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ABSTRACT

Air temperature is one of the most critical climatic factors controlling rice growth, development, and production in current and future climatic scenarii predicting increasingly frequent situations of extreme and/or fluctuating temperatures. With its large spectrum of geographical origins and cropping areas, one can credit tropical japonica rice subspecies of a probable genetic diversity of its response to air temperature, which is of major interest for the breeding of better adapted rice varieties. A panel of 195 rice accessions (175 *japonica* plus 20 reference cultivars) was studied in controlled environment to estimate cardinal (base, optimum, and maximum) temperatures based on the monitoring of the elongation rate (*LERmax*) of the sixth leaf on the main stem in response to six fixed thermal treatments ranging from 16 to 35 °C. A dedicated statistical framework was elaborated for estimating *LERmax*, cardinal temperature and related uncertainties. Developed statistical framework enhanced the precision of cardinal temperatures estimated compared to previously reported methods, especially for base temperature. Maximum temperature was trickier to estimate and will require further studies. A significant genotypic variability for base and optimal temperature was pointed out, suggesting tropical *japonica* subspecies represents a relevant genetic pool to breed for rice genotypes adapted to various thermal situations. These results also suggested that using genotype-dependent cardinal temperature values should enhance the way crop growth models account for genotype × environment interactions hence their predictive value in current and future climatic conditions.

Introduction

Climate change and particularly increasingly fluctuating and extreme temperatures strongly impact on crop growth and development and ultimately crop production particularly for rice (Challinor et al., 2007; Hatfield & Prueger, 2015). Nevertheless, the response of plant growth and development to temperature is complex and still partially understood. First, growth (organ expansion, C assimilation, and respiration) and development (organ initiation) do not correspond to the same physiological processes, nevertheless they are commonly considered with identical responses to air temperature (Zhang & Tao, 2013) and there are physiological evidences for so (Parent et al., 2010). Crop growth and development response to temperature is classically modeled through the duration of phenological phases measured in thermal time. This is consistent with the simple hypothesis that growth and development rates are linear functions of air temperature above a base temperature. This simple approximation is only valid for a small range of temperatures; for wider ranges, more complex models have been published (Yan & Hunt, 1999, Zhang & Tao, 2013). For example, growth rate can be viewed as a linear function of the temperature between a base temperature (*Tbase*) and an optimum temperature (*Topt*), and then display a plateau and even further a descending line down to a 0 at maximum temperature *Tmax*. *Tbase*, *Topt,* and *Tmax* are called cardinal temperatures. This type of piecewise linear modeling can be made more complex but the higher the number of linear components, the higher the number of parameters, and the more difficult their estimation is. Parameter estimation is even hardened when the number of components is not known initially and varies from one case study to the other, e.g. when some varieties display a plateau while others do not. In addition, piecewise linear models can generate unrealistic curves with too abrupt changes compared to that observed.

Models with smoother curves such as the Beta distribution models, proposed by Yin et al. (1995) and Yan and Hunt (1999), provide a more realistic response curve and

require fewer parameters: the maximum growth rate over temperature, *Rmax,* and the cardinal temperatures *Tbase*, *Topt,* and *Tmax*. Schematically, below the base temperature (*Tbase,* or *Tmin* for Yan & Hunt, 1999), crop growth and development stop. Above this base temperature, the rate of growth and development increase with temperature up to an optimum at *Topt*, beyond which they decrease until a maximum temperature (*Tmax*) is reached and no further growth or development occur. Between *Tbase* (or *Tmin*) and *Tmax*, growth rate is supposed to have an asymmetric bell-shape evolution. By definition no growth can be observed below *Tbase* or over *Tmax*, so the estimation of *Tbase* and *Tmax* parameters must rely on extrapolations that may result in a lack of precision. Parent et al. (2010) proposed another paradigm to model plant growth and development response to temperature in analogy with the response observed for underlying enzymatic activity. However, the adjustment of this model requires data acquired under extreme temperatures rarely met in field conditions and hardly reproducible in non-dedicated growth chambers.

Usually, crop growth models use the same cardinal temperatures for all cultivars within a given species such as rice (Kumar et al., 2016) or other crops (Brisson et al., 1998; Wang et al., 2002). This is mainly due to the experimental difficulty to estimate these parameters, although several studies already demonstrated that these parameters are genotype dependent, in particular within the rice *indica* subspecies (Dingkuhn & Miézan, 1995 and Dingkuhn, Sow et al. 2015 on a larger indica panel). This should imply considerable errors in the way crop models simulate the genotype × environment interactions (GxE) underlying crop growth and production in response to thermal conditions. To our knowledge, such a study was not performed yet on tropical *japonica* rice. As this subspecies is originating from and cultivated in a large spectrum of environments from sea level to altitudes above 2000 m. asl, it should show some genetic variability in plant response to temperature, which is of major interest to breed for adaptation to climate change and extreme temperatures (Lv et al.,2016).

The present study aims at exploring the genetic variation of cardinal temperatures within the tropical *japonica* rice subspecies. The response of maximum leaf expansion rate (*LERmax*) to air temperature was chosen as an easy-to-measure trait to estimate cardinal temperatures. *LERmax* of the sixth leaf on the main stem was chosen, since during the vegetative phase and more precisely between the appearance of the fourth and the eighth leaf, rice developmental pattern is stable along time for a given genotype and environment (Katayama, 1951; Yoshida, 1981). Based on the measurement of sixth leaf elongation under six temperature modalities, a statistical framework was elaborated to (1) model *LERmax* response to temperature using

a model adapted from Yan and Hunt (1999) and (2) estimate cardinal temperatures and evaluate their variability within the rice *japonica* panel.

Once described the genetic material, experimental design and data, the modeling tools, calibration method, and results are presented and discussed with respect to the added value of characterizing the intraspecific variability of developmental parameters and its impact on the predictive value of crop models.

Materials and method

Experimental data

Genetic material

A panel composed of 175 tropical *japonica* rice accessions, augmented with 20 reference accessions belonging to other genetic groups: *indica*, aus and aromatic, was studied. This panel gathered both traditional and improved varieties originating from 32 different countries. Its description is available at (http://ricephenonetwork.irri. org/diversity-panels/orytage-diversity-panels).

Experimental design and plant measurements

The elongation of the sixth leaf was monitored on the 195 accessions in six thermal treatments applied in growth chambers. Two temporal replicates were performed in CIRAD facilities (Montpellier, France), one in 2010 and the other in 2011. Each year, for each temperature, each variety appeared once in a unique pot. Each year, an auxiliary chamber and two main chambers were used. The auxiliary chamber had an average air temperature of 27 °C during the day and 23 °C during the night, a 70% relative air humidity day and night and a 12-h photoperiod. Of the two main chambers, one was dedicated to the 16 °C target temperature and in the other, the 20, 23, 26, 30, and 35 °C target temperatures succeeded each other in a random order. In each main growth chamber, temperature was automatically regulated and a 12-h photoperiod was supplied with metal halid lamps (OSRAM HQI/TS 250 W) that provided a photosynthetically active radiation (PAR) of 600 µmol m^{-2} s^{-1} at canopy level. Temperature and relative humidity sensors (Type T Thermocouple, Copper/Constantan), three per chamber, were evenly distributed among the plants and their data recorded with a datalogger (CR1000 Campbell Scientific Ltd, 80 Hathern Road, Shepshed, Leicestershire LE12 9GX UK). For each replicate and for each target temperature and variety in a replicate, four seeds were selected and germinated in cleaned and dried Petri boxes. Seeds were placed on a filter paper and wetted with distilled water. They were incubated at 30 °C for two days. The two most homogenous and vigorous seedlings of each accession were selected and planted at two cm depth in a one-liter pot filled with a substrate
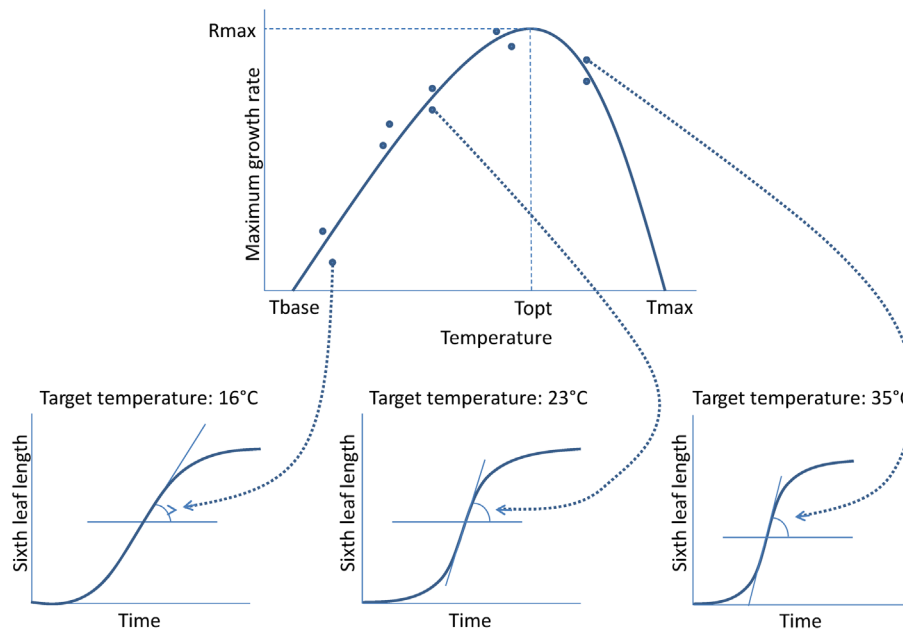
Figure 1. Hierarchical model of the leaf length as a function of the time and temperature. Bottom: the sixth leaf length is a function of time. Top: LERmax, the maximum derivative of this function is governed by the temperature following a second function with parameters Tbase, Topt, Tmax, and Rmax.

made of compost Nehaus-S and podzolane (5.7%) mixed with two grams of Plantacote fertilizer. Pots were positioned in the auxiliary growth chamber. Potted plants were grown under well-watered aerobic conditions all along the trial. At the two-leaf stage for a given accession, the most vigorous seedling was selected and the other was thinned. When the fifth leaf on the main stem appeared for a given accession, the corresponding pot was transferred into a main growth chamber in order to get acclimated to the target temperature before the sixth leaf appeared and its growth was monitored. The positions of the plants in the room were exchanged every day to minimize the effect of any possible heterogeneity in light intensity and temperature.

From the day of its appearance until it reached its final length, the sixth leaf length was daily measured approximately at the same time of the day, i.e. at around 10 h in the morning. Leaf length was measured from the ligule of the fifth leaf to the tip of the sixth leaf, using a vertically mounted ruler.

Statistical and modeling framework to estimate cardinal temperatures from leaf length measurements

Estimating LERmax and correcting for departures from each target temperature

At any given temperature, leaf length is supposed to follow a logistic function of time. The maximum derivative of this function, i.e. the maximum leaf expansion rate (*LERmax*), is in turn a function of temperature. Thus, the resulting model is hierarchical (Figure 1); it is non-linear, because the leaf growth is a non-linear function of the parameters. It is also mixed because the measurements are repeated on the same leaf and parameters are likely to fluctuate randomly from one plant to another according to individual and environmental fluctuations.

The first step of the hierarchical model analysis consisted in modeling the sixth leaf length for each rice plant as a function of time, at constant six target temperatures 16, 20, 23, 26, 30 and 35 °C. The model used was a logistic function

$$f(t) = K \frac{1}{1 + ae^{-rt}} \tag{1}$$

where t is the time and K, a and r real are positive parameters to estimate.

This logistic function has a point of symmetry I with coordinates $\left(x_I = \frac{ln(a)}{r}; y_I = \frac{K}{2}\right)$ (Figure 2). This point is also the inflexion point of the curve. f', the first derivative of f, models the leaf elongation rate (LER). *LERmax*, the maximum of f' is reached at point I and its value is $f'\left(\frac{ln(a)}{r}\right) = \frac{Kr}{4}$.

LERmax was estimated by nonlinear least squares using proc nlin of Sas/Stat version 9.3 (SAS Institute Inc., 2011). The standard error of *LERmax* was estimated with the Delta method (see for example Ver Hoef, 2012).

The second step consisted in evaluating the environmental effects on *LERmax* estimation by estimating the
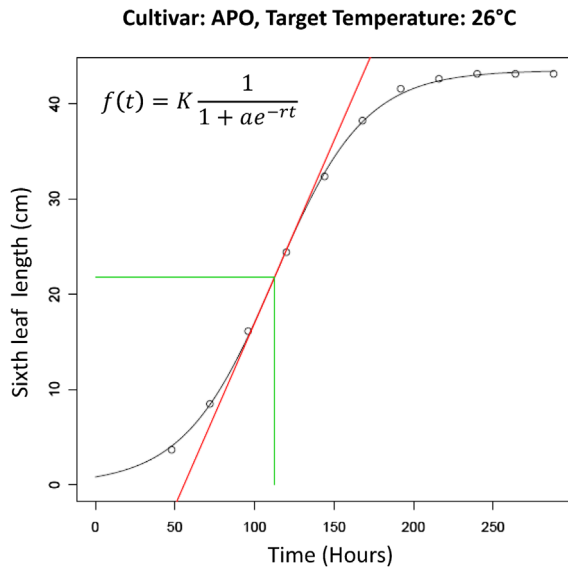
Cultivar: APO, Target Temperature: 26°C

Figure 2. Leaf length as a logistic function of the time.
Notes: The inflexion point is represented at the intersection of the vertical and the horizontal green segments. The slope of the tangent of the logistic function at its inflexion point (red line) is the maximum elongation rate (LERmax). Example of Apo accession at target temperature of 26 °C.

year effect and the lack of reproducibility variance. Out of the 196 cultivars tested, up to 14 were missing for a given year and temperature. Any difference in environmental conditions of the two different years that affects the mean of *LERmax* would then result in a bias in the *LERmax* mean for the cultivars observed only one year when compared to those observed the two years.

As the actual temperatures fluctuated around the target temperatures, of ±1.5 °C for 90% of the measurements, we fitted an analysis of covariance, with the variety as factor and the temperature as covariate (Equation (2)), despite *LERmax* being a non-linear function of the temperature. For this, the small variations of actual temperature around their targets were supposed to have an approximately linear effect on *LERmax*, by considering a first-order Taylor expansion around the actual mean temperature and neglecting the variations in slope among the varieties. After this adjustment for temperature fluctuations, a year effect was still significant and was retained for final model.

Adding these three effects of variety, actual temperature and year, a linear mixed model was fitted to *LERmax* for each target temperature k

$$LERmax_{ijk} = LERmax_{i0k} + b_k\left(T_{ijk} - T_{0k}\right) + c_{jk} + D_{ijk} + \varepsilon_{ijk}$$
(2)

where

- $LERmax_{ijk}$ is the maximum leaf expansion rate obtained at actual temperature T_{ijk} for variety i during year j with target temperature k;
- $LERmax_{i0k}$ is the expected maximum expansion rate at target temperature T_{0k} for variety i;

- b_k is the locally linear response of *LERmax* to temperature in the vicinity of T_{0k} (cm day^{-1} °C^{-1});
- c_{jk} is the mean effect of year j (2010 or 2011), with $\sum_j c_{jk} = 0$, for target temperature k;
- D_{ijk} is the random effect of the lack of reproducibility on variety i the year j with target temperature k $D_{ijk} \sim \mathcal{N}(0, \sigma^2_{Dk})$;
- ε_{ijk} is the error of estimation of *LERmax* from the length measurements, of variance $\sigma^2 \varepsilon_{ijk}$ (already estimated at step 1).

Using the mixed procedure of SAS/STAT software version 9.3, this model allowed us to estimate a mean year effect on *LERmax* for each temperature. The *LERmax* estimates were then adjusted for this year effect before proceeding to the next modeling step.

Modeling the response of LERmax to temperature

This third step of the statistical analysis consisted in modeling the effect of air temperature on *LERmax* and estimating cardinal temperatures using values previously estimated for each accession at six target temperatures and in each replicate separately. Beta-linear (Beta-L) model was devised as an alternative to Yan and Hunt's Beta model, from which it is derived. It can be defined as follows:

$$BetaL(Rmax, Tbase, Tmax, Topt, T)$$

$$= \begin{cases} Rmax\left(\dfrac{Tmax-T}{Tmax-Topt}\right)\left(\dfrac{T-Tmin}{Topt-Tmin}\right)^{\left(\frac{Topt-Tmin}{Tmax-Topt}\right)} & \text{, if } T \geq x_J \quad (3) \\ y_J \dfrac{T-Tbase}{x_J-Tbase} & \text{, if } Tbase \leq T \leq x_J \\ 0 & \text{, otherwise} \end{cases}$$

with $x_J = 2\,Topt - Tmax$

$$y_J = 2Rmax\left(\frac{2Topt - Tmax - Tmin}{Topt - Tmin}\right)^{\left(\frac{Topt-Tmin}{Tmax-Topt}\right)}$$

$$Tmin = \frac{2TbaseTopt - Tbase(2Topt - Tmax) - (2Topt - Tmax)^2}{Tbase - 4Topt + 3Tmax}$$

When the temperature is greater or equal to x_J defined above, the model coincides with Yan and Hunt's (1999) Beta model. When the temperature is lower than $x_{J'}$ the model is defined as the left half-tangent to the Beta model curve at the inflexion point J with coordinates (x_J, y_J). Then *Tbase* is defined as the intersection of this half-line with the x axis. For the sake of clarity, the above expression is voluntarily over-parameterized. Only four parameters *Rmax*, *Tbase*, *Topt* and *Tmax* are needed to entirely define the Beta-L model. Thereafter, $\theta_i = (Rmax_i, Tbase_i, Tmax_i, Topt_i)$ will refer to the vector of parameters related to the variety i.
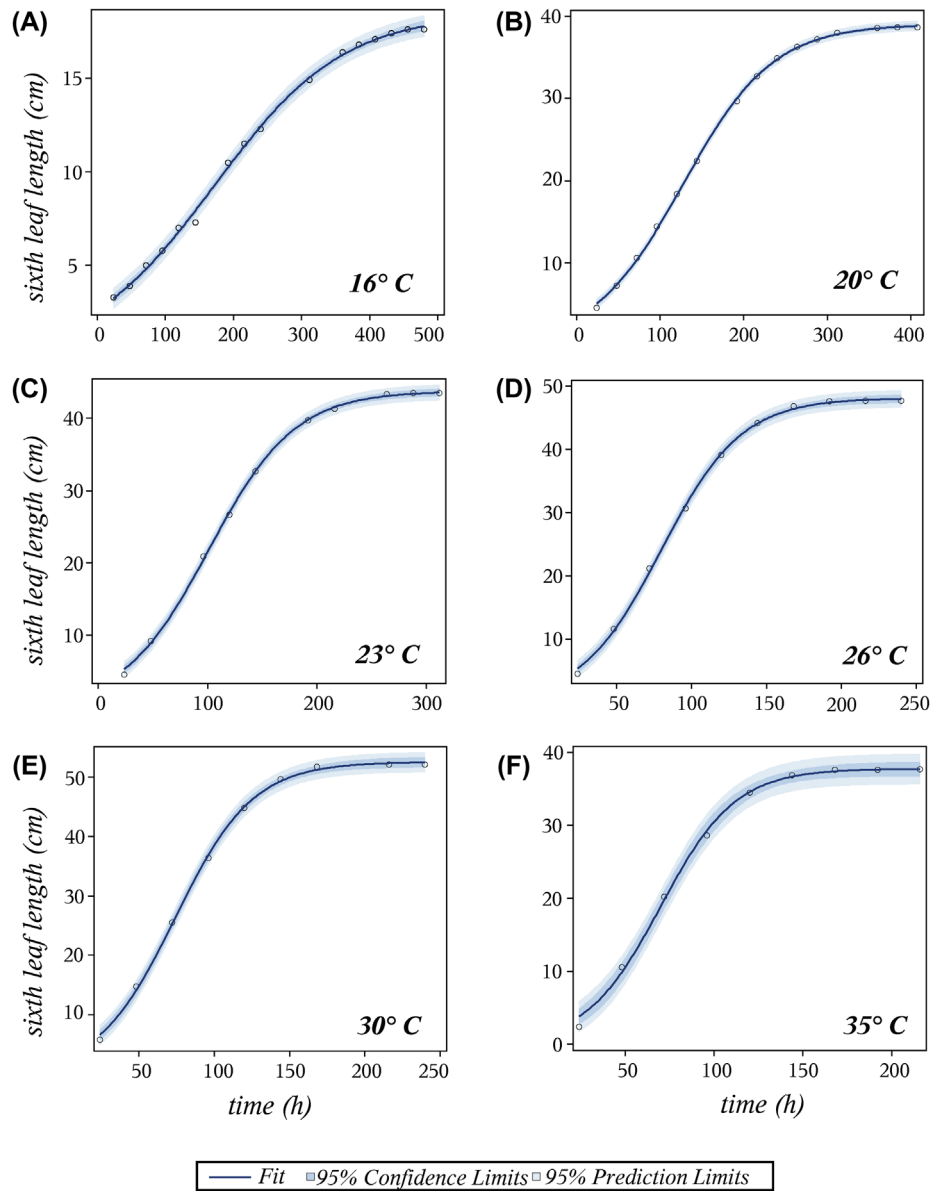
Figure 3. Observed (dot) and modeled (blue line) leaf length of Curinca variety, for one replication of the experiment, at each target temperature 16, 20, 23, 26, 30, and 35 °C (subplot a, b, c, d, e, and f, respectively).

In order to take into account the error propagated from leaf measurements to *LERmax* through its estimation and also a possible lack-of-repeatability of the experiment, a non-linear mixed model was used with two error components:

$$LERmax_{ijk} = BetaL\left(\theta_i, T_{ijk}\right) + D_{ijk} + \varepsilon_{ijk}$$

where

- *LERmax$_{ijk}$* is the maximum leaf expansion rate obtained at actual temperature T_{ijk}

for variety *i* during year (or replicate) *j* with target temperature *k*, adjusted for year effect using analysis of covariance (Equation (2));

- *BetaL(θ_i, T_{ijk})* is the expected maximum expansion rate with variety *i* at the actual temperature T_{ijk}, modeled as defined in Equation (3);
- D_{ijk} is the random effect of the lack of reproducibility on variety *i* the year *j* at target temperature *k*; $D_{ijk} \sim \mathcal{N}(0, \sigma^2_{Dk})$ (variance already estimated at step 2);
- ε_{ijk} is the error of estimation of *LERmax* from the length measurements, of variance $\sigma^2\varepsilon_{ijk}$ (already estimated at step 1).

From this, the parameters of the Beta-L model including *Tbase* could be estimated along with their standard errors. The same process was performed with the Beta model to obtain *Tmin*.

Table 1. Standard error of the lack of repeatability and mean standard error of estimation of maximum leaf expansion rate of leaf 6 on the main stem (LERmax).

	Target temperature (°C)					
	16	20	23	26	30	35
Mean of						
Standard error of lack of repeatability	0.014	0.028	0.040	0.040	0.049	0.057
Standard error of estimation from an individual curve	0.003	0.007	0.012	0.017	0.022	0.021
Global standard error	0.014	0.029	0.042	0.043	0.054	0.061
Global CV (%)	19.6	12.8	11.7	9.3	9.4	12.3
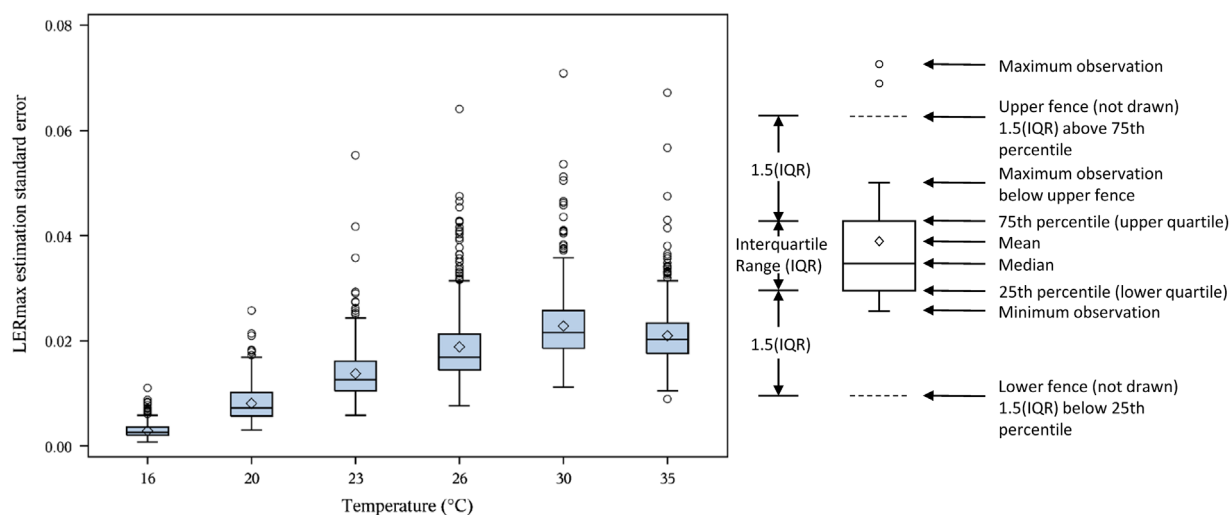
Figure 4. Boxplots of the frequency distributions of the standard errors of the LERmax estimators obtained at each target temperature.

Comparison of Beta-L and Beta models to estimate cardinal temperatures

The Vuong closeness test (Vuong, 1989) was used to evaluate which one of the two models, Beta or Beta-L, fits the best the *LERmax* evolution over temperature. Based on the Kullback-Leibler information criterion, it tests the null hypothesis that two models, nested, not nested or overlapping, is equally close to the data, against the alternative hypothesis that one of them is closer to the data than the other. Vuong's *Z*-statistic was calculated for each variety, resulting in a sample of 195 *Z*-values. Vuong's *Z*-statistic asymptotically follows a standard normal distribution. A large enough deviation towards negative or positive values indicates a better fit of one model or the other.

Test for significant variability of Tbase and Topt

An analysis of variance was conducted using proc mixed of SAS software to assess the genotypic variability of the *Tbase* and *Topt* estimates obtained using the previously described modeling framework.

Graphical representations and statistical analysis

All the graphics presented in the present article were made using either R 3.3.1 (R Development Core Team, 2016) or

SAS 9.3 statistical softwares while all the statistical results were obtained with SAS 9.3.

Results

Estimation of maximum leaf expansion rate LERmax

Leaf growth plotted against time of the day confirmed the assumed logistic shape of this relationship. Sample curves are shown for one replication in Figure 3(a)–(f) for variety *curinca* at temperatures 16, 20, 23, 26, 30, and 35 °C, respectively. As the frequency of length measurements was the same for all temperatures, more data were collected at lower temperatures, where leaf expansion took longer. As a result, the *LERmax* estimation was generally more precise at lower than at higher temperatures (Table 1 and Figure 4). For a given temperature, the number of measurements and their positions on the curve varied according to leaf expansion rate and the time the sixth leaf appeared (Figure 3). As a result, for a given temperature, *LERmax* estimation precision was not the same for all the varieties (Figure 4).

The standard deviation of the individual *LERmax* estimation error was smaller on average than that of the lack of repeatability (Table 1). However, as it varies from one pot to another (Figure 4), it can occasionally exceed the standard error of lack of repeatability.

Modeling the effect of temperature on LERmax using the Beta-L model

Comparison of Beta-L and Beta models to estimate cardinal temperatures

Vuong's Z-statistic was calculated for each variety, resulting in a sample of 195 Z-values. The Z-values' unimodal distribution fitted approximately the standard normal distribution, with a slight left shift. Its variance was slightly lower than 1 ($\sigma^2 = 0.98$), and its negative mean showed a non-significant leaning ($p = 0.0957$) towards the Beta-L model. Thus, no sign of heterogeneity of the response shapes could be detected, suggesting the same model can be used for all of them. Overall, the Beta-L model fits the data at least as well as the Beta model.

The median of the standard error for *Tbase* estimated using Beta-L model was 0.30 °C, and was never higher than 0.78 °C, whereas this median was 1.5 °C for the standard error of *Tmin* estimated using Beta model, and its third quartile was 2.4 °C (Figure 5(A)). The difference in precision of *Topt* was less pronounced (Figure 5(B)), still the Beta-L model provided a more precise estimation. Results for *Tmax* showed a strong imprecision for both models, due to the fact that this parameter was estimated by extrapolating the model curves. Also *Tmax* will not be further analyzed in this study. Because of its better precision in *Tbase* and *Topt* estimation, with an equivalent fit to data, the Beta-L model was preferred to the Beta model.

Genotypic variability of cardinal temperatures obtained with the Beta-L model

The distributions of *Tbase* and *Topt* estimated for each accession in the japonica panel are plotted in Figure 6(A) and (B) together with their standard error. Both *Tbase* and *Topt* showed a significant genotypic variability, confirmed by their significant variety effects ($p < 0.0001$) (results not

shown). *Tbase* varied between 12.8 °C (SE = 0.36) and 15.6 °C (SE = 0.55) and *Topt* between 28.2 °C (SE = 0.50) and 35.2 °C (SE = 1.89). *Tbase* was thus systematically higher than values commonly used in crop models that vary from 8 to 13 °C.

Discussion and conclusion

The present study explored the genetic variation of cardinal temperatures (base, optimal and maximal) within the *japonica* rice subspecies. The maximum expansion rate of the sixth leaf (*LERmax*) was chosen as the reference growth process and studied on 195 accessions. A statistical framework was elaborated to model *LERmax* response to temperature using a new model, called Beta-L model, adapted from the Beta model of Yan and Hunt (1999). This new model improved the estimation of cardinal temperatures at least in the case of rice. These key results are discussed below with respect to their implications and perspectives for rice crop modeling, phenotyping, and genetic studies.

Advantages and limits of methodological choices

In this study, the Beta-L model enabled to estimate more accurately the base temperature (*Tbase*) than the minimum temperature (*Tmin*) of the Beta model classically used in literature (e.g. Yin et al., 2003). The Beta model has a curved response to low temperatures, whereas linear, piecewise linear and our Beta-L models have a linear response to low temperatures. To our knowledge, no study previously compared the goodness of fit of curve vs. straight line fitting regarding this response to low temperatures, and the present study did not show a clear winner in that respect. This may be due to the technical difficulties in observing low plant growth rates while keeping them
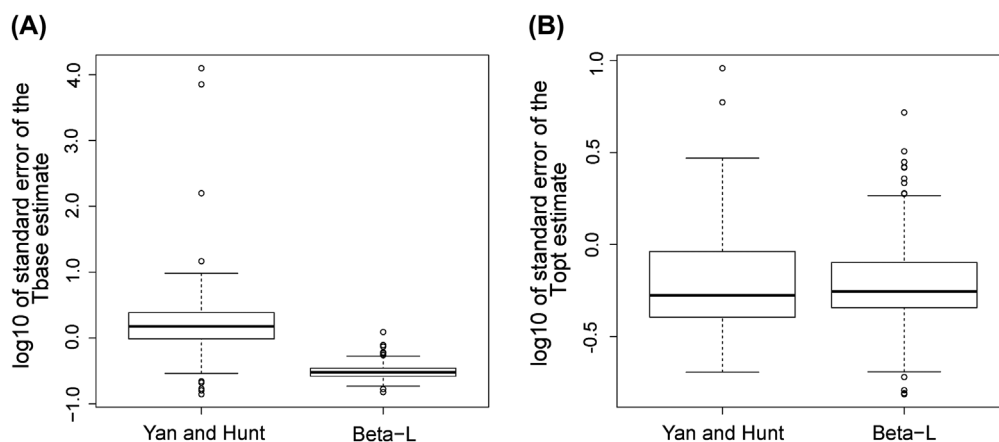

Figure 5. Boxplots for the standard errors of parameter estimations of the two models. (A) The Tbase parameter of the Beta–L model is more precisely estimated than the Tmin parameter of the Yan and Hunt's Beta model. (B) This is less pronounced for the Topt parameter.
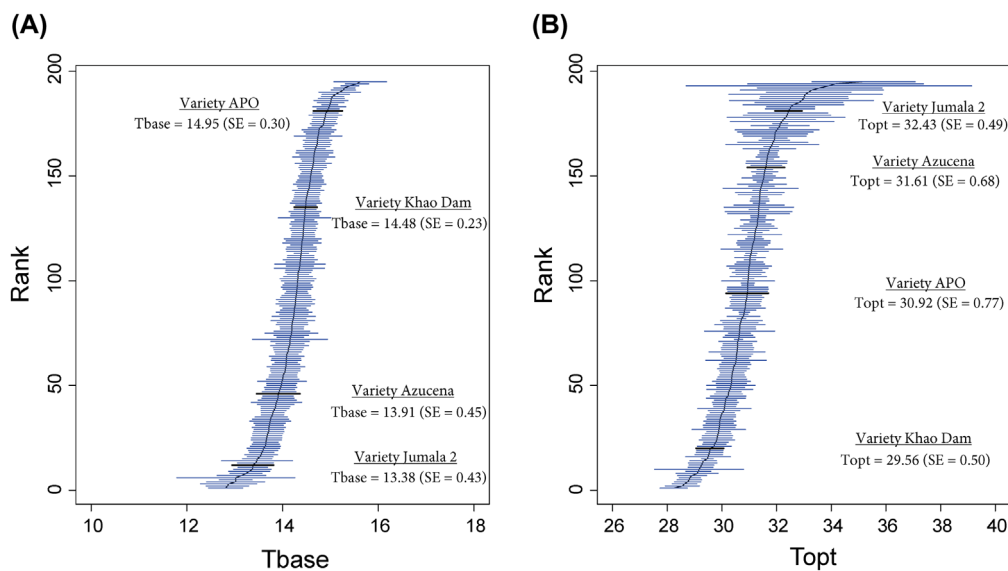Note: Boxplot legend is the same as in Figure 4.

Figure 6. Sorted base and optimum temperatures of the 195 varieties and their standard errors show a genotypic variability of Tbase (A) and Topt (B).

Notes: Cultivars were put in order from the smallest to the highest base (resp. optimum) temperature values. The rank of a particular cultivar is its position in the resulting sorted list.

alive. By contrast, the *Tbase* parameter of the Beta-L model was more accurately estimated than the *Tmin* parameter of Yan and Hunt's Beta model certainly because it requires less extrapolation. This made of *Tbase* a better candidate than *Tmin* for selection and marker association. Moreover, in its linear part, the Beta-L model was consistent with the concept of thermal time underlying most crop models. Using *Tbase* estimated by the Beta-L model should thus be more appropriate in a modeling context than using *Tmin* estimated by the Beta model. *Topt* was also more accurately estimated with Beta-L than with Beta model, though the superiority of Beta-L was less obvious than for *Tbase*. As the maximum target temperature was 35 °C, the standard error of *Topt* got higher as *Topt* got closer to 35 °C. A similar behavior is not observed for *Tbase*, although it results from an extrapolation under the minimum 16 °C target temperature. Apart from these general trends, some heterogeneity in standard error was observed and probably resulted from the different patterns of missing data for some cultivars. *Tmax* could not be estimated accurately for all varieties, as 35 °C was already a maximum attainable target for our growth chambers. With equipment better fitted for high temperatures, it is likely that useful estimates could be obtained for *Tmax* as they were for *Tbase*. There again, when data is available, the linearization of the beta model for the high temperatures may be an option to consider. However, attention must be paid at high temperatures to maintain air vapor pressure deficit (VPD) at an acceptable value in order to avoid water stress and ultimately leaf burning. It would be also interesting to explore whether there is genetic variability in the maintenance of

rice leaf tissue growth and function under heat conditions and further methodological set up must be performed for improving the estimation of *Tmax*.

Implications for crop modeling

Cardinal temperatures are simplifying concepts classically used to summarize the response of the plant to the air temperature. As model parameters, they make it possible to render the general shape of the response of growth to temperature. They also define a range of favorable temperatures for the enzymatic activities, related to the cell division and elongation, underlying the different growth processes observable at the plant level (Parent et al., 2010). This is not to say they define absolute thresholds: some variation is indeed observed around the modeled curves, and this is true at all temperatures. Thus, one could not affirm that no growth is to be observed outside the estimated (*Tmin*, *Tmax*) or (*Tbase*, *Tmax*) range.

As said in the introduction, it is a common practice in crop modeling to consider, for a given species, a unique value for these cardinal temperatures. Here, both the distributions of *Tbase* and *Topt* estimated for each accession in the *japonica* panel showed a significant genotypic variability which was not demonstrated yet to our knowledge. In the particular case of *Tbase*, the 175 tropical *japonica* accessions showed values ranging between 12.8 °C (SE = 0.36) and 15.6 °C (SE = 0.55), whereas most of studies and crop models commonly use from 8 to 13 °C as a fixed value for rice (Bouman et al., 2001; Luquet et al., 2006). This raises the question of

the impact of considering, within a given species, fixed vs. variable value for these parameters when modeling and predicting crop growth and ultimately yield in a given environment. This was also suggested by Dingkuhn et al. (2015) in the case of a model-based study of the genetic variability in phenological traits with the rice *indica* subspecies. Cardinal temperatures indeed are key parameters in the modeling of crop phenology and development in almost all crop models, which is known to strongly drive and impact on crop growth and yield (Zhang & Tao, 2013). A preliminary simulation experiment with the crop growth model Ecomeristem (Luquet et al., 2016) forced with *Tbase* values estimated in the present study (other parameters being fixed at values estimated for Azucena, a reference tropical japonica genotype, Rebolledo et al., 2015) in sub-optimal growing conditions (average climatic data met in a greenhouse, data presented in Rebolledo et al., 2012) pointed out a potential propagated variability of 70% on shoot biomass accumulation at 40 days after sowing. This concern takes even more importance in the context of an increasing application of crop modeling to explore ideotypes as the combination of traits represented by model parameters (Luquet et al., 2016; Martre et al., 2014; Rötter et al., 2015) and more particularly in a climate change context (Kumar et al., 2016).

Perspectives for genetic studies and model based ideotype definition

Cardinal temperatures estimated in the present study come in complement to the set of traits and model parameters that were previously phenotyped on the same tropical *japonica* rice panel by Luquet et al. (2012, 2016), Courtois et al. (2013) and Rebolledo et al. (2015). This novel data-set will be used in a short term to perform genome wide association study using recently refined genotyping resources with 16664 SNP markers. This will reinforce the connection between key crop model parameters and molecular marker and allelic effects and by there the capacity to *in silico* explore optimal trait and marker combinations toward ideotype definition for targeted environmental conditions.

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Disclosure statement

The authors declare that they have no competing interests. Local, national or international guidelines and legislation were followed with the required and appropriate permissions and licenses during the experimental work of this study.

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