climate change scenarios are highly sensitive to the formalism parameterization used to represent the RUE-temperature relationship. These findings highlight the critical importance of refining crop models considering temperature response and cardinal temperatures (optimal range: 30–33°C) to enhance projections of sugarcane yield under future climate conditions. We discussed physiological processes that may explain differences in RUE_A among varieties. Incorporating these refined mechanisms into models will support more accurate climate impact assessments and aid breeding programs focused on developing high-yield sugarcane varieties.

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Glossary

Acronyms	Units	Definitions
RUE	g DM MJ^{-1}	Radiation-use efficiency, the rate at which a plant is able to convert intercepted solar radiation into dry biomass.
RUE_A	g DM MJ^{-1}	Apparent radiation-use efficiency, calculated as total aboveground biomass at final biomass sampling date divided by cumulative intercepted shortwave (global) solar radiation since crop start.
RUE_{MAX}	g DM MJ^{-1}	The maximum radiation-use efficiency calculated across a sequence of biomass sampling dates in a single cropping season.
RUE_O	g DM MJ^{-1}	Theoretical maximum radiation-use efficiency under ideal water, temperature, and nutrient conditions.
ADM	t ha^{-1}	Aboveground dry biomass per area
SRAD	MJ m^{-2} d^{-1}	Daily shortwave radiation (global solar radiation)
PAR	MJ m^{-2} d^{-1}	Daily photosynthetically active radiation
*fi*RAD	MJ MJ^{-1}	Canopy interception fraction of shortwave (global) solar radiation
*i*RADc	MJ m^{-2}	Cumulated canopy-intercepted shortwave (global) solar radiation
Anet	μmol m^{-2} s^{-1}	Instantaneous leaf net photosynthesis
GPP	μmol m^{-2} s^{-1}	Gross primary productivity

1. Introduction

Sugarcane (*Saccharum* spp.) is a perennial C_4 tropical grass belonging to the Poaceae (Gramineae) family and the genus *Saccharum* (Moore et al., 2013). It is a crop of significant economic importance worldwide, cultivated primarily to produce sugar, ethanol, electricity, and other by-products such as fertilizers, specialty chemicals, paper, and compost (Moore and Botha, 2013). In 2022, around 1.9 billion tons of sugarcane were produced from 26 million ha globally (FAOSTAT database). The demand for sugarcane-derived products is projected to rise in the future, driven by population growth and increasing industrial applications, including biofuels, bioplastics, and other innovative uses (Goldemberg et al., 2014; Leal et al., 2013). To meet this demand, there is a need to avoid extensification and increase yield in existing cultivated areas.

Climate change, driven by increases in air temperature in response to increasing concentrations of greenhouse gases (carbon dioxide, methane, and nitrous oxide), is expected to impact future sugarcane production (Dias and Inman-Bamber, 2020; Linnenluecke et al., 2018; Marin et al., 2014; Singels et al., 2021). As temperature change is a primary response to greenhouse gas accumulation in the atmosphere, projected increases in temperature are associated with a relatively low level of uncertainty (Thornton et al., 2014). Global surface mean temperatures have risen by 1.1°C over the last century and are projected to reach +1.5°C in the near term (2030–2035). By 2100, temperatures are expected to increase further, ranging from +1.4°C under a low-emission scenario to +4.4°C under a high-emission scenario (IPCC, 2023). Tropical regions, where sugarcane is predominantly grown, are expected to experience significant increases in the annual hottest day temperatures (IPCC, 2023).

While global warming's impacts on other climatic variables, such as rainfall, involve great uncertainty, there remains a substantial risk that precipitation may decrease or become more variable in many sugarcane-producing regions in the future (Feng et al., 2013). Water performs numerous critical functions in plants, with cooling through evaporation requiring the largest volume of water. Thus, decreases in rainfall can exacerbate heat stress in plants by effectively increasing the temperatures they experience (Inman-Bamber et al., 2012). Consequently, accurate projections of climate change impacts on sugarcane production depend on robust modeling of how changes in temperature influence key plant physiological processes.

One of the advantages of sugarcane is its exceptional ability to use sunlight to drive photosynthesis and produce biomass. The efficiency with which a crop converts canopy-intercepted solar radiation into biomass can be quantified using a parameter known as radiation-use efficiency (RUE, g MJ^{-1}) (Monteith et al., 1997). Sinclair and Muchow (1999) reported a sugarcane RUE of about 2.0 g DM MJ^{-1} SRAD and stated that this is the highest value of all economically significant field crops. However, there is ongoing debate regarding whether RUE is a stable trait across varieties and the growing season, excluding yield-limiting factors (Acreche, 2017; Acreche et al., 2015; De Silva and De Costa, 2012; Dias et al., 2021a; Donaldson et al., 2008; Robertson et al., 1996). This controversy reduces the accuracy of climate change projections on biomass production in different regions.

Resolving the RUE-variety debate requires some interpretation of how RUE is measured and what different reported RUE values represent (see Glossary, which includes detailed acronyms, and their definitions and units of measure). In principle, RUE is calculated as the change in dry biomass between two points in time, divided by the solar radiation intercepted by the crop during that period (Monteith et al., 1997). Typically, biomass measurements exclude root biomass, and intercepted radiation can refer to either shortwave (global) (SRAD, MJ m^{-2} d^{-1}) or photosynthetically active radiation (PAR, MJ m^{-2} d^{-1}). When RUE is calculated as the total crop biomass at harvest (or final biomass sample) divided by total radiation intercepted since crop start, it is referred to as 'apparent' RUE (RUE_A, g MJ^{-1}) (Robertson et al., 1996; Sinclair and Muchow, 1999). Conversely, RUE calculated for a period between two biomass sampling events is termed RUE_P (g MJ^{-1}). RUE_A can be lower than RUE_P if stresses (e.g., very hot or cold conditions, drought, low nutrient availability) or other processes (high maintenance respiration, lodging) reduce biomass accumulation rates during specific sampling periods. The highest sugarcane RUE_P value for sugarcane in a single cropping season has been termed RUE_{MAX} (g MJ^{-1}) (Jones et al., 2019; Muchow et al., 1994; Park et al., 2005; Robertson et al., 1996; Sinclair and Muchow, 1999). For a large dataset, the highest RUE_{MAX} approaches the theoretical maximum RUE for sugarcane (or a specific variety), referred to as RUE_O (Jones et al., 2019; Singels, 2013).

Sugarcane RUE has been observed to be sensitive to air temperature (Dias et al., 2021a; Donaldson et al., 2008). Crop species with the C_4 photosynthesis pathway, such as sugarcane, are better adapted to higher temperatures ($>$ 25°C) compared to species with C_3 photosynthesis (Long, 1999). This adaptation underscores the importance of C_4 crop species in warmer future climatic conditions. It is also acknowledged that C_4 crop species are significantly sensitive to variations in air temperature within the 20–30°C range (Long, 1999). This temperature range is typical of current sugarcane-producing regions worldwide (Dias and Inman-Bamber, 2020). The anticipated economic importance of sugarcane in the future underscores the urgent need to project the impacts of climate change on sugarcane productivity accurately. This is essential for planning effective adaptation strategies to mitigate the adverse effects of climate change and, where possible, capitalize on its positive impacts. In this context, RUE remains as a critically important emergent physiological trait in sugarcane. The magnitude of expected future temperature changes is substantial enough to significantly impact the RUE of typical C_4 crops by shifting sugarcane-growing environments closer to, or further from, their optimal temperature range.

RUE is an important parameter in many dynamic sugarcane simulation models, including DSSAT-CSM-CANEGRO (referred to as 'DSSAT-Canegro' from now on; Jones and Singels, 2018) and APSIM-Sugar (referred as 'APSIM' from now on; Keating et al., 1999), which are the most widely used worldwide to date (see Dias and Inman-Bamber, 2020 for a complete list of sugarcane models). MOSICAS (Christina et al., 2021) and DSSAT-CSM-SAMUCA (Vianna et al., 2020) have gained attention in the past five years. These models differ in their representation of RUE_O and its response to temperature, which includes both the cardinal temperature as well as the formalism for response to temperature (Jones et al., 2019; Vianna et al., 2022) usually using linear (e.g.

DSSAT-Canegro and APSIM) or symmetric curvilinear (e.g. MOSICAS) responses. Some of these differences can be linked to the difference in RUE representation in crop models, whether considering net (APSIM) or gross (DSSAT-Canegro and MOSICAS) photosynthesis (Jones et al., 2021). To explore the impact of climate change on sugarcane productivity, crop models are essential tools to represent biomass accumulation response to temperature through the RUE concept, and literature suggests that formalisms that represent the nonlinear and non-symmetric response of photosynthesis to temperature (Johnson et al., 2010; Wang and Engel, 1998) can be used to improve the ability of crop models to make reliable predictions under current or projections under future climate scenarios (Wang et al., 2017). Thus, having confidence in the sugarcane RUE response to temperature in these models is critical.

The broad objective of this study was to characterize the sugarcane RUE response to temperature using field data spanning environments and varieties across important sugarcane-producing regions worldwide to ensure that projections of future sugarcane yield are as accurate and representative as possible. Specific objectives were to i) evaluate if RUE_{MAX} varies across varieties in major producing countries, ii) assess whether the formalisms used in crop models appropriately represent the RUE response to temperature, and iii) investigate the impact of different formalisms on biomass projections in crop models and their sensitivity to the choice of RUE-temperature response in the context of warming climates.

2. Material & methods

2.2. RUE datasets

The data used in this study included sugarcane in-field experimental data previously published in the literature and whose original data were collected from the authors (including plant growth, meteorological data; Table 1). Two experiment datasets were gathered: i) varietal experiment datasets, where experiments included variety comparisons in the same field, and ii) crop model calibration and sensitivity datasets, including only one variety per experiment. The first dataset was used to assess variety differences in RUE_{MAX} and RUE_A, and the second was used for crop model calibration and sensitivity analysis.

The "varietal experiment" dataset included measurements of the fraction of intercepted radiation (*fi*RAD) by the sugarcane canopy considering the incident global solar radiation (SRAD, in $MJ\ m^{-2}\ d^{-1}$) and periodic aboveground dry mass (ADM, in tons, g or kg DM ha^{-1}) sampling over the crop season.

The "calibration and sensitivity" dataset included periodic ADM, *fi*RAD, and Leaf Area Index (LAI), except for South African data (SAF-PONG and SAF-MEDG), which only included observations of accumulated intercepted radiation (*i*RADc) with ADM. All experiments were fertilized under optimal conditions. Most of the experiments were irrigated except for a few, which were rainfed (experiments in Argentina and the RUN-SALS experiment in La Reunion) when rainfall was enough to meet sugarcane water demand. In this paper, a trial was defined as a one-year growth cycle in a specific site and country (Table 1).

2.3. Leaf photosynthesis and GPP datasets

In addition to RUE, in-field data of instantaneous leaf net photosynthesis (A_{net}, $\mu mol\ m^{-2}\ s^{-1}$) and gross primary productivity (GPP, $\mu mol\ m^{-2}\ s^{-1}$) were gathered from the literature and original data were collected from the authors. A_{net} and GPP variables were normalized between 0 and 1 using the 99% upper quantile as the higher observed values. The sources, experimental conditions, and measurements are briefly described below.

The first dataset measured leaf photosynthesis in sugarcane (plant crop cycle) in Campinas, Sao Paulo State, Brazil (Magalhães Filho, 2014). The design included four varieties (SP79-1011, IACSP94-2094, IACSP94-2101, and IACSP95-5000) with four replicates grown under optimal fertilization and irrigation. A_{net} was measured on eleven dates, from 125 to 477 days after planting, from 7:00 to 17:00, every 2 hours. Measurements were taken using an infrared gas analyzer (LI-6400XT, LICOR, Lincoln NE, USA) under natural variations of air temperature, relative humidity and light intensity. Measurements were recorded under low coefficient of variation ($CV < 5\%$) and temporal stability. Leaf and air temperature were measured with the LI-6400XT. Note that leaf and air temperature were similar in this experiment, and thus, the response to air temperature was chosen in the following analysis.

In the second dataset, GPP was estimated in a highly monitored rainfed experimental site with eddy-covariance measurements during the second and third ratoons of sugarcane variety SP83-2847 at an hourly time step, in Luiz Antonio, São Paulo State, Brazil (Cabral et al., 2013, 2012). The filtered and gap-filled net ecosystem exchange (NEE) data was partitioned into GPP and Ecosystem respiration (Reco) through the "nighttime partitioning" method (Wutzler et al., 2018), applying the temperature response function of nighttime NEE fluxes to estimate Reco during daytime, based on the Lloyd & Taylor model (Lloyd and Taylor, 1994). GPP and air temperature above the canopy were used in our analysis.

Table 1

RUE datasets used for the varietal experiment analysis or the calibration and sensitivity analysis, including country, experiment identification, number (No.) of plant and ratoon crop cycles, and number of varieties compared in each site and data source.

			No. of Crop Cycle			
Datasets	**Country**	**Experiment ID**	**Plant**	**Ratoon**	**No. of varieties**	**Source**
Varietal experiment	La Reunion	RUN-DEL1*	1	0	18	(Christina et al., 2020)
		RUN-ICSM*	1	1	5	(Jones et al., 2019)
	Brazil	BRA-MGSR*	2	0	6	(Dias et al., 2020, 2021a)
		BRA-PIGL*	3	0	6	(Dias et al., 2020, 2021a)
		BRA-CRU	1	1	3	(Cruz et al., 2021)
	South Africa	SAF-ICSM*	1	1	5	(Jones et al., 2019)
	USA	USA-ICSM*	0	1	6	(Jones et al., 2019)
	Zimbabwe	ZIM-ICSM*	1	0	6	(Jones et al., 2019)
	Argentina	ARG-SAEZ	1	2	5	(Saez et al., 2019)
Calibration & Sensitivity	La Reunion	RUN-SALS	0	3	R579	(Viaud, 2023)
		RUN-LINV	1	0		(Christina et al., 2020)
	Brazil	BRA-VIAN	0	2	RB867515	(Vianna et al., 2020)
		BRA-PIGL	3	0		(Dias et al., 2020, 2021a)
	South Africa	SAF-PONG	0	3	NCo376	(Donaldson, 2009)
		SAF-MEDG	0	2		(Singels et al., 2005)
	Argentina	ARG- SAEZ	1	2	LCP 85-384	(Saez et al., 2019)

* used in the variety x environment interaction analysis in this study (section 2.3)

2.4. RUE calculation and varietal effect analysis

RUE was calculated as the increase in sugarcane ADM divided by the accumulated daily *i*RAD in each plot from each trial. Two RUEs were calculated: RUE_A, defined as the final ADM at harvest divided by the cumulated intercepted global radiation over the crop cycle since planting, and RUE_{MAX}, calculated as the maximum RUE observed between successive biomass sampling dates during the crop cycle. The corresponding mean air temperature to this RUE_{MAX} was calculated as the mean between these two sampling dates. To calculate RUE, the daily *fi*RAD was estimated over the growth season based on a logistic growth function (Verhulst, 1838), a common sigmoidal-style curve used in agricultural studies (Archontoulis and Miguez, 2015):

$$fiRAD(d) = \frac{fiRADmax}{1 + 100\ e^{-b\ d}} \tag{1}$$

$$RUE_A = \frac{ADM(harvest)}{\sum_{d=0}^{d=harvest} fiRAD(d)\ SRAD(d)} \tag{2}$$

$$RUE_{MAX} = \max_{0 \le d1, d2 \le harvest} \left(\frac{ADM(d2) - ADM(d1)}{\sum_{d=d1}^{d=d2} fiRAD(d)\ SRAD(d)} \right) \tag{3}$$

Where *d* is the number of days since planting or previous harvest, *fi*RADmax is the maximum intercepted radiation reached, and *b* is an empirical fitting parameter.

Regressions were performed in each plot from the varietal experiment dataset using the *nlsLM* function (*minpack.lm R* package, Elzhov et al., 2016). A comparison between predicted *fi*RAD and measured *fi*RAD can be found in Supplementary Material Fig. S1, which yielded a root mean square error (RMSE) of 0.11 and a mean bias of -0.03.

First, the RUE response to the interaction between the variety and its environment (defined as a trial) was assessed using a subset of the varietal experiment where the same variety was tested in different sites (Table 1). The effect of the interaction between variety and trial, and crop class (CropClass, i.e., plant or ratoon crop) on RUE_A and RUE_{MAX} was assessed using a linear analysis of variance:

$$RUE \sim CropClass + Variety + Trial + CropClass : Variety + Trial : Variety \tag{4}$$

To ensure residue normality, the RUE variables were transformed using a Box-Cox transformation (*powerTransform* and *bcPower R* function, *car* R package, Fox et al., 2023). As non-significant interaction was found (see 3.1 result section), the influence of crop class and variety on the whole varietal experiment dataset was assessed using a mixed linear analysis of variance with the trial as a random effect (*nlme R* package, Pinheiro et al., 2022):

$$RUE \sim CropClass + Variety + (1|Trial) \tag{5}$$

Variables were also Box-Cox transformed to ensure residue normality. Predicted means and confidence intervals per variety or CropClass were estimated using the *emmeans* function (*emmeans R* package, Lenth et al., 2023). The *emmeans* function was also used to perform pairwise comparison with a Tukey *p*-adjustment method.

2.5. Description of RUE - temperature formalisms in crop models

In most sugarcane crop models, the influence of daily mean temperature (T_{MEAN}) on RUE is applied as an efficiency response function of temperature (fT_{RUE}, unitless 0-1), and the daily potential biomass production results from fT_{RUE}, total intercepted radiation, and RUE_{MAX}. Crop models use different formalisms of temperature effects on RUE, and four of them were compared in this study. The first formalism (referred to as ApsimCanegro), used in the APSIM (Keating et al., 1999) and DSSAT-Canegro (Jones and Singels, 2018) models, consists of a trapezoidal function, with a linear increase or decrease between two optimal temperatures:

$$if(T_{MEAN} \le T_B \mid T_{MEAN} \ge T_X)\ \{fT_{RUE} = 0\} \tag{6}$$

$$if(T_{MEAN} \ge T_{OPT1} \mid T_{MEAN} \le T_{OPT2})\ \{fT_{RUE} = 1\ \} \tag{7}$$

$$if\left(T_{MEAN} > T_B \middle| T_{MEAN} < T_{OPT1}\right) \left\{ fT_{RUE} = \frac{T_{MEAN} - T_B}{T_{OPT1} - T_B} \right\} \tag{8}$$

$$if\left(T_{MEAN} > T_{OPT2} \middle| T_{MEAN} < T_X\right) \left\{ fT_{RUE} = \frac{T_X - T_{MEAN}}{T_X - T_{OPT2}} \right\} \tag{9}$$

Where T_B, T_{OPT1}, T_{OPT2}, T_X are base, first, and second optimum (optimum range), and maximum temperature, respectively.

The second formalism (referred to as Mosicas), used in the MOSICAS crop model (Christina et al., 2021), was a symmetric curvilinear response with only one optimal temperature and no base and maximum temperature but a rate of decrease with suboptimal temperatures:

$$fT_{RUE} = 1 - \ T_{DEC}|T_{MEAN} - T_{OPT}|^{\gamma} \tag{10}$$

$$if(fT_{RUE} \le 0)\ \{fT_{RUE} = 0\} \tag{11}$$

Where T_{OPT} is the optimal temperature and T_{DEC} and γ are parameters controlling the rate of decrease in RUE with temperature.

The third formalism (referred to as Wang-Engel) proposed by Wang and Engel (1998) has been shown to be effective in simulating the phenology and photosynthesis response of varied annual crops to temperature (Streck et al., 2007; Wang et al., 2017, 2018). It is a non-symmetric curvilinear response with an optimal temperature, base temperature, and maximum temperature:

$$if(T_{MEAN} \le T_B \mid T_{MEAN} \ge T_X)\ \{fT_{RUE} = 0\} \tag{12}$$

$$if\ \ (T_{MEAN} > T_B | T_{MEAN} < T_X) \left\{ \begin{array}{c} \alpha = \dfrac{\ln(2)}{\ln(T_X - T_B/T_{OPT} - T_B)} \\ fT_{RUE} = \left(\dfrac{2(T_{MEAN} - T_B)^{\alpha}(T_{OPT} - T_B)^{\alpha} - (T_{MEAN} - T_B)^{2\alpha}}{(T_{OPT} - T_B)^{2\alpha}} \right)^{\beta} \end{array} \right\} \tag{13}$$

Where T_{OPT} is the optimal temperature, T_B and T_X are the base and maximum temperature for RUE, and β is a parameter controlling the curvature.

The fourth formalism (referred to as Johnson), a modified beta function to describe the photosynthesis response to temperature, proposed by Johnson et al. (2010), was similar to the Wang-Engel formalism but with a maximum threshold:

$$fT_{RUE} = \left(\frac{(1+c)T_{OPT} - T_B - c\ T_{MEAN}}{(1+c)T_{OPT} - T_B - c\ T_{REF}} \right) \left(\frac{T_{MEAN} - T_B}{T_{TREF} - T_B} \right)^{c} \tag{14}$$

Where T_{OPT} and T_{REF} are optimal temperatures, T_B is the base temperature, and *c* a curvature coefficient.

2.6. Temperature response regression analysis

The parameterization of the fT_{RUE} functions was performed based on a quantile regression to assess the envelop curve of RUE response to temperature, as many other processes could reduce RUE_{MAX} other than temperature in the dataset, such as variation in water and nutritional status in field-grown plants even under well-managed conditions. The dataset used to assess the change in RUE_{MAX} with air temperature included the dataset used in the varietal experiment (averaged per variety and trial, Table 1) as well as additional RUE_{MAX} values published in the literature (Araújo, 2016; Barbosa, 2017; De Silva and De Costa, 2012; Donaldson, 2009; Donaldson et al., 2008; Muchow et al., 1997; Olivier et al., 2016; Park et al., 2005; Schwerz et al., 2018; Silva, 2009; Singels and Smit, 2002). To parameterize the fT_{RUE} response, a normalized RUE_{MAX} was defined as the measured RUE_{MAX} divided by the maximum predicted RUE_{MAX} obtained in the varietal effect analysis (i.e., 3.0 g DM MJ^{-1} SRAD).

Despite including published RUE data, the dataset did not include RUE_{MAX} response to very high (above 32°C) or very low (below 15°C) air temperatures and could not be used alone to parameterize RUE response to very low and high temperatures. Consequently, the change in leaf photosynthesis and canopy GPP to temperature was also explored through two additional datasets as a proxy for crop RUE (see Section 2.2). The change in A_{net} and GPP with air temperature was parameterized for each formalism using a 99% quantile regression (*nlrq* function from *quantreg R* package, Koenker, 2009). For formalisms including a minimum temperature, a lower boundary was defined for minimum temperature as 7°C in the regression, based on previous studies on canopy GPP or net ecosystem exchange responses to temperature (Colmanetti et al., 2024; Cuadra et al., 2012) as well as leaf photosynthesis response (Peixoto and Sage, 2017; Sage et al., 2013).

For high-temperature response, two strategies were defined for RUE response to air temperature: i) a Leaf-type response, where temperature parameters at high temperatures (T_{OPT2}, $T_{MAX,}$ and T_{REF}) were fixed to the same value obtained in the A_{net} response regression, and ii) a GPP-type response, in which the temperature parameters at high temperatures were fixed to the same value obtained in the GPP regression. Note, as the Mosicas formalism did not require minimum and maximum temperatures, no parameters were fixed for this formalism. The change in RUE_{MAX} with mean air temperature in each formalism was parameterized using a 90% quantile regression due to a lower number of observations ($n = 179$) compared to A_{net} ($n = 1{,}055$) or GPP ($n = 8{,}436$).

To compare formalisms and assess the quantile regression quality, we calculated the quantile loss (or pinball loss) index QLI as follows:

$$QLI = \frac{1}{n}\sum_{i=1}^{n}\begin{cases} \tau\ (y_i - \hat{y}_i)\ if(y_i \geq \hat{y}_i) \\ (1-\tau)\ (y_i - \hat{y}_i)\ if(y_i < \hat{y}_i) \end{cases} \tag{15}$$

Where y_i is the observation, $\hat{y}_i$ is the corresponding predicted quantile, τ is the quantile level (e.g., 0.9), and n is the number of observations. A lower QLI indicated a better quantile fit (note that only comparison at the same quantile level is appropriate).

The default RUE parameterization for the different formalisms referred to the parameter values obtained from the literature (Jones et al., 2021 for ApsimCanegro; Christina et al., 2021 for Mosicas; Wang et al., 2018 with maize parameters for Wang-Engel; Johnson et al., 2010 with C_4 species parameters and $T_{OPT} = 33$°C for Johnson) and QLI was calculated for this default parameterization.

2.7. Crop model sensitivity to RUE-T formalism and parameterization

The influence of model formalism and parameterization on RUE_A and ADM simulations was explored in different locations under current and future climates. To this aim, we adapted the MOSICAS crop model v1.1.0 (Christina, 2025a), which was written in *R* in open-access (https://gitlab.cirad.fr/mathias.christina/mosicas), and thus the RUE – temperature response equation was easily changed. MOSICAS, a deterministic thermoradiative type model that accounts for water stress, consists of daily growth and carbon balance modules linked to a water balance module. The canopy is represented by LAI following a "big-leaf" approach, whereas the intercepted radiation is calculated based on the extinction coefficient approach. The model converts the daily intercepted radiation into daily gain in total dry mass, considering temperature-reducing factors, water stress, and maintenance respiration. To use the aboveground RUE measured in this study, we modified the model to express RUE based on SRAD. Note that the MOSICAS model uses the air temperature above the canopy in the RUE temperature response curve, so the input temperature from the weather station is directly used in the calculation.

For each variety (Table 1, calibration and sensitivity analysis dataset) and depending on available observations, we first calibrated the model on the dynamics of LAI, fraction of intercepted radiation (*fi*RAD), or cumulated intercepted radiation (*i*RADc). Details on calibrated parameters can be found in Supplementary Material Table S1. The RUE_{MAX} value was assumed constant across varieties and fixed to the same higher value as the one used to normalize RUE_{MAX} (3.0 g DM MJ^{-1} SRAD, see Section 2.6). Parameter optimizations were performed using the *RGenoud* optimization code provided with the MOSICAS model (see *gitlab* repository). Then, we changed the RUE temperature response equations using the new parameter values obtained during the procedure described in section 2.4. In addition, the sensitivity of each variety to water stress was calibrated to simulate ADM observations accurately. Simulation's accuracy was assessed by comparing observations (calculated in Section 2.5) and predictions based on the coefficient of determination (R^2), relative RMSE (rRMSE) and Willmott's index of agreement (d):

$$rRMSE = \frac{\sqrt{\frac{1}{n}\sum_{i=1}^{n}(S_i - O_i)^2}}{\overline{O}} \tag{16}$$

$$d = 1 - \frac{\sum_{i=1}^{n}(S_i - O_i)^2}{\sum_{i=1}^{n}\left(|S_i - \overline{O}| + |O_i - \overline{O}|\right)^2} \tag{17}$$

Where S_i and O_i are the simulated and observed values, $\overline{O}$ the mean observed values, respectively, and n the number of observations.

We assessed the long-term sensitivity of the crop model to the choice of formalism in three sites on Reunion Island with contrasting temperature patterns. We chose Reunion Island as a study case due to its high climate variability, with sugarcane ranging from sea level to 1,000 m a.s.l. (Christina et al., 2021). Climate change scenarios were available at a high spatial resolution (3×3 km; Leroux et al., 2021) for Reunion Island. The projections were produced as part of the BRIO project (Building Resilience in the Indian Ocean) by coupling the large-resolution scale CNRM-ESM2-1 model (from CMIP6) and the high-resolution scale ALADIN model to better represent climate projections in the main Indian ocean territories, including Reunion Island (Leroux et al., 2021). In this study, we used climate change data from the RCP 8.5 scenario to illustrate the sensitivity to high change in temperatures over time. Based on a previous climate change study on sugarcane yield (Christina et al., 2024b), we selected three sites with contrasting average annual temperatures (12.7, 22.1, and 25.1°C, average over the 2016-2025 period) but similar average daily global radiation (8.6, 9.4, and 8.7 MJ m^{-2} d^{-1}). These sites were located (latitude/longitude) at -20.93/55.66, -21.11/55.75, and -21.14/55.72 at 20, 135, and 730 m a.s.l. Simulations were performed following the method applied by Christina et al. (2024b) in these areas using the R579 variety. Potential ADM under non-limiting water conditions was simulated to isolate the projected ADM's response to the temperature increase.

At each site, and for each model formalism and parameterization, the difference in ADM between future years and a baseline was calculated, using the period 2016-2025 as the average reference baseline. Then, the simulated yearly increase in ADM was calculated as the slope between the difference in ADM and the year. To assess model sensitivity to the formalisms and parameterizations, we calculated the coefficient of variation (CV) of the yearly increase in ADM among formalisms or parameterizations. In addition, the relative contributions of model formalism and model parameterization to uncertainties were quantified by investigating the response of the simulated average yearly increase in ADM to the combination of the different model formalisms and parameterization based on a linear analysis of variance (Tao et al., 2018). The share of variance by model formalism, parameterization, and interaction was calculated based on their respective sum of squares.

3. Results

3.1. RUE response to variety and crop cycle

The maximum and apparent RUE showed high variability depending

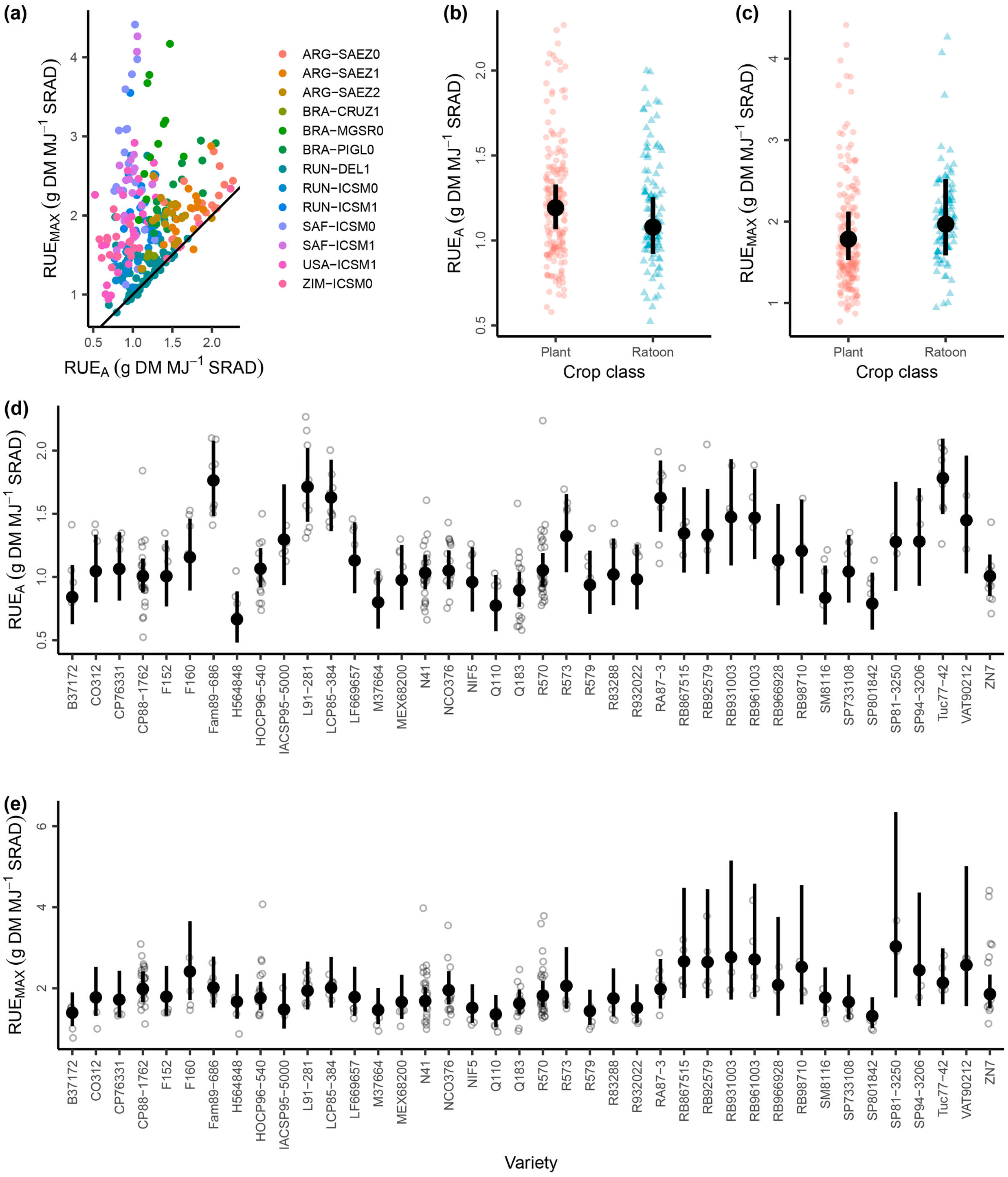

Fig. 1. Apparent ($\mathrm{RUE_A}$) and maximum ($\mathrm{RUE_{MAX}}$) radiation use efficiency (g DM MJ^{-1} SRAD) depending on trials in the varietal experiment dataset (a), crop class (plant or ratoon crop, b, c), and variety (d, e). Black points and bars represent the predicted means and confidence interval by the mixed model. Small transparent points indicate the observed values.

on countries, sites and varieties with RUE_A values ranging from 0.5 to 2.5 g DM MJ^{-1} SRAD and RUE_{MAX} ranging from 1.0 to 4.5 g DM MJ^{-1} SRAD (Fig. 1a). In our varietal experiment dataset, there was no interaction between variety and trial for RUE_A ($F_{21,141} = 1.06$; $p = 0.398$) or RUE_{MAX} ($F_{21,141} = 0.88$; $p = 0.613$). Similarly, neither RUE_A ($F_{10,141} = 0.78$; $p = 0.644$) nor RUE_{MAX} ($F_{10,141} = 1.26$; $p = 0.258$) presented interaction between crop class and variety. In the mixed model without interaction, the crop class did not influence RUE_A ($F_{1,11} = 0.14$; $p = 0.71$) or RUE_{MAX} ($F_{1,11} = 0.004$; $p = 0.95$, Fig. 1b,c). On the contrary, RUE_A ($F_{39,236} = 3.08$; $p < 0.0001$) and, to a lesser extent, RUE_{MAX} ($F_{39,236} = 1.54$; $p = 0.027$) differed between varieties.

Considering RUE_A, and crossed confidence intervals, a high number of significant differences were noticed among varieties, with mean predicted values ranging from 0.66 to 1.78 g DM MJ^{-1} SRAD (Fig. 1d). The highest RUE_A values were observed in varieties from Argentina (e.g., Fam, L91, RA or Tuc varieties) and Brazil (RB varieties). The change

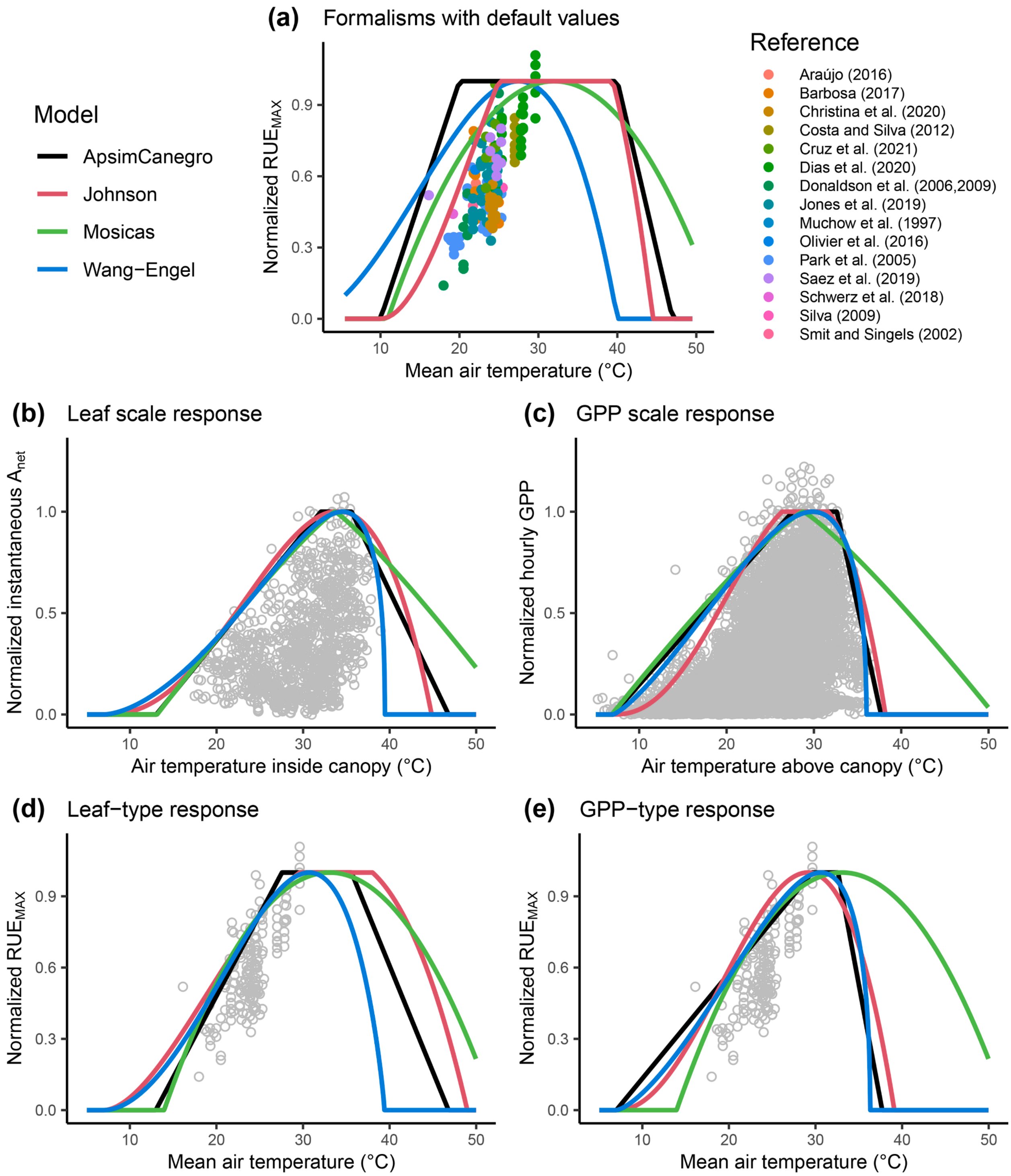

Fig. 2. Change in normalized maximum radiation use efficiency (RUE_{MAX}) with mean air temperature depending on formalism (ApsimCanegro, Johnson, Mosicas, and Wang-Engel) based on default parameters values (a) and quantile regression using a Leaf-type (d) or GPP-type response (e) for very high and very low temperatures. Leaf-type and GPP-type response parameters for very low and high temperatures were obtained from the change in normalized net leaf photosynthesis (A_{net}, b) or normalized gross primary productivity (GPP, c) with temperature.

in RUE_{MAX} among varieties was much lower compared to RUE_A. The mean RUE_{MAX} predicted values ranged from 1.32 to 3.04 g DM MJ^{-1} SRAD (Fig. 1e). Nonetheless, considering pairwise regressions, only two varieties differed among themselves in the RUE_{MAX} pairwise comparison at 5%, the SP80-1842 and F160 varieties ($p = 0.0491$). All others showed no significant differences in the pairwise comparisons.

3.2. Change in RUE with temperature

Based on the current default RUE formalism parameterizations (default temperature response parameter values), ApsimCanegro and Mosicas formalisms did not allow an appropriate envelope curve of normalized RUE_{MAX} response to mean air temperature with high quantile loss index (QLI, Fig. 2a, Table 2). ApsimCanegro and Mosicas overestimated RUE_{MAX} for temperatures ranging from 10 to 20°C (Fig. 2a). Considering the net photosynthesis (A_{net}) response at leaf level or GPP response to air temperature, all formalisms were able to accurately represent the observed values range with low 99% QLI ranging from 0.0055 to 0.0057 for A_{net} and 0.0061 to 0.0065 for GPP (Fig. 2b,c Table 2). Based on a visual assessment, the Johnson formalism represented a slightly lower increase in GPP for temperatures ranging from 10 to 20°C compared to other formalisms. Based on A_{net} and GPP regressions, we have fixed the base (T_B) and high temperature (T_X, T_{OPT2}, or T_{REF}) parameters in ApsimCanegro, Wang-Engel, and Johnson formalisms to propose two options based on the leaf photosynthesis or GPP dynamics at very high temperature (Fig. 2d,e, Table 3). In the normalized RUE_{MAX} – temperature response, whether based on A_{net} or GPP dynamics, all formalisms presented similar QLI, lower than the default parameterization (Table 2). Nonetheless, the Mosicas formalism failed to predict realistic base temperature in the GPP-type regression.

3.3. Change in RUE_A simulations depending on formalism and parameterization

Dynamics of LAI, fraction of intercepted radiation (*fi*RAD), and cumulative intercepted radiation were calibrated for each variety, allowing accurate prediction of *fi*RAD with rRMSE ranging from 0.08 to 0.16 depending on varieties (Fig. 3). Different parameters were calibrated, including a parameter controlling the daily rate of increase in LAI, the sensitivity of LAI to water stress, and the extinction coefficient (Table S1). A unique optimal RUE_{MAX} value was used for all varieties (3.0 g DM MJ^{-1} SRAD), based on the maximum predicted value per variety in the variance analysis (Fig. 1) and used to normalize the RUE – temperature response (Fig. 2). Nonetheless, to accurately simulate the aboveground dry mass dynamics, the sensitivity of RUE to water stress was calibrated for each variety and lowered for LCP85384 and NCo376 varieties (Fig. 3d, Table S1). With a unique RUE_{MAX} across varieties, simulated aboveground dry biomass (ADM) rRMSE ranged from 0.19 to 0.43 (considering all formalism and parametrization combined, Fig. 3d). However, the choice of formalism and parameterization influenced the accuracy of simulated RUE_A (Fig. 3e). Using the default parameterization, the ApsimCanegro, Mosicas, and Wang-Engel formalisms tended to overestimate RUE_A values. For all four formalisms, the GPP-type and Leaf-type parameterization showed a lower rRMSE on RUE_A compared to default parameterization (Fig. 3e). In addition, GPP-type and Leaf-type parameterization showed similar rRMSE in the Mosicas and Wan-Engel formalisms. Still, the GPP-type showed a slightly lower rRMSE (0.188) compared to Leaf-type parameterization (0.200) with ApsimCanegro, and it was the opposite for Johnson formalism.

Table 2
Quantile loss index (QLI) in the different RUEMAX – temperature response formalisms depending on the quantile regressions on net leaf photosynthesis (A_{net}), gross primary productivity (GPP), and radiation use efficiency (RUE). The quantiles used for regressions were 0.99, 0.99, and 0.9 for A_{net}, GPP, and RUE due to differences in the number of observations.

Formalism	Index	A_{net}	GPP	RUE (default)	RUE (Leaf-type)	RUE (GPP-type)
ApsimCanegro	QLI	0.00551	0.00613	0.0411	0.0248	0.0238
Mosicas	QLI	0.00570	0.00626	0.0280	0.0249	0.0249
Wang-Engel	QLI	0.00549	0.00628	0.0357	0.0242	0.0241
Johnson	QLI	0.00554	0.00646	0.0313	0.0240	0.0272

3.4. Biomass response to climate change and sensitivity to formalism and parameterization

The influence of model formalism choice and parameterization in model responses to future climate was explored using three selected sites with contrasting mean air temperatures in Reunion Island (Fig. 4), evaluated through projected potential ADM (without water stress). Regarding parameterization, the change from the default parameterization to the new Leaf-type or GPP-Type parameterization significantly affected the rate of increase in ADM over the years in most sites (Fig. 4a). With the ApsimCanegro, Mosicas, and Wang-Engel formalisms, the default parameterization projected a lower increase in ADM over the years compared to the new Leaf and GPP-Type parameterization. For example, with ApsimCanegro in the intermediate site ($T_{MEAN} = 22.1$°C), the average yearly increase in ADM was 0.09 t ha^{-1} yr^{-1} with the default parameterization. At the same time, it was 0.36 and 0.28 t ha^{-1} yr^{-1} with Leaf-type and GPP-type parameterizations (Fig. 4a). In addition, the difference was higher in the warmer site. With ApsimCanegro, the yearly increase in ADM was higher by 21, 200, and 307% with the GPP-type parameterization compared to the default one in the 18.7°C, 22.1°C, and 25.1°C sites, respectively (Fig. 4a). Similar behavior was observed for the Wang-Engel formalism and, to a lesser extent, the Mosicas formalism. With the Johnson formalism, lower differences between default and new parameterization were observed, except in the coldest site, where the increase in ADM was lower with the new parameterization than with the default one.

The sensitivity to the choice of formalism or the choice of model parameterization was evaluated with the coefficient of variation (CV) in the yearly increase in ADM due to change in formalism (Fig. 4b) or parameterization (Fig. 4c). The sensitivity to the choice of formalism was low with the new parameterization (whether Leaf-type or GPP-type) compared to the default parameterization (Fig. 4b). Small differences were observed between Leaf-type and GPP-type regarding sensitivity to the choice of formalism with similar CV between 4.2% and 11.6% depending on sites, except for the GPP-type sensitivity in the warmest site with a CV of 21.6% due to lower early increase with the Johnson formalism. Regarding sensitivity to model parameterization, the ApsimCanegro formalism was the most sensitive, with CV ranging from 24 to 58%, depending on the sites. By comparison, the Mosicas and Johnson formalism had CV ranging from 11% to 32% depending on sites. Nonetheless, differences in sensitivity to model parameterization mainly reflected the difference between the default parameterization and the newly proposed ones. Globally, except for the coldest site, model parameterization was the primary source of variability in the simulated increase in ADM (Fig. 4d). In the coldest site, model formalism had a strong influence due to discrepancies in RUE-temperature response at low temperatures among formalisms (Fig. 2).

4. Discussion

4.1. Contrasted response of RUE_A and RUE_{MAX} to variety

It is well known that sugarcane RUE declines with crop age, even when temperature, water, and nutrient status are not apparently limiting. This phenomenon was termed the “reduced growth phenomenon” (RGP) by Park et al. (2005) and later on further explored by Van Heerden et al. (2010). Our results, based on a network of field experimental trials, suggest that the RUE before its decline, equivalent to

Table 3

Parameter values in the different RUE_{MAX} – temperature response formalisms depending on the quantile regressions on net leaf photosynthesis (A_{net}), gross primary productivity (GPP), and radiation use efficiency (RUE).

Formalism	Parameter	A_{net}	GPP	RUE_{MAX} (default)	RUE_{MAX} (Leaf-type)	RUE_{MAX} (GPP-type)
ApsimCanegro	T_B	13.0	7.0	10	13.0*	7.0*
	T_{OPT1}	32.1	27.6	20	27.8	29.6
	T_{OPT2}	35.6	32.6	40	35.6*	32.6*
	T_X	46.8	37.7	47	46.8*	37.7*
Mosicas	T_{OPT}	33.7	28.7	32	33.1	33.1
	T_{DEC}	0.032	0.027	0.0025	0.0027	0.0027
	γ	1.14	1.17	2.0	2.0	2.0
Wang-Engel	T_B	7.0	7.0	0	7.0*	7.0*
	T_{OPT}	34.5	29.9	27.5	30.7	30.6
	T_X	39.4	36.0	40	40.6*	36.0*
	β	0.39	0.44	1	0.84	0.44
Johnson	T_B	7.0	7.0	10	7.0*	7.0*
	T_{OPT}	33.4	26.4	25	29.6	29.1
	T_{REF}	34.0	29.1	33	34.0*	29.1*
	c	2.50	2.45	2	1.80	2.21

* fixed values in the regression.

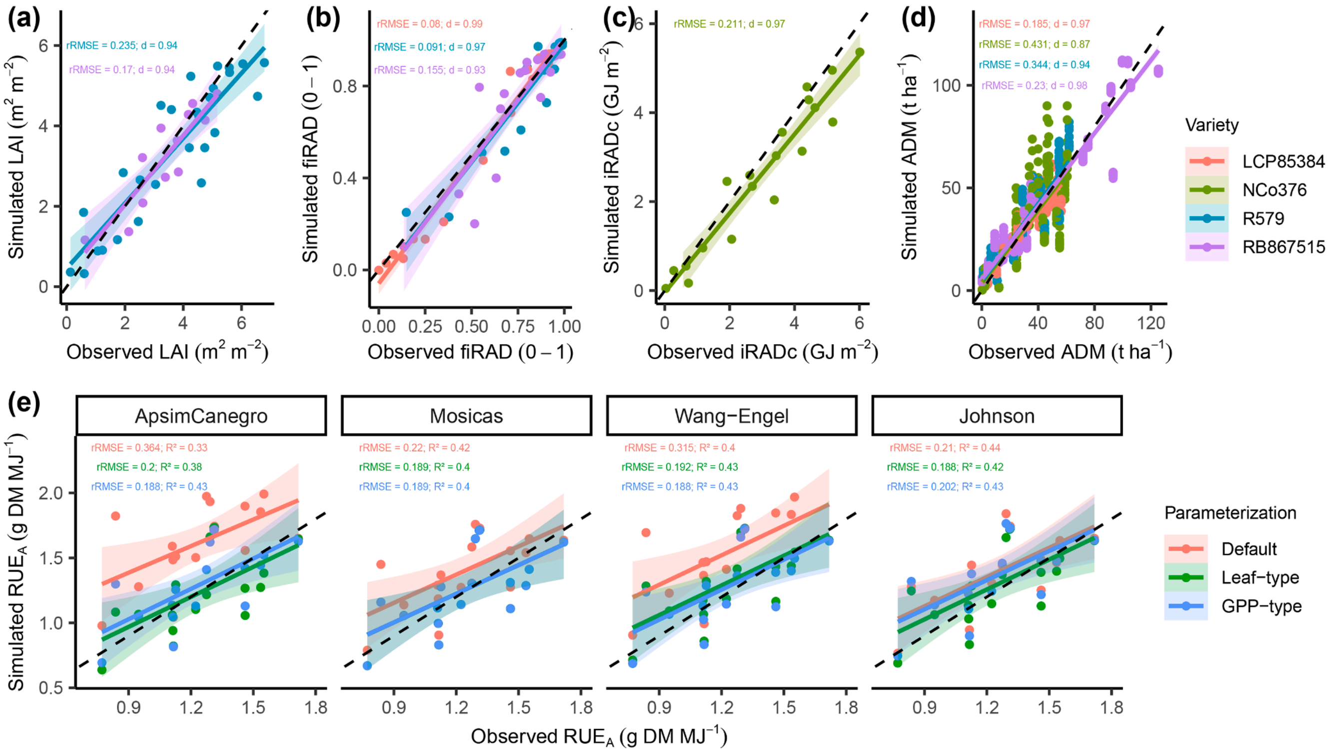

Fig. 3. Comparison between observed and simulated leaf area index (LAI, a), fraction of intercepted radiation (*fi*RAD, b), cumulated intercepted global radiation (*i*RADc, c), aboveground dry mass (ADM, d), and apparent radiation use efficiency (RUE_A, e) depending on the formalism used (ApsimCanegro, Mosicas, Wang-Engel, and Jonhson) and the parameterization (Default, Leaf-type, and GPP-type). The relative rRMSE, Willmott d index and R^2 were indicated per variety or formalism parameterization. The dashed lines represent the identical curve (1:1).

RUE_{MAX}, is minimally influenced by varieties, not only locally as observed in high-yielding sites in Brazil (Dias et al., 2021a), but also for 40 varieties across six producing countries in our study where only two varieties differed in RUE_{MAX} (SP80-1842 and F160). Sugarcane breeders worldwide have likely involuntarily selected high RUE_{MAX} genotypes while screening for high sucrose yields. Despite the expectation that RUE_{MAX} is closely linked to crop yield, existing evidence does not always support this, likely due to RGP (De Silva and De Costa, 2012; Donaldson et al., 2008; Jones et al., 2019). Our results highlight how RUE_A strongly differs among varieties. Thus, there are opportunities to understand the reasons better and exploit that for crop and agronomic intervention improvements to increase sugarcane production. As the RGP varies among sugarcane varieties (Dias et al., 2021a), growth slowdown sensitivity could explain differences in RUE_A despite similar RUE_{MAX} among varieties.

Lodging, declining leaf nitrogen (N) status with age, localized feedback inhibition of photosynthesis by high sugar content in leaf and/or high stalk sucrose content, and high respiration were hypothesized to be the causes of RGP (Park et al., 2005; Van Heerden et al., 2010) but none of them are conclusive to date and perhaps will not be because these phenomena might have concomitant causes operating together to decrease RUE over time. Lodging is definitely involved with RGP (Van Heerden et al., 2015), and recent studies showed how lodging sensitivity differed significantly among varieties according to aerial traits such as

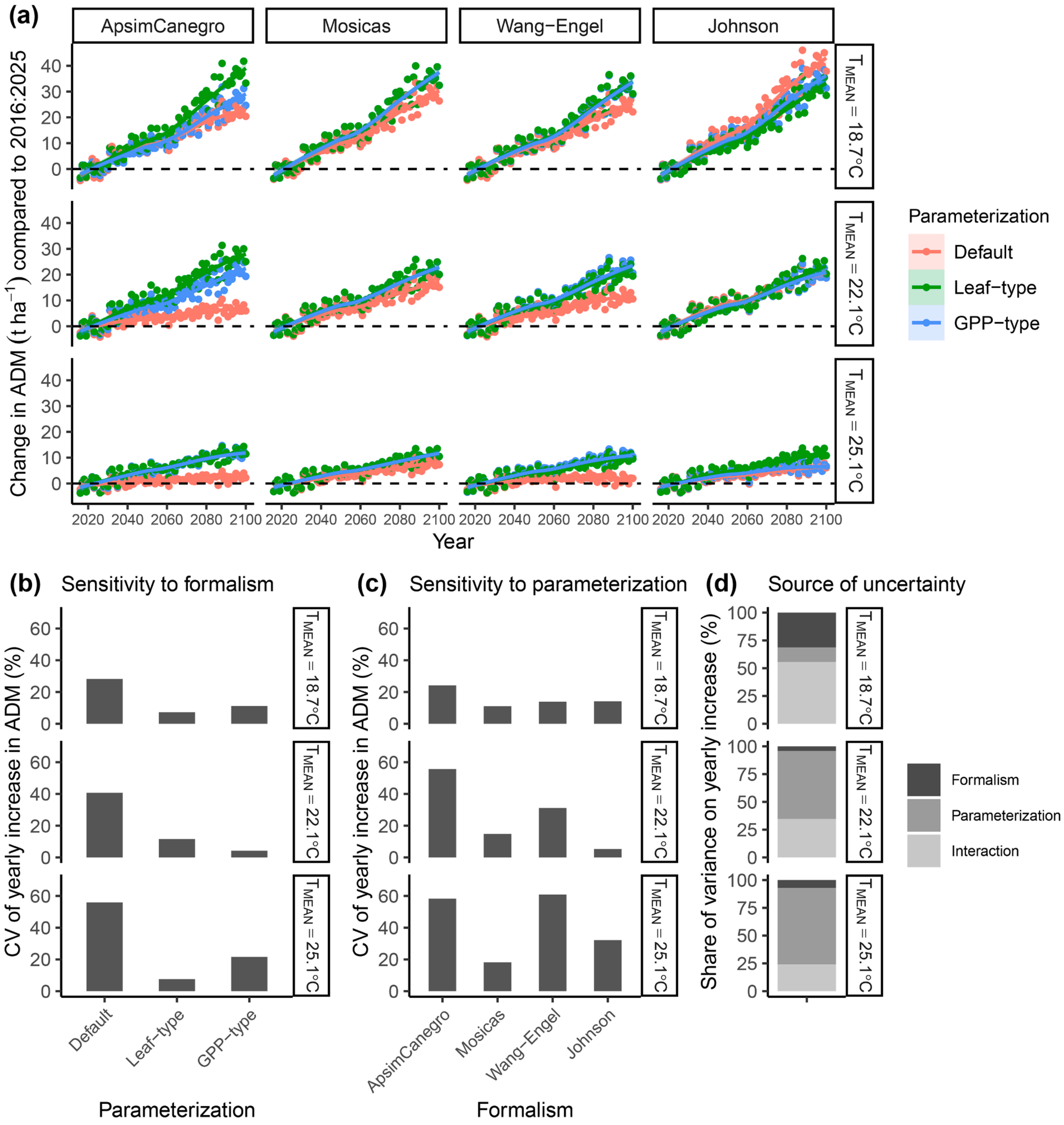

Fig. 4. Change in projected potential sugarcane aboveground dry mass (ADM without water stress, t ha^{-1}) from 2015 to 2100 compared to the average 2016 to 2025 period (a) and coefficient of variation (CV) of the average yearly increase in ADM among model formalisms depending on the parameterization (b) and among the parameterization depending on the formalism (c) in three selected sites of Reunion Island with contrasted mean air temperatures (T_{MEAN} = 18.7, 22.1, and 25.1 °C, respectively). (d) represent the share of variance in yearly increase in ADM depending on formalism choice, parameterization choice, and their interaction in the three selected sites. Sugarcane growth was projected under the RCP 8.5 climate change scenario.

tillering and plant height (Christina et al., 2024a) but also potentially to belowground traits (Jongrungklang et al., 2018). However, there were many situations where crops did not lodge, but RUE still declined towards harvest under unlimited growth conditions (Park et al., 2005; Van Heerden et al., 2010).

Differences in RGP among varieties may represent differences in sensitivity to environmental limitations when considering two key physiological processes - photosynthesis and respiration. Leaf N status is closely linked to photosynthesis, and previous studies suggest that as the sugarcane canopy begins to expand, the plant relies substantially on its internal N reserves (Sage et al., 2013). As a result, the available N is distributed across a larger leaf area, therefore declining A_{net} over time. However, evidence suggests that the N use efficiency varies among sugarcane genotypes (Robinson et al., 2007), which has a close relationship with photosynthesis, as most leaf N is invested in photosynthetic proteins such as Rubisco and PEPC (Sage et al., 2013). Alternatively, sugarcane photosynthesis can be inhibited by the accumulation of sugars in leaves (McCormick et al., 2009, 2008, 2006). When comparing the sensitivity of sugarcane to sucrose spraying – a way to inhibit photosynthesis, there was a significant variation between genotypes when considering Rubisco and PEPC abundances and activities (Ribeiro et al., 2017). In that regard, one could argue that other leaves within the sugarcane canopy could compensate for the inhibitory effect of carbohydrates on the photosynthesis of light-exposed leaves and prevent or even reduce a decline in overall canopy photosynthesis (Inman-Bamber et al., 2011), a topic that deserves more research. In fact, leaf photosynthesis in sugarcane is modulated more by the leaf carbohydrate dynamics than by leaf carbohydrate concentration (Ribeiro et al., 2017). When active sinks demand energy and carbon, leaf photosynthesis in sugarcane is stimulated (Ribeiro et al., 2017). In such a scenario, high-yielding genotypes might present stronger sinks and higher stimulation of photosynthesis compared to low-yielding genotypes. Taken together, these findings would suggest that the extension of down- or up-regulation of photosynthesis by sugars is genotype-dependent and could justify variations in RGP and RUE_A among sugarcane cultivars studied herein.

Regarding respiration and its components, the scientific literature is very limited when considering its importance in field-grown crops, such as sugarcane. For instance, both maintenance and growth respiration would increase due to high temperatures (Amthor, 2025), and literature suggests that increased biomass production for summer-started crops limits high sugarcane yields compared to winter-started ones under well-watered and managed conditions, possibly due to elevated maintenance respiration of larger crops (Van Heerden et al., 2010). As the RGP occurs during the final months of the crop cycle during stalk maturation in dry and cold winter seasons (Martins et al., 2025), one could argue that changes in respiration are not key in determining RGP in tropical conditions. However, the same is not true when considering photosynthesis, which is significantly reduced during winter and certainly reduces RUE_A in sugarcane plants (Martins et al., 2024, 2025). Although there is a significant variation in leaf respiration rate among sugarcane genotypes (Almeida et al., 2021; Ribeiro et al., 2017; Tejera et al., 2007), the impact of such a process on overall canopy respiration and then on RGP and RUE_A of sugarcane remains unknown. Understanding this response may be a crucial target for crop improvement (Amthor, 2025).

In addition to RGP sensitivity, other processes could explain the difference in RUE_{MAX} and RUE_A response to variety, such as the diffuse radiation effect (determining yield factor) or the water stress sensitivity (limiting factor). RUE is well known to increase with the fraction of diffuse radiation (Sinclair et al., 1992). Under diffuse radiation, light penetrates more evenly through the canopy, allowing not only the upper but also the lower and middle leaves to photosynthesize efficiently, which improves the overall canopy photosynthetic productivity. However, the extent to which different sugarcane canopy architectures among varieties may induce different responses to diffuse radiation still needs deeper investigation (Luo et al., 2014, 2013). Under water-limited conditions, there is evidence that some varieties are better than others regarding water deficit tolerance (Inman-Bamber and Smith, 2005; Venkataramana et al., 1986). Such differences in key periods of sugarcane growth could explain why RUE_A may differ among varieties while variability in RUE_{MAX} is low. Nonetheless, previous studies on an extensive range of varieties showed that the genotype × water stress interaction effect on stomatal conductance and yield were small compared to the genotype effect (Basnayake et al., 2015, 2012), suggesting that differences in water-stress resistance may not be a significant effect explaining the high difference in RUE_A. In our study, most of the experiments were irrigated, so no or limited water stress should have occurred, supporting the hypothesis that differences in RUE_A may be primarily linked to differences in growth slowdown sensitivity (Dias et al., 2021a).

Taken together, our findings highlight the value of RUE_A as an empirical framework to capture varietal differences, while also underscoring its limitations for mechanistic understanding. Future research should aim to disentangle how processes such as respiration, biomass partitioning, N and sucrose dynamics, under contrasting temperature regimes and crop age contribute to RUE_A variation. Strengthening these physiological links would improve their predictive capacity and usefulness in supporting breeding and climate adaptation strategies. In addition to the phenomena mentioned, elite genotypes have different strategies to achieve high yields, e.g., differences in water and N use efficiency (Acreche, 2017), and even differences in the number of sinks and early source-sink dynamics (Saez et al., 2019). Although these varietal strategies do not directly explain the variability in RUE_A and RUE_{MAX}, it would be important to consider them as physiological traits indirectly selected by breeders. Moreover, whether through models or designed trials, it would be feasible to detect the timing and duration within the cycle during which genotypes grow with RUE_{MAX} as a selection trait.

4.2. *Modeling the RUE response to temperature*

Improving the temperature response in crop models is essential to reduce the uncertainty of crop yield projections in the context of global warming (Maiorano et al., 2017; Wang et al., 2017). Our study underscores that the sensitivity of biomass production response to temperature is more influenced by the choice of cardinal temperatures (base, optimal, and maximum) than the choice of formalism itself. Furthermore, improvements in the parameterization significantly reduced the differences between formalisms. Therefore, the development of a better strategy for parameterizing appropriate cardinal temperatures in sugarcane crop models takes precedence over improving the formalism’s structure.

One limitation of this study is that the RUE-temperature responses were partly derived from literature datasets, which originated from experiments conducted under diverse environmental and management conditions. As a result, differences in measurement protocols and site-specific factors may have introduced additional variability into the analysis. Despite this limitation, the environmental variability experienced in the dataset is its greatest strength, and it would be very costly to consider a multi-environment trial to parameterize the models. In this context, the use of envelope curves to describe the RUE-temperature response minimize the influence of study-specific biases, as this approach assesses the upper boundary of physiological response. Future research based on multi-location trials explicitly designed to investigate the interaction between temperature and RUE would provide more mechanistic insights and reduce uncertainty in parameterization.

Based on our study, we recommend that crop models using daily RUE_O as a parameter apply a base temperature of 7°C and an optimal temperature ranging from 30 to 33°C, depending on formalisms, should be encouraged. This base temperature is lower than the ones historically adopted to represent photosynthesis in the widely used sugarcane crop models (T_B = 9°C, APSIM, Keating et al., 1999; T_B = 10°C, DSSAT-Canegro, Jones and Singels, 2018), but it is consistent with carbon exchange measurements at the canopy (Colmanetti et al., 2024; Cuadra et al., 2012) and leaf-scale photosynthesis (Peixoto and Sage, 2017; Sage et al., 2013). Nevertheless, estimating the maximum mean daily temperature based on RUE_{MAX} is difficult considering the usual sugarcane-cultivated regions since average temperature above 35°C is not observed in such areas. Therefore, obtaining the uppermost RUE_{MAX} temperature response based on biomass accumulation will require experiments in controlled environments or specific experiments under very warm regions.

With the currently available datasets, we recommend using GPP-type maximum temperatures between 36 and 38°C for models based on air temperature above the canopy (e.g., DSSAT-Canegro, APSIM-Sugar, and MOSICAS) and using Leaf-type maximum temperatures between 41 and 47°C for models based on the air temperature inside the canopy (e.g., STICS, Kebalo et al., 2025) depending on formalism. Nonetheless, for models that use a daily time step, our study suggests that the maximum temperature adjustments are less sensitive since those conditions are not common over regions where sugarcane is cultivated (neither nowadays nor in the future). However, it should be important for models using photosynthesis at an hourly scale (e.g., JULES, Vianna et al., 2022). Even if our study highlights a low sensitivity to the choice of RUE-temperature formalism, we recommend Wang-Engel as a more appropriate formalism for future studies, as i) the parameters have clearer meanings compared to Johnson formalism, ii) the ApsimCanegro formalism was found to be highly sensitive to the cardinal temperature values compared to other formalisms, and iii) Mosicas does not allow a base temperature to be specified.

Whether the RUE_O response to temperature may differ among varieties remains unsolved in our analysis. The absence of interaction between variety and the trial on RUE_{MAX} in our study suggests that varieties should respond similarly to temperature (as suggested by Parent and Tardieu, 2012, in various crops). Previous studies on an international dataset also showed low interaction between genotype and environments with stable RUE_O in four countries (Jones et al., 2019). Nonetheless, previous studies at the leaf scale suggest that some sugarcane varieties or species may differ in their photosynthetic rate response to chilling (Du et al., 1999) or heat stress (Kohila and Gomathi, 2018; Liu et al., 2020; Peixoto and Sage, 2017). Currently, we recommend fixing the cardinal temperature parameters for the sugarcane species, regardless of varieties and across environments. More detailed datasets may reveal that RUE_{MAX} response to temperature significantly differs among varieties.

As highlighted by our study, the estimation of cardinal temperatures (base, optimal, and maximum) for RUE has substantial consequences for application in climate change studies, with potential underestimation of the increase in ADM in previous studies using the two most used models, APSIM-Sugar (e.g., Dias et al., 2021b) and DSSAT-Canegro (e.g., Marin et al., 2013; Singels et al., 2014). While we are confident that our new parameterization should reduce the uncertainty of ADM estimates under projected changing climates, the current formalisms in crop models still contain an inherent bias by not considering the daily temperature range (minimum at night and maximum during the day). High temperatures at hourly time scales are strongly correlated with high vapor pressure deficit (VPD) and could reduce photosynthesis at midday and potentially daily RUE despite non-stomatal control of water loss (Márquez et al., 2024). For example, a modeling approach using an hourly time scale model (JULES) simulated an abrupt negative impact on sugarcane yields when daytime temperatures above 35°C become more frequent in Brazil (Vianna et al., 2022). In addition, we cannot rule out the influence of low night temperatures in reducing sugarcane photosynthesis, as reported in other species (Santos et al., 2011). To overcome such limitations in current crop models, a first option would be to develop hourly time-scale routines into crop models, but it becomes potentially more difficult to use in climate change scenario assessments. A second option would be to use an empirical effect of the difference between day and night VPD on transpiration efficiency and RUE to account for the effect of extreme daily temperatures (as done in APSIM, Lobell et al., 2013). However, it may increase the level of empiricism in model parametrization. Most importantly, an appropriate compromise has to be found between biological reality and parsimony in crop models (Hammer et al., 2019; Yin et al., 2021).

4.3. Recommendation for calibration strategy in crop models and varietal-sensitivity improvements

Our results illustrate that the implications of parameterization differ across production environments. In hot regions, where mean annual temperatures approach or exceed 25°C (e.g., northern Brazil, northern Australia, India, Thailand), biomass predictions may become particularly sensitive to the parameterization of RUE cardinal temperatures. By contrast, in cooler regions (e.g., Argentina, South Africa, Louisiana in USA), the choice of formalism tends to have a stronger influence on model outcomes than the exact parameter values. These findings suggest that varietal-specific parameterization would be most beneficial when simulating sugarcane performance in high-temperature environments or when evaluating genotypes with contrasting sensitivities to RGP.

As discussed in the previous section, the first step in calibrating crop models is to standardize the cardinal temperatures for sugarcane across all environments and varieties. If the cardinal temperatures or formalisms are modified from previous model versions, it may necessitate reparametrizing RUE_O in crop models. This does not imply that earlier studies were incorrect, but rather that they may have used an inappropriate RUE_O (e.g., very high RUE in Marin et al., 2011), or changed other parameter values (e.g., distinct extinction coefficient among sites, Dias et al., 2021a, 2019), to compensate for underestimating the effect of temperature.

This study used an RUE_O value of 3.0 g DM MJ^{-1} SRAD using ADM and *i*RAD. It was derived from trials conducted under optimal temperature and irrigation conditions in high-yielding environments in Brazil. This value is higher than the ones used in previous studies modeling sugarcane growth in South Africa, Zimbabwe, USA, Australia, or La Reunion, with RUE_O ranging from 1.3 to 2.1 g DM MJ^{-1} SRAD depending on crop models and varieties (Jones et al., 2021; Thorburn et al., 2010), which were conducted under lower temperature conditions. Nevertheless, our value is lower than the one used in modeling studies in Brazil with Canegro in DSSAT v4.5 (Singels et al., 2010), with RUE_O values around 4.6 g DM MJ^{-1} SRAD (Dias and Sentelhas, 2017; Marin et al., 2015). Herein, the RUE_O chosen is directly linked to the dataset used and may be subjected to biases, such as measurement errors or the absence of data from even higher temperature conditions. This value can be used as a reference, but the choice of the RUE_O value must also consider the processes incorporated into carbon assimilation in crop models (Table 4). This includes factors such as the type of radiation used (RAD vs. PAR), whether the biomass considered includes above- and belowground components or only aboveground, and whether maintenance respiration is considered before (net RUE) or after (gross RUE) C assimilation.

As an initial approach, we recommend fixing the RUE_O across all environments. However, while most models account for water stress, other processes influencing carbon assimilation are not always included

Table 4
Processes included in the RUE_O concept and daily RUE calculations in four crop models, and possibility to perform a varietal calibration on these processes.

		DSSAT-Canegro	APSIM	MOSICAS	STICS
Processes included in RUE_O	Biomass	whole	ADM	whole	ADM +perennial reserve
	Radiation	PAR	RAD	PAR	PAR
	Respiration	gross RUE	net RUE	gross RUE	net RUE
Processes accounted for in daily RUE calculation	Water stress	yes	yes	yes	yes
	Nitrogen stress	no	yes	no	yes
	Diffuse radiation effect	no	no	yes	no
	Change in root-to-shoot	yes	yes	yes	yes
	Lodging	yes	yes[1]	no	no
	RGP	no	yes[1]	no	no
Possibility to perform a varietal calibration	Water stress sensitivity	yes	yes	yes	yes
	Nitrogen stress sensitivity	no	yes	no	yes
	Diffuse radiation effect	no	no	yes	no
	Change in root-to-shoot	no	yes	yes	no
	Lodging	yes	yes[1]	no	no
	RGP	no	yes[1]	no	no

*RGP: reduce growth phenomenon; RAD: global radiation; PAR: photosynthetic active radiation; ADM: aboveground dry mass

[1] See section ‘2.2.3. Reduced growth phenomenon (RGP)’ in Dias et al. (2019) for further details.

(Table 4). The processes not necessarily included in the models are diverse: N stress, lodging and other RGP processes in high-yield environments, unpredictable variations in the root-to-shoot ratio (which is highly influenced by environmental factors, as highlighted by Chevalier et al., 2025), and, for example, the effects of diffuse radiation. When the crop models do not consider these processes, it may be necessary to calibrate the RUE_O for a homogeneous environment (in terms of soil and climate). Nonetheless, modelers should remain aware that this calibration might inadvertently compensate for other environmental factors the model cannot adequately represent.

Regarding varietal effects, our results suggest that RUE_O should be standardized across varieties. Therefore, varietal calibration should focus on other processes that influence the daily RUE calculation in crop models, as mentioned in the discussion on variety in section 4.1. Many processes that vary among varieties are not currently accounted for in crop models or are accounted for but not easily calibrated per variety (Table 4). In such cases, a varietal calibration of RUE_O may be necessary with the same limits as previously mentioned. Still, to effectively use these models as tools for evaluating varieties and potential adaptations to climate change, it is essential to incorporate these processes in future crop model development, especially for high-yielding varieties. For these high-yielding varieties, two key processes warrant further investigation: i) integrating RGP mechanisms into crop models more mechanistically, as suggested by Van Heerden et al. (2015) in Canegro structure, and ii) assessing how respiration is incorporated into crop models, given its critical role and sensitivity to varying temperature.

5. Conclusion

This study provides critical insights into sugarcane RUE, showing that RUE_{MAX} is stable across elite varieties and is highly temperature-dependent, while RUE_A varies significantly for these factors. Therefore, in crop modeling, RUE_{MAX} should be assumed constant across genotypes and environments. Based on an international dataset, the analysis emphasizes the importance of accurately parameterizing crop model formalisms and cardinal temperatures (optimal: 30–33°C) to improve projections of sugarcane yield under climate change. Additionally, it offers a reference for calibrating RUE temperature response formalisms in major crop models and provides guidelines for model calibration. While RUE_{MAX} remains consistent, the sensitivity of RUE_A to environmental factors highlights the need for refining crop models to capture better varietal responses to factors related to RGP (i.e., lodging, the decline in N use efficiency with age, and respiration of large crops). Incorporating these mechanisms will enable crop models to more accurately simulate sugarcane productivity dynamics, supporting climate impact assessments and breeding programs for high-yield, climate-resilient varieties.

Data availability

Experimental datasets used in the analysis included open and restricted data. Details on data availability were given in Supplementary Material. *R* scripts codes used to perform analyses are available in open-source on Zenodo (Christina, 2025b).

CRediT authorship contribution statement

Mathias Christina: Writing – original draft, Visualization, Software, Project administration, Methodology, Formal analysis, Data curation, Conceptualization. **David Clark:** Writing – review & editing, Project administration, Methodology, Data curation. **Fabio Ricardo Marin:** Writing – review & editing, Project administration, Methodology, Data curation. **Rafael Vasconcelos Ribeiro:** Writing – review & editing, Investigation, Data curation. **Julio Victor Saez:** Writing – review & editing, Investigation, Data curation. **Tendai Polite Chibarabada:** Writing – review & editing, Investigation, Data curation. **Murilo dos Santos Vianna:** Writing – review & editing, Investigation, Data curation. **Matthew R. Jones:** Writing – original draft, Methodology. **Santiago Vianna Cuadra:** Writing – review & editing, Investigation, Data curation. **Osvaldo Machado Rodrigues Cabral:** Writing – review & editing, Investigation, Data curation. **Martin Moises Acreche:** Writing – review & editing, Investigation. **Henrique Boriolo Dias:** Writing – original draft, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2025.110854.

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