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RiceGrow: A rice growth and productivity model

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ABSTRACT

Growth and yield formation in rice (*Oryza sativa* L.) depend on integrated impacts of genotype, environment and management. A rice growth simulation model can provide a systematic and quantitative tool for predicting growth, development and productivity of rice under changing environmental conditions. Existing rice models perform well but are somewhat difficult to use because of the large number of parameters that users must estimate. Experience in modelling wheat suggested that using physiological development time (*PDT*) as a scaler for phenology and a partitioning index for organ growth could result in fewer parameters while providing good predictability and applicability. RiceGrow was developed using *PDT* and a partitioning index to quantify relations among rice growth and environmental factors, genotypic parameters and management practices. RiceGrow includes seven sub-models for simulating phenology, morphology and organ formation, photosynthesis and biomass production, dry matter partitioning, yield and quality formation, water relations and nutrient balance. The model was calibrated with three datasets involving various cultivars, sowing dates and N rates at multiple sites. Validation with independent datasets showed the model had good predictability and applicability. The RiceGrow model was compared with the ORYZA2000 model, showing that both provided satisfactory estimates for phenology, shoot biomass and yield. Overall, RiceGrow can be used to predict rice growth and development with varied genotypes, environmental conditions and management practices for multiple uses including scientific understanding, policy formulation and optimizing crop management.

1. Introduction

Rice (*Oryza sativa* L.) is the most important grain crop in China, its planting area accounting for 30% of all grain crops, and its yield for 40% of the grain yields. More than half of world's population relies on rice as its primary food staple. China and other rice producing countries face problems of feeding an increasing population, global warming and a reduction in rice planting area. Accurate prediction of rice growth and productivity under varying environmental conditions will be helpful in developing appropriate agricultural policies and ensuring adequate food production.

Crop simulation models can dynamically describe the biophysical and physiological processes of growth, development and yield, and provide a quantitative tool for predicting the productivity level of a crop in relation to genotype, environment and management [1–3]. Several growth simulation models have been developed for rice, including SIMRIW [4], CERES-Rice [5,6] and ORYZA [7,8], each performing well. These models use development stage (DS) or a development index to predict phenology, and use partitioning coefficients to estimate organ biomass. Some coefficients have different values at different stages, which complicates their application. Cao et al. [9,10] developed a wheat growth model using physiological development time (*PDT*) as a scaler for phenology and a partitioning index for organ growth, resulting in fewer parameters while providing good predictability and applicability.

The primary objectives of this study were (1) to develop an eco-physiological process-based simulation model of rice growth, development, and yield (RiceGrow) by quantifying and integrating the fundamental relations of developmental and growth processes with environmental factors, genotypic parameters and management practices by using physiological development time and a partitioning index, and (2) to compare results from the RiceGrow model with results from the ORYZA2000 model using the same datasets to determine if RiceGrow, with fewer input parameters, would provide similar or improved results compared with ORYZA2000 [8].

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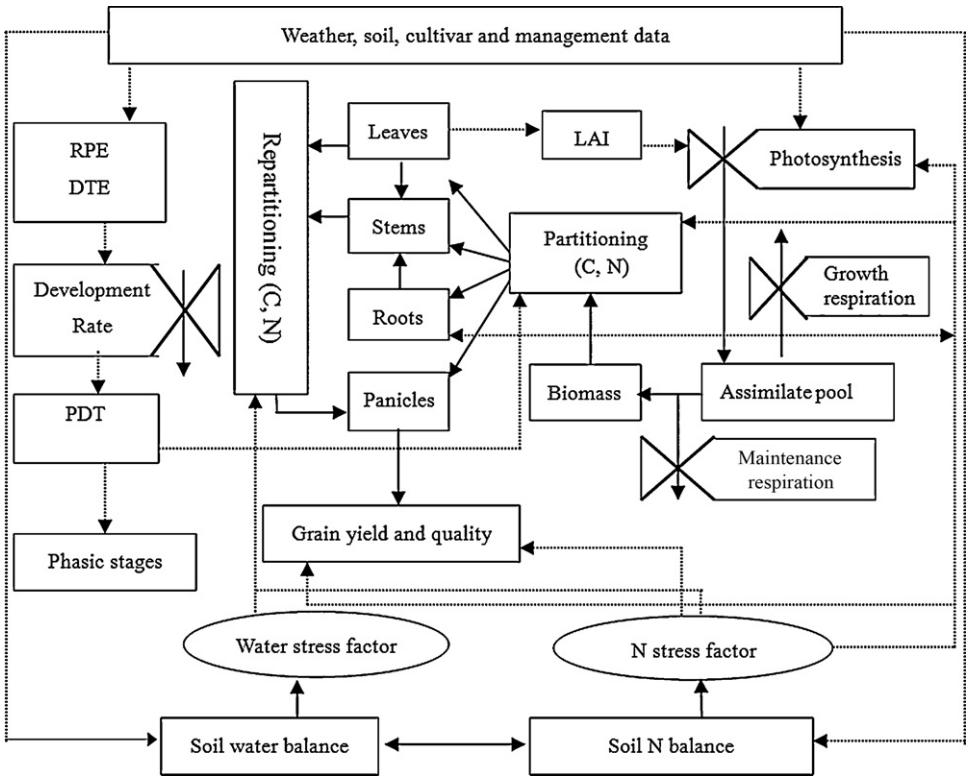

Fig. 1. Structural framework of the model RiceGrow.

2. Materials and methods

2.1. Description of RiceGrow[1]

2.1.1. General

RiceGrow was developed by analysing and integrating the relationships between rice growth and development and environment through the use of published studies [1–3] and field data. The model simulates phenology, morphology and organ formation, photosynthesis and biomass accumulation, biomass partitioning, yield and quality formation of various genotypes in response to environmental factors and management practices. The structure of RiceGrow is outlined in Fig. 1.

2.1.2. Phenology

Phenology was simulated by using physiological development time (*PDT*) to quantify the effects of temperature and photoperiod. *PDT* is defined as the development time accumulated under an optimum environment and has been used previously for wheat [9,10]. *PDT* for rice is a state variable that has values of 0 at emergence, 8 at the beginning of the photoperiod-sensitive phase, 13 at panicle initiation, 18 at the end of the photoperiod-sensitive phase, 32 at heading and 57 at maturity. The interaction of daily thermal effectiveness (*DTE*), relative photoperiod effectiveness (*RPE*) and an intrinsic earliness (*IE*) and basic filling factors (*BFF*) determine the daily physiological effectiveness. These daily values of effectiveness were summed to obtain *PDT*. The Beta [11] and quadratic functions were used to describe daily thermal effectiveness (*DTE*, Eqs. (1) and (2)) and daily photoperiod effectiveness (*DPE*, Eqs. (3) and (4)), respectively. Five specific genetic parameters were used to adjust the genotypic differences in rice development so that all cultivars would reach the same physiological development time at a given development stage (Eqs. (5) and (6)). These parameters were: temperature sensitivity (*TS*), photoperiod sensitivity (*PS*), optimum temperature (T_o), intrinsic earliness (*IE*), and basic filling factor (*BFF*). Thermal time from sowing to emergence was determined by adding the increased thermal requirement for seeding depth (7 °C per cm) to the soil surface thermal time (47 °C), using 10 °C as the base temperature) (Eq. (7)).

2.1.3. Leaf area development

The *LAI* submodel has two phases: (1) an exponential growth phase and (2) a non-exponential growth phase. The exponential growth phase occurs during early growth (when $LAI < 1.6$). During this phase, it is assumed that leaf growth is driven by temperature without water or nutrient limitations [7,12], and leaf area increases exponentially with thermal time (°C d, base 10 °C) (Eq. (8)). Potential relative growth rate (R_p) was regulated by a nitrogen nutrition index (*NNI*) [12,13] (Eq. (9)) and a water deficit factor (*WDF*), which was calculated from actual and potential canopy transpiration. In the non-exponential growth phase (when $LAI > 1.6$), the increase in *LAI* was calculated as a product of the increment in leaf dry weight and specific leaf area (*SLA*) of the green leaves (Eq. (10)). *SLA* was calculated using a quadratic function based on thermal time until it exceeded 1200 °C d, after which *SLA* was set to a constant value (Eq. (11)).

2.1.4. Photosynthesis and biomass accumulation

Gaussian integration was introduced to calculate daily canopy photosynthesis, by integrating the instantaneous photosynthetic rate over the day and leaf area index. The three-point method and the five-point method were used to calculate the photosynthesis rate, allowing a depth- or time-dependent photosynthetic response curve to be introduced [8,14]. The reflection coefficient of the canopy changed with the sine of the solar angle, and the relationship between the extinction coefficient for PAR and *PDT* was quantified (Eq. (12)). The actual CO_2 assimilation rate was

[1] For equations and variables see Appendices A and B.

influenced by CO_2 concentration, physiological age, average temperature, N nutrition and water stress (Eqs. (13)–(16)) based on maximum CO_2 assimilation rate (*Am*), which was regarded as a genetic parameter. The CO_2 concentration factor was quantified by Eq. (14) [15], and the physiological age factor was determined by *PDT* according to Hasegawa et al. [16,17] (Eq. (15)). The average temperature factor was calculated from cardinal temperatures (Eq. (16)). Daily total dry matter was calculated from daily total gross assimilation of canopy (*DTGA*) and respiration consumption (Eq. (20)). Respiration was expressed as a daily loss of total dry matter. Maintenance respiration and growth respiration were both accounted for in the present model: maintenance respiration was calculated from the maintenance coefficient and biomass (Eqs. (17) and (18)) according to Penning de Vries [15]. The maintenance coefficient, which declines with physiological age, was expressed as a function of *PDT* (Eq. (18)), and growth respiration was determined from daily total gross canopy assimilation (*DTGA*) (Eq. (19)).

2.1.5. Partitioning and yield formation

A partitioning index was introduced to simulate time-course dynamics of dry matter distribution among organs during development. The shoot and root partitioning indices were defined as a fraction of dry weight in plant biomass, and for green leaves, stems and ears as the proportion of their dry weights in shoot mass [10]. The partitioning index changed with *PDT* (Eqs. (21)–(25)), whereas the potential partitioning index for panicle dry weight (*PPIP*) was regarded as a genetic parameter. Since water deficit affects biomass allocation [15,18], a water deficit factor (*WDF*) was used to adjust shoot and root dry matter partitioning, with daily biomass allocated to green leaves being adjusted by both the *WDF* and the *NNI*. Biomass allocated to spikes was determined by high and low temperature-based functions [4] (Eqs. (26a)–(26c)). The proportion of weight in panicles was between 82% and 92%, with an average of 87%. The average moisture content of paddy rice grains is about 14%, which was used as default value to calculate final rice yields. If the actual grain moisture content is not 14%, the simulated grain yield should be adjusted.

2.1.6. Soil–plant water and nitrogen relations

The soil–plant water and nitrogen balance sub-models in RiceGrow were based on work by Ye [19], who described water dynamics based on a water and nitrogen balance model in wheat [20,21]. The water balance sub-model for semi-arid and flooded conditions was developed according to the soil water budget method following the CERES-Wheat [22] and MACROS models [15]. The processes of water interception by crops, irrigation, rainfall, surface drainage/runoff, field evaporation and transpiration, and root water uptake were included. The drought stress factor was based on the critical soil water content, which is the point of limited soil water availability. The waterlogging stress factor was quantified by integrating soil water content, waterlogging duration and plant sensitivity at the different growth stages. In the nitrogen sub-model, critical plant-nitrogen content, nitrogen uptake and allocation were quantified to describe the relationships between soil-N supply, plant uptake, dry matter production and N accumulation in the grains. The partitioning indices were used to simulate nutrient distribution among organs in relation to *PDT*.

2.1.7. Grain quality formation

Rice grain quality, including the formation of starch and protein, which are the primary components of the rice grain, depends on the processes of carbon and nitrogen assimilation pre-anthesis and translocation post-anthesis, as detailed by Zhu et al. [23] and Li [24]. The relationships between grain starch and protein accumulation and environmental factors (temperature, nitrogen, water) were analysed using data from field experiments with different cultivars and nitrogen rates. Based on these results, algorithms for starch and protein accumulation in the rice grain were developed on the basis of non-structural carbohydrate formation, nitrogen uptake, and carbon and nitrogen flow dynamics in the plant that were driven by physiological development time (*PDT*). In addition, based on the patterns of the differential starch and protein partitioning among panicle branches, spatial distribution models for starch and protein accumulation in grains of the primary and secondary branches on the panicle were established.

2.2. ORYZA2000

The ORYZA2000 model is a product of the modelling by the 'School of De Wit' [1,25]. It is one of the most famous growth models for rice, simulating growth and development of lowland rice in situations of potential production, water limitations, and nitrogen limitations [8]. ORYZA2000 also follows a daily calculation scheme for the rate of dry matter production of the plant organs and for the rate of phenology development. By integrating these rates over time, dry matter production and development stage are simulated throughout the growing season.

The photosynthesis and dry matter production modules in ORYZA2000 are well documented [14,26], and these modules in RiceGrow are similar. In grain crops, carbohydrate production (source size) during grain-filling can be higher or lower than the storage capacity of the grains (sink size). Spikelet sterility due to either too high or too low temperatures is adjusted by the method described by Horie [27,28]. Leaf area growth includes a source- and sink-limited phase. In the early growth phases, leaf area increases exponentially as a function of temperature sum times a relative leaf growth rate. When the *LAI* is larger than 1, the increase in leaf area is calculated from the increase in leaf weight times specific leaf area. Carbohydrates produced are partitioned among roots, leaves, stems, and panicles using experimentally derived partitioning factors as a function of development stage, which is tracked as a function of daily average temperature and photoperiod.

2.3. Experiments

Five experiments were conducted.

2.3.1. Experiment 1

This experiment was conducted at the Nanjing Agricultural University Experiment Station in Nanjing (32°02′N, 118°50′E) in 2000 and 2001. Two Japonica rice cultivars were evaluated: Koshihikari and RR109, with two sowing dates in 2000 (13 and 20 May) and six sowing dates in 2001 (29 April, 10 and 18 May, 3 June, 15 July, and 1 August). The experiment was of a split-plot design with three replications. Plot size was 10 m^2, with row and hill spacings of 23.1 and 13.2 cm, respectively, two plants per hill. Fertilizer application rates for N, P_2O_5 and K_2O were 270, 150 and 150 kg ha^{-1}, respectively.

Measurements in 2001 were taken primarily from the following sowing dates (SD): 29 April (SD1), 3 June (SD2) and 15 July (SD3). During the experimental period, sample plants were randomly selected every 4 d at the panicle differentiation stage and every 7 d at other stages. Depending on which organs were present, each sample was separated into four fractions: roots, sheaths and stems, leaves and panicles. Green leaf blade area was measured with a CI-203 area meter (CID, Vancouver, WA, USA). Aboveground organ dry weights were determined by oven-drying at 80 °C to constant weight. Total N contents of roots, sheaths and stems, leaves and panicles were determined using the semi-micro Kjeldahl method. Weather data (minimum and maximum air temperature, precipitation, sunshine hours) were obtained from a meteorological station within 1 km of the experimental fields.

2.3.2. Experiment 2

This experiment was conducted at the Jiangsu Academy of Agricultural Sciences Experiment Station in Nanjing (32°02′N, 118°50′E) in 2001. Four nitrogen rates were tested (0, 135, 270 and 405 kg N ha^{-1}) on cultivar 9325. The experiment was of a randomized complete block design with three replications and a plot size of 12 m^2. Sowing and transplanting date were 8 May and 12 June, respectively. Row and hill spacing were 25.0 and 13.2 cm, with two plants per hill. The application rate for both P_2O_5 and K_2O was 150 kg ha^{-1}. Other management followed local standard practices. Measured variables were as in Experiment 1.

2.3.3. Experiment 3

This experiment was conducted in 2001 at three sites: Chiang Mai, Thailand (18°45′N, 98°58′E), Kyoto, Japan (35°03′N, 139°44′E) and Nanjing, China (32°02′ N, 118°50′ E), with three Indica type cultivars: Takanari (TAK), IR72 and Ch86, and two Japonica types: Nipponbare (NIP) and Takenari (TEN). The sowing and transplanting dates were 13 July and 7 August at Chiang Mai, 12 May and 13 June at Nanjing, and 2 and 25 May at Kyoto. Application rates for N, P_2O_5 and K_2O were all 120 kg ha^{-1}. The experiment was of a randomized complete block design with three replications and a plot size of 15 m^2. Row and hill spacing were 30 and 15 cm, respectively, with one plant per hill. Other management followed local standard practices. Plants were sampled at the key development stages. Measured variables were as in Experiment 1.

2.3.4. Experiment 4

This experiment was a 'virtual experiment' in which data were used from previously published rice experiments [29]. The experiment included 13 sowing dates and six sites (including Yanxian, Guangzhou, Changsha, Nanjing, Tianjin, Gongzhuling and Tianjin, located from 43°31′N to 18°20′N). The development stages at which data had been collected included emergence, panicle initiation, heading and maturity. In addition, 13 different daylength treatments (20-min steps in the range from 11.5 to 14.5 h and daylengths 15, 18 and 24 h) had been imposed in Guangzhou, with heading data recorded for each treatment. Six cultivars were evaluated: Guoguang, Nantehao, Bolizhan, Huangkezaonianri, Laolaiqing and Qingguzhong. Daily weather data were obtained from the National Meteorological Center (NMC) in Beijing.

2.3.5. Experiment 5

This experiment was conducted in Jiangning district, Nanjing, China (32°02′N, 118°50′E) in 2007 and 2008. Rice cultivar Wuxiangjing 14 was evaluated. The experiment was of a random design with three replications. In 2007, the sowing and transplanting dates were 18 May and 18 June, respectively. Plot size was 27 m^2, with row and hill spacings of 4.5 and 6 cm, respectively. Two nitrogen rates were tested: 0 and 360 kg N ha^{-1}. In 2008, the sowing and transplanting dates were 24 May and 25 June, respectively. Plot size was 29.25 m^2, with row and hill spacings of 4.5 and 6.5 cm, respectively. Other management followed local standard practices. Measured variables were the same as in Experiment 1.

The data from Experiments 1, 2 and 4 were used for model development and parameterization, and those from Experiments 3 and 4 were used for model validation. In Experiment 4, the 13 different daylength treatments and five sowing dates were used for calibration, and the other eight sowing dates were used for validation. The data from Experiment 5 in 2007 were used to calibrate, and the data from Experiment 5 in 2008 were used to validate the two models.

3. Results and discussion

3.1. Model calibration

The RiceGrow sub-models were parameterized by using literature values or regressions based on experimented data. The phenology development, *LAI* growth and dry matter partitioning sub-models were calibrated separately by using observed data to avoid the accumulated error from data transmission between sub-models. The soil water and nutrient sub-models had been constructed and tested previously [19–21].

3.1.1. Phenology modelling

Five specific genetic parameters: temperature sensitivity (*TS*), photoperiod sensitivity (*PS*), optimum temperature (T_o), intrinsic earliness (*IE*), and basic filling factor (*BFF*) were used for predicting development stages of different rice cultivars (Table 1). Photoperiod sensitivity (*PS*) was most closely related to cultivar maturity and had values from 0 for early-maturing Japonica rice to 16.85 for late-maturing Indica rice, reflecting large genotypic differences. The values of *TS* and T_o for different cultivars ranged from 2.0 to 5.3 and from 28 to 30, respectively, which showed that the sensitivity temperature for rice cultivars varied little. No correlation was found between *IE* and *BFF* for the cultivars tested in this study, in which values ranged from 0.21 to 1.0 and from 0.58 to 0.96, respectively.

3.1.2. Specific leaf area simulation

Specific leaf area (*SLA*) decreased rapidly with growing degree days (*GDD*) during the early growth period (*GDD* less than 1200 °C d), and then remained stable at about 0.002 ha kg^{-1} (Fig. 2). The cultivars Koshihikari and RR109 showed the same pattern for the three sowing dates. Thus, sowing date and cultivar had little impact on model calibration. Nitrogen application rate had a slight effect on *SLA*, with the high-N rate depressing *SLA* when *GDD* was greater than 1200 °C d (Fig. 3). Thus, the *NNI* was used to modify *SLA* values under varied N levels.

Table 1
Genetic parameters[a] for predicting development stages of different rice cultivar types (Experiments 1 and 4).

Cultivars	Type	$PS \times 10^{-2}$	*TS*	T_o (°C)	*IE*	*BFF*	RMSE (d)		
							Emergence	Heading	Maturity
Guoguang	Early-maturity Japonica	0	5.0	28	1.00	0.75	1.39	3.83	2.48
Nantehao	Early-maturity Indica	0	2.7	28	0.32	0.84	1.44	5.36	4.50
Koshihikari	Middle-maturity Japonica	2.1	4.0	28	0.60	0.67	1.13	3.34	2.98
Bolizhan	Middle-maturity Indica	0.61	2.0	30	0.21	0.96	1.57	4.37	1.84
Huangkezaonianri	Middle-maturity Japonica	4.18	2.3	31	0.53	0.71	1.65	3.21	3.91
Laolaiqing	Late-maturity Japonica	5.82	3.0	31	0.62	0.63	1.85	5.78	3.56
RR109	Late-maturity Japonica	6.12	4.2	28	0.63	0.58	1.09	3.28	3.51
Qingguzhong	Late-maturity Indica	16.85	5.3	30	0.73	0.72	1.67	6.64	4.25
Average								4.58	3.37

[a] For abbreviations see Appendix B.

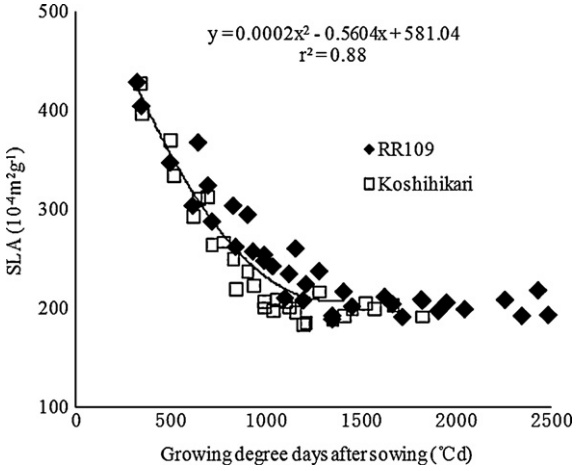

Fig. 2. Specific leaf area (*SLA*) in relation to growing degree days after sowing for the rice cultivars RR109 and Koshihikari.

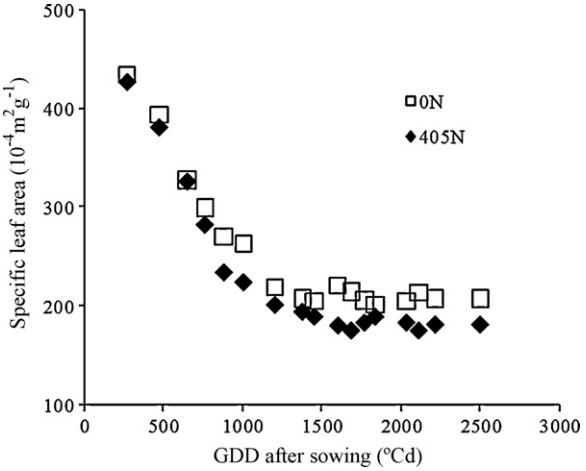

Fig. 3. Specific leaf area (*SLA*) in relation to growing degree days (GGD) after sowing for the rice cultivar 9325 at two N levels.

3.1.3. Dry matter accumulation and partitioning

The values for maximum CO_2 assimilation rate (*Am*) showed little change, about 46 kg CH_2O ha^{-1} h^{-1}, compared with reported values of 42–50 kg CH_2O ha^{-1} h^{-1} [1,7,17]. This may reflect a narrow range of this characteristic for the cultivars used in our experiments.

Dry matter partitioning into leaves, stems and panicles was affected by genotype, sowing date and nitrogen level (Figs. 4 and 5). The partitioning indices for organs were quantified using the dataset of SD2 of experiment 1, which represented a conventional sowing date and N application rate. The potential partitioning index for panicles (*PPIP*) of different cultivars showed a large variation; *PPIP* for the cultivar RR109 was 0.58, whereas for the cultivar Koshi-

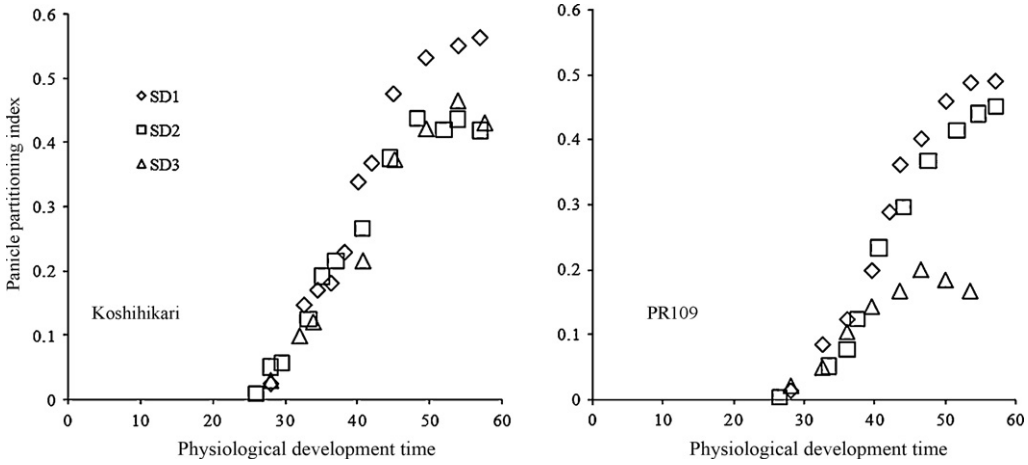

Fig. 4. Panicle partitioning index (*PPI*) in relation to physiological development time (*PDT*) for rice cultivars Koshihikari and RR109 sown on 3 different dates (SD).

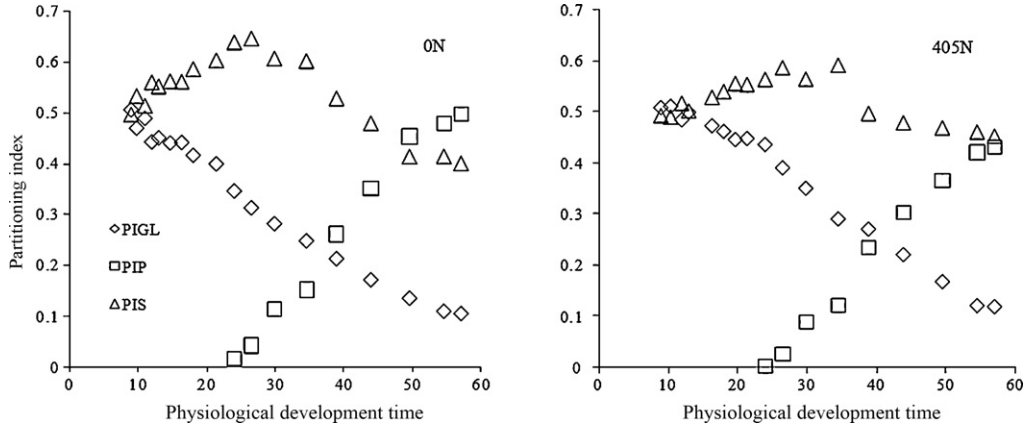

Fig. 5. Partitioning indices for green leaf dry weight (PIGL), panicle dry weight (PIP) and stem dry weight (PIS) in relation to physiological development time for the rice cultivar 9325 at two N levels.

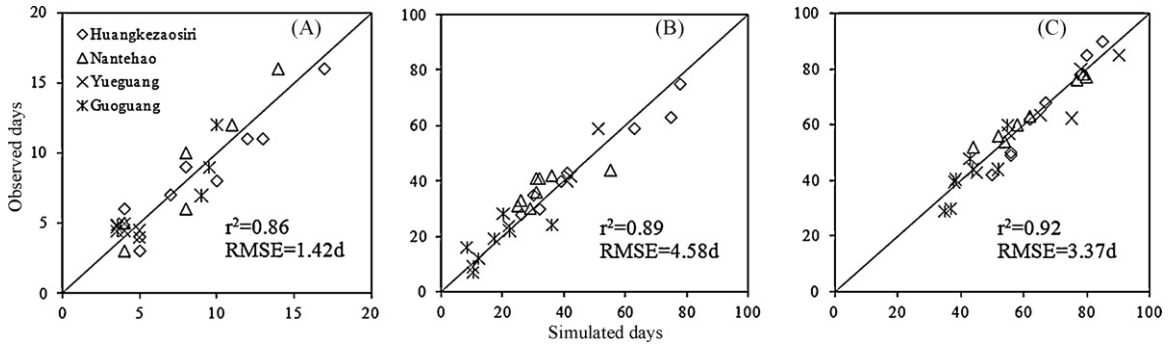

Fig. 6. Simulated versus observed days from sowing to emergence (A), emergence to heading (B) and heading to maturity (C) for various rice cultivars.

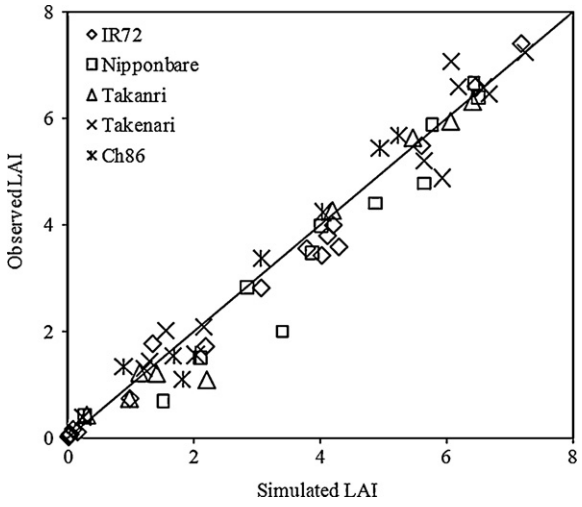

Fig. 7. Simulated versus observed *LAI* values at key development stages for various rice cultivars.

hikari the value was only 0.49. Seed setting rate was reported by Horie et al. to be decreased when daily maximum temperatures exceeded 32 °C at heading and anthesis stages [4]. Fig. 4 shows the relationship of *PPI* with *PDT* for the cultivars Koshihikari and RR109 for different sowing dates. The *PPI* for the cultivar Yoshihikari with the SD1 treatment decreased about 15% compared with SD2, which could have been caused by high temperatures at heading. Cultivar RR109 escaped high-temperature injury because it is an early-maturing late Japonica type and heading occurred during lower temperatures. The *PPI* in SD3 was reduced due to low temperatures delaying the heading stage, especially for cultivar RR109. Both *PIGL* and *PIS* were reduced when N level was increased for cultivar 9325 in Experiment 2 (Fig. 5).

Table 2
Genetic parameters for rice cultivar Wuxiangjing 14 derived from RiceGrow.

Genetic parameter[a]	Value for Wuxiangjing 14	Units
PS	0.0506	
TS	3.82	
T_o	30.2	°C
IE	0.34	
PDF	0.61	
Am	46	kg CH_2O ha^{-1} h^{-1}
PPIP	0.54	
R_p	0.0067	°C d^{-1}

[a] For abbreviations see Appendix B.

3.2. Model validation

3.2.1. Growth stage

The experimental data involved a wide range of photoperiod and temperature values, including daily mean temperatures from 19 to 30 °C, daylengths from 11 to 15.5 h, and observed days from 35 to 116. There was generally good agreement between the predicted

Table 3
Genetic parameters for rice cultivar Wuxiangjing 14 derived from ORYZA2000.

Development stage (DVS)			Specific leaf area (*SLA*)		Partitioning				Maximum grain weight (kg grain^{-1})
Phase[a]	DVR[b] (°C d^{-1})	PPSE[c] (h^{-1})	DVS	*SLA* (ha kg^{-1})	DVS	Leaf	Stem	Panicle	
DVRJ	0.000773	0.15	0.00	0.0040	0.00	0.60	0.40	0.00	0.0000245
DVRI	0.000749		0.16	0.0038	0.50	0.60	0.40	0.00	
DVRP	0.000785		0.33	0.0028	0.75	0.30	0.70	0.00	
DVRR	0.001281		0.65	0.0023	1.00	0.00	0.40	0.60	
			2.10	0.0020	1.20	0.00	0.00	1.00	

[a] DVRJ = juvenile phase; DVRI = photoperiod-sensitive phase; DVRP = panicle formation phase; DVRR = grain-filling phase.
[b] DVR = development rate.
[c] PPSE = photoperiod sensitivity.

Table 4
Calibration results for RiceGrow and ORYZA2000.

Parameter	Predicted by RiceGrow	Predicted by ORYZA2000	Observed
Panicle initiation (DAS)[a]	82	80	79
Flowering (DAS)	101	103	102
Maturity (DAS)	159	157	155
Grain yield (kg ha^{-1})	9629	12,007	11,304
Biomass at harvest (kg ha^{-1})	20,165	20,082	18,232

[a] DAS = days after sowing.

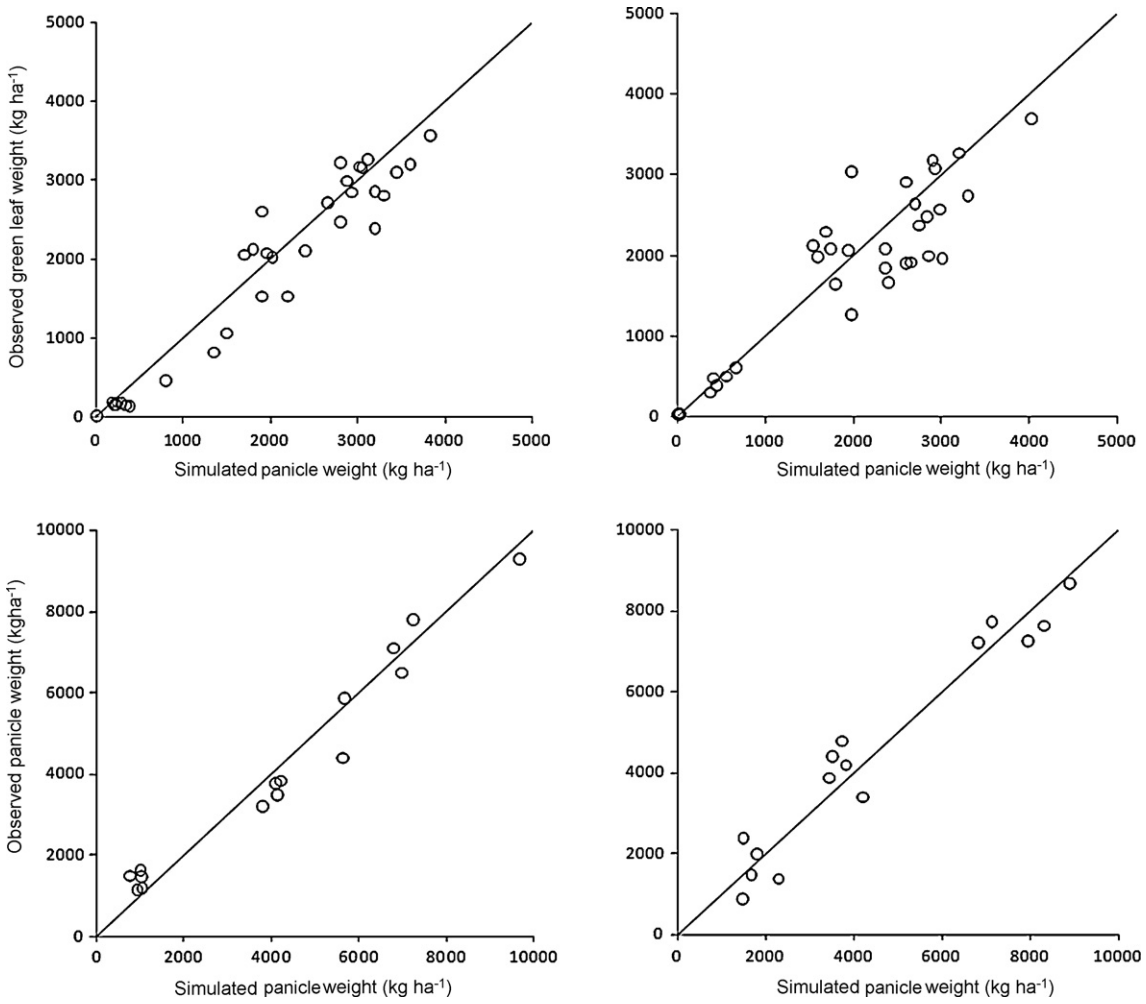

Fig. 8. Simulated versus observed dry weights of panicle and green leaves of various rice crops grown at Kyoto, Japan and Nanjing, China.

and observed days (Fig. 6), with the RMSE values ranging from 1.0 to 1.9 d for emergence, from 3.2 to 6.6 d for heading and from 1.8 to 4.5 d for maturity (Table 1), respectively, and with r^2 values for emergence, heading, and maturity of all cultivars of 0.86, 0.89 and 0.92, respectively.

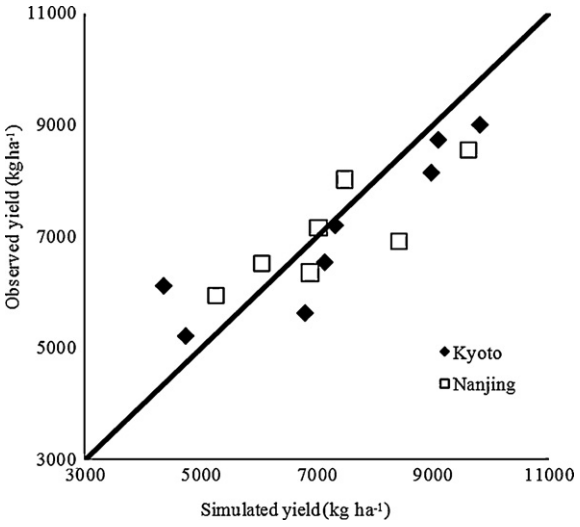

Fig. 9. Simulated versus observed yields for five rice crops grown at Kyoto, Japan and Nanjing, China.

3.2.2. Leaf area index

Simulated *LAI* values were compared with field observations involving several sites, sowing dates and cultivars. The *LAI* of the various cultivars at the main development stages were well predicted, with a highly significant fit (r^2 = 0.97), low RMSE (0.47) and low mean absolute error (0.28) (Fig. 7). However, there was a slight over-estimation for low *LAI*, because *SLA* decreased rapidly with increasing *GDD* at an early stage. This relationship needs to be further evaluated in future investigations.

3.2.3. Biomass partitioning and yield

The simulated biomass partitioning for leaves and panicles, and the yields were compared with observed data from Experiment 3 (Figs. 8 and 9). The r^2 between simulated and measured values for leaves, panicle and grain yield based on the 1:1 line were 0.89, 0.85 and 0.77, respectively, and the RMSE between those was 278, 569 and 832 kg ha^{-1} in Kyoto, and 467, 612 and 856 kg ha^{-1} in Nanjing. These values indicate that the model performed well.

3.3. Comparison of RiceGrow and ORYZA2000

3.3.1. Model calibration

The measured data from Experiment 5 in 2007 were used to calibrate RiceGrow. The genetic parameters of RiceGrow are listed in Table 2. The high-N treatment (360 N kg ha^{-1}) in Experiment 5 in 2007, which was regarded as optimal, was used for estimating the genetic parameters of cultivar Wuxiangjing 14 for ORYZA2000. The

Table 5
Validation results for RiceGrow and ORYZA2000.

Parameter	Predicted by RiceGrow	Predicted by ORYZA2000	Observed
Panicle initiation (DAS)[a]	74	76	72
Flowering (DAS)	102	101	100
Maturity (DAS)	155	154	151
0 N treatment (N0)			
Shoot biomass after harvest (kg ha^{-1})	11,037	10,495	9744
RMSE for shoot biomass (kg ha^{-1})	718.1	873.3	
Yield (kg ha^{-1})	624	5709	6028
390 kg N ha^{-1} treatment (N390)			
Shoot biomass after harvest (kg ha^{-1})	17,320	19,093	17,081
RMSE for shoot biomass (kg ha^{-1})	1393.2	1079.1	
Yield (kg ha^{-1})	9615	10,947	9053.1

[a] DAS = days after sowing.

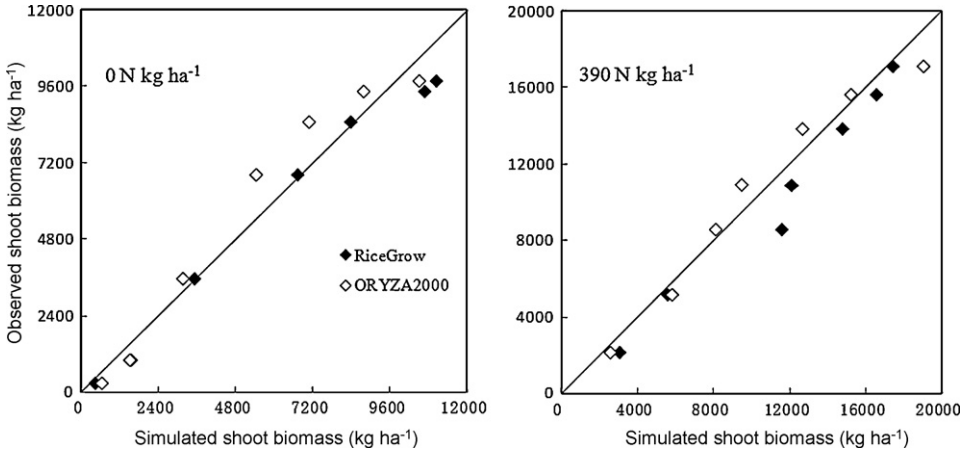

Fig. 10. Simulated versus observed shoot biomass at two N levels, for RiceGrow and ORYZA2000.

main parameters for ORYZA2000 are listed in Table 3; the parameters that are not listed were used as default parameters for the cultivar IR72 as given by ORYZA2000 [8]. The calibrated results for the two models are listed in Table 4. ORYZA2000 and RiceGrow both simulated phenology, shoot biomass at harvest and yield satisfactorily.

3.3.2. Model validation

The two N treatments in Experiment 5 in 2008 were used to validate the two models, the high-N treatment (390 N kg ha^{-1}; N390) was regarded as non-N-limited conditions to simulate ORYZA2000 and RiceGrow. Table 5 lists the validated results of phenology, shoot biomass after harvest, and yield of the two models. Both models simulated the phenology satisfactorily, with an RMSE value of 2.94 d for ORYZA2000 and 2.83 d for RiceGrow. Shoot biomass was simulated satisfactorily too (Fig. 10), with an RMSE value for predicted shoot biomass under N0 treatment of 718.1 kg ha^{-1} for RiceGrow and 873.3 kg ha^{-1} for ORYZA2000, and under N390 treatment 1393.2 kg ha^{-1} for RiceGrow and 1079.1 kg ha^{-1} for ORYZA2000. These results indicate that the performance of RiceGrow in predicting shoot biomass under the non-N-application condition was better than that of ORYZA2000, whereas the performance of ORYZA2000 was better under the optimal N condition. The yield under N0 treatment was simulated well by the two models, but the yields simulated by the two models under the N390 treatment were both overestimated (Table 5).

4. Conclusions

An eco-physiological process-based simulation model for rice growth (RiceGrow) was developed by quantifying the fundamental growth processes and their response to environmental factors, genotypic parameters and management practices. The model used physiological development time and partitioning index methodology similarly to that previously reported for a wheat growth model [9,10].

The model is composed of seven sub-models, including phenology, photosynthesis and biomass production, biomass partitioning, yield and quality formation, water and nitrogen relationships. Eight parameters relating to rice yield were used: temperature sensitivity, photoperiod sensitivity, optimum temperature, intrinsic earliness, basic filling factor, maximum CO_2 assimilation rate, potential partitioning index for panicle and potential relative growth rate for leaf area index. The model was calibrated and validated using five datasets that involved various cultivars, sowing dates and experimental sites, and showed good predictability and applicability.

The model ORYZA2000 was compared with RiceGrow. In RiceGrow, the waterlogging stress factor is quantified by integrating soil water content, waterlogging duration and plant sensitivity at the different development stages, whereas ORYZA2000 only can simulate the water-limited growth. Also the grain quality formation processes were simulated in RiceGrow, but are not simulated in ORYZA2000. The outputs of RiceGrow and ORYZA2000 were compared using a dataset involving 2 years and two N rates. The results showed that the two models simulated phenology, shoot biomass and yield satisfactorily, with RiceGrow providing results similar to ORYZA2000.

However, further studies are needed to ensure accurate model predictions with diverse cultivars and under diverse production environments. It would be valuable to quantify the stress of high and low temperature in phenology and to simulate the influence

of varied CO_2 levels on photosynthesis, which currently is only explained in simple terms in RiceGrow. RiceGrow and ORYZA2000 were simply compared with two different conditions and should be further compared in comprehensive conditions in the future.

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Appendix A.

RiceGrow submodel equations for phenology, leaf area index, photosynthesis and dry matter accumulation and partitioning (variables are described in Appendix B).

Submodel	Equations	
Phenology	$RTE(I) = \left[\left(\frac{T(I)-Tb}{T_o-Tb}\right)\left(\frac{Tc-T(I)}{Tc-T_o}\right)^{Tc-T_o/To-T_b}\right]^{TS}$	(1)
	$DTE_i = \frac{1}{24}\sum_{I=1}^{24} RTE(I)$	(2)
	$RPE_i = \begin{cases} 1 & P \le P_o \\ 1 - PS \times (P-P_o)^2 & P_o < P \le P_c \end{cases}$	(3)
	$PC = P_o + \left(\frac{1}{PS}\right)\frac{1}{2}$	(4)
	$DPE_i = \begin{cases} DTE_i \times IE & 0 \le PDT \le 8 \\ DTE_i \times RPE_i & 8 \le PDT \le 18 \\ DTE_i & 18 \le PDT \le 32 \\ DTE_i \times BFF & 32 \le PDT \le 57 \end{cases}$	(5)
	$PDT_i = PDT_{i-1} + DPE_i$	(6)
	$EM = 45 + 7 \times SDEPTH$	(7)
Leaf area index	$LAI_P = LAI_o \times \exp(R_P \times GDD) \quad LAI \le 1.6$	(8)
	$R = R_P \times MIN(NNI, WDF)$	(9)
	$LAI = SLA \times AWL$	(10)
	$SLA_P = \begin{cases} -0.0002GDD^2 - 0.5604GDD + 581.04 & GDD \le 1200 \\ 200 & GDD > 1200 \end{cases}$	(11)
	$K = 0.0087 \times PDT + 0.2222$	(12)
Photosynthesis and dry matter accumulation	$AMAX = Am \times FCO_2 \times FPA \times FT \times MIN(NNI, WDF)$	(13)
	$FCO_2 = 1 + \beta \ln\left(\frac{Cx}{340}\right)$	(14)
	$FPA = \begin{cases} 1 & PDT < 28 \\ \exp[-a(PDT-28)] & 28 \le PDT \le 57 \end{cases}$	(15)
	$FT = \begin{cases} \exp\left[\frac{-(T-T_o)^2}{(T-T_b)(T_c-T)}\right] & T_b < T < T_c \\ 0 & T < T_b;\ T > T_c \end{cases}$	(16)
	$RM = RM(T_o) \times ABIOMASS \times Q_{10}^{(T-To)/10}$	(17)
	$RM(T_o) = 0.0091 - 0.0001 \times PDT$	(18)
	$RG = Rg \times DTGA$	(19)
	$GCR = \frac{DTGA - RM - RG}{1-b}$	(20)
	$PISH = -8.42 \times 10^{-5} \times PDT^2 + 0.01 \times PDT + 0.63$	(21)
	$PIRO = 1 - PISH$	(22)
Dry matter partitioning	$PIGL = \begin{cases} 0.54 - 0.0046 \times PDT & PDT < 26 \\ 1.4532 \times \exp(-0.0492 \times PDT) & PDT \ge 26 \end{cases}$	(23)
	$PIP = \begin{cases} PPIP \times \frac{1}{1+\exp[-0.2804 \times (PDT-39)]} & PDT \ge 24 \\ 0 & PDT < 24 \end{cases}$	(24)
	$PIS = 1 - PGIL - PIP$	(25)
	$HTF = \frac{1}{1+\exp[-0.853 \times (T_m - 36.6)]} \quad 32 \le PDT \le 39$	(26a)
	$LTF = 1 - \left(\frac{4.6 + 0.054 \times Q_t^{1.56}}{100}\right) \quad 26 \le PDT \le 39$	(26b)
	$Q_t = \sum(22 - T_4) \quad T_4 \le 22$	(26c)

Appendix B.

Description of variables used in RiceGrow.

Symbol	Unit	Description
ABIOMASS	$kg\,ha^{-1}\,d^{-1}$	Daily actual biomass
Am	$kg\,CO_2\,ha^{-1}\,h^{-1}$	Maximum CO_2 assimilation rate
AMAX	$kg\,CO_2\,ha^{-1}\,h^{-1}$	Actual CO_2 assimilation rate
AWL	$kg\,ha^{-1}$	Actual dry weight of green leaves
AWP	$kg\,ha^{-1}$	Actual dry weight of panicle
BFF		Basic filling factor
Cx	ppm	Actual CO_2 concentration
DPE		Daily physiological effectiveness
DTE		Daily thermal effectiveness
DTGA	$kg\,CH_2O\,ha^{-1}\,d^{-1}$	Daily total gross assimilation
EM	°C d	Thermal time from sowing to emergence
FCO_2		CO_2 factor
FPA		Physiological age factor
FT		Temperature factor
GDD	°C d	Growing degree days
HTF		High-temperature factor
K		Radiation extinction coefficient
IE		Intrinsic earliness
LAI	$m^2\,m^{-2}$	Leaf area index
LAI_o	$m^2\,m^{-2}$	Initial leaf area index value
LAI_P	$m^2\,m^{-2}$	Potential leaf area index value
LTF		Low temperature factor
NNI		Nitrogen nutrition index
P	h	Daylength
Pc	h	Critical daylength for heading
PDT		Physiological development time
PIGL		Partitioning index for green leaves dry weight
PIP		Partitioning index for panicle dry weight
PIRO		Partitioning index for underground biomass
PIS		Partitioning index for stem dry weight
PISH		Partitioning index for aboveground biomass
Po	h	Optimum daylength
PPIP		Potential partitioning index for panicle
PS		Photoperiod sensitivity
Qt	°C d^{-1}	Respiration temperature coefficient
R	°C d^{-1}	Actual relative growth rate for leaf area index
RG	$kg\,CH_2O\,ha^{-1}\,d^{-1}$	Growth respiration consumption
Rg		Growth respiration coefficient
RM (To)	$kg\,CH_2O\,ha^{-1}\,d^{-1}$	Maintenance coefficient
R_p		Potential relative growth rate for leaf area index
RPE		Relative photoperiod effect
RTE		Relative thermal effectiveness
SDEPTH	cm	Sowing depth
SLA	$10^{-4}\,m^2\,g^{-1}$	Specific leaf area
SLAp	$10^{-4}\,m^2\,g^{-1}$	Potential specific leaf area
T	°C	Daily mean temperature
T4	°C	Daily mean temperature from end of photoperiod Sensitivity to fourth day after anthesis
Tb	°C	Minimum temperature for rice growth
Tc	°C	Maximum temperature for rice growth
T(I)	°C	Hourly temperature
T_o	°C	Optimum growth temperature for rice growth
TS		Temperature sensitivity
WDF		Water deficit factors
β		Coefficient of CO_2 factor function
A		Coefficient of CO_2 factor function
B		Content of non-carbon substances

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