



A two-step approach to quantify photothermal effects on pre-flowering rice phenology



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ARTICLE INFO

Article history:

Received 20 July 2012

Received in revised form 30 July 2013

Accepted 30 September 2013

Keywords:

Aerobic rice

Photothermal response

Flowering

Phenology parameterisation

Reciprocal transfer experiment

ABSTRACT

Decreasing water availability for rice based systems resulted in the introduction of water saving production systems such as aerobic rice and alternate wetting–drying technology. To further improve resource use efficiency in these systems, water management should be attuned to critical growth stages, requiring accurate prediction of crop phenology. Photoperiod-sensitivity of aerobic rice genotypes complicates the estimation of the parameters characterising phenological development and hence impairs predictions. To overcome this complication, we followed a two-step approach: (1) the photoperiod response was determined in growth chambers, through a reciprocal transfer experiment with variable day length, conducted at a fixed temperature, and consecutively, (2) the temperature response was studied by combining the obtained photoperiod parameters with data from field experiments. All four aerobic rice genotypes tested exhibited strong photoperiod-sensitivity. Durations of basic vegetative phase (BVP) i.e. when plants are still insensitive to photoperiod, photoperiod-sensitive phase (PSP), and post-PSP (PPP) varied among genotypes. The temperature response of the genotypes was explored by combining phenological observations in the reciprocal transfer experiment with observations in two field experiments. The temperature range in the field experiments was too narrow to obtain convergence to a unique set of temperature response parameters, regardless whether a bilinear or a beta model was used. Sensitivity analysis however provided clear arguments in support of the recent doubts on the validity of a commonly used set of cardinal temperatures for rice phenology. Using standard cardinal temperatures, the rate of development at temperatures below 31 °C was overestimated. This finding stresses the need for experiments on rice phenology under a wider range of temperatures.

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1. Introduction

Within crops resource accumulation and the efficiencies of their use are strongly coupled to the timing and interplay of plant growth and development. Understanding phenological chronology is important for fine-tuning genotype selection and adjusting sowing dates (Vergara and Chang, 1985; Fukai, 1999). Accurate prediction of critical growth stages is also crucial for designing appropriate crop management. The timing of resource application is particularly important when these resources are scarce. Temperature and photoperiod (PP) are the two principal factors controlling pre-flowering development of plants. Studies on photothermal responses thus facilitate the selection of adapted genotypes for target environments as well as the optimisation of crop management in order to minimise the adverse consequences of seasonal constraints (Collinson, 1992; Fischer et al., 2003). For rice crops

careful genotype selection and scheduling of resource application is essential for the success of water saving systems such as aerobic rice (AR) and alternative wetting–drying technology (Belder et al., 2005; Lafitte et al., 2002; Xiaoguang et al., 2005).

Rice (*Oryza sativa* L.) is a short-day plant and the degree of PP-sensitivity varies among genotypes. Since the 1960s, IRRI has been breeding for less PP-sensitive genotypes, thus allowing these genotypes to be grown in multiple cropping systems. IR8, a less PP-sensitive genotype developed in 1966 showed a wider adaptability and stable growth duration compared with the traditional genotypes (Vergara and Chang, 1985; Prasad et al., 2001). In the higher latitudes of Japan and Northeast China, early maturing japonica PP-insensitive genotypes allow for growing rice under adverse conditions i.e. short and cool summers under long days of more than 15 h (Okumoto et al., 1996; Wei et al., 2008). However, PP-sensitivity may have advantages as a safety mechanism when exact planting dates are not followed. Within a wide range of sowing dates, a PP-sensitive genotype would still flower and mature at the same time. The synchronised maturation of crop might help prevent the ripening of the crop to occur under unfavourable

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conditions (Vergara and Chang, 1985; Prasad et al., 2001). For that reason, PP-sensitivity is an important trait that can be used in breeding programmes that target improved crop performance in resource-limited environments (Poonyarit et al., 1989; Li et al., 1995; Fischer et al., 2003). Long duration, PP-sensitive genotypes can better withstand unfavourable conditions such as early drought, transplanting shock and low soil fertility (Vergara and Chang, 1985; Fukai, 1999).

Phenology calibration from field observations is especially difficult in case of PP-sensitive genotypes (van Oort et al., 2011). The two main problems are: (a) finding the start and end of the PP-responsive period and (b) disentangling photoperiod and temperature effects. Temperature and photoperiod are correlated; during summer day length (photoperiod) is generally longer and temperatures are higher. The question arises: if a delay in flowering is observed during summer, is this due to the longer day length, temperatures above the optimum temperature for development, or both? Often this question can simply not be answered from field experiments. To disentangle both effects, we applied a two-step approach. Firstly, the photoperiod parameters were estimated in a PP-controlled reciprocal transfer experiment at constant temperature. In a second step these photoperiod parameters were used to study the temperature response under field conditions. The temperature response calibration problem becomes relatively simple when default values for cardinal temperatures can be assumed. In that case the only remaining parameters to be estimated are the temperature sums needed to complete the consecutive development stages. For rice, commonly used cardinal temperatures are 8, 30 and 42 °C for the base, optimum and maximum temperature, respectively (Matthews et al., 1995; Bouman et al., 2001). However, two recent studies (Zhang et al., 2008; van Oort et al., 2011) questioned the validity of these commonly used default parameters and showed that these could lead to bias in simulated phenology.

The objectives of this paper were therefore to (1) present a two-step approach for estimating the photothermal phenology of rice genotypes, (2) apply this approach to four modern aerobic rice genotypes and (3) study the validity of a set of standard cardinal temperatures commonly used for simulating rice phenology.

2. Materials and methods

In this section we first outline the set of equations used to describe the photothermal response to pre-flowering rice phenology (Section 2.1). In Section 2.2 the phytotron study for determining PP-sensitivity is presented, whereas the details regarding the field experiments on temperature sensitivity are outlined in Section 2.3. Both sections start with a description of the experimental set-up, followed by an outline of the procedures for parameter estimation.

2.1. Development stages and equations

Rice development can be partitioned into two main phases: the pre-flowering phase from emergence ($\theta = 0$) to flowering ($\theta = 1$) and the grain filling phase from flowering to maturity ($\theta = 2$). The pre-flowering phase can be further dissected into three sub-phases: the basic vegetative phase (BVP, $0 < \theta < \theta_1$), the PP-sensitive phase (PSP, $\theta_1 < \theta < \theta_2$) and the post-PSP phase (PPP, $\theta_2 < \theta < 1$). In the above θ (–) is the development stage with values of zero at emergence, 1 at flowering and 2 at maturity. Parameters θ_1 and θ_2 mark the start and the end of PSP, respectively. Durations of BVP, PSP, and PPP are expressed in days (d) and the value of θ increases daily with

development rate (DR; d^{-1}). Eq. (1) is used for obtaining development rate in the pre-flowering phases:

$$DR(T, P) = \begin{cases} \frac{g(T)}{f_0} & \theta \leq \theta_1 \text{ or } \theta \geq \theta_2 \\ \frac{g(T) * r(P)}{f_0} & \theta_1 < \theta < \theta_2 \end{cases} \quad (1)$$

In this equation, $g(T)$ and $r(P)$ are unit less temperature- and PP-response functions respectively, and f_0 is duration (in days) from emergence to flowering under optimal temperature and optimal day length. Eq. (1) is a simplified version of the equation used by Yin et al. (1997a,b) in which the photoperiod sensitive (PSP) and non-photoperiod sensitive (BVP and PPP) phases are distinguished, but a single function $g(T)$ is used for temperature effect and no distinction is made between the effects of day and night temperature. Function $r(P)$ represents the photoperiod response function.

In our two step approach, we first estimated the values of θ_1 and θ_2 and selected the most appropriate photoperiod response function $r(P)$ for each genotype separately. For the shape of $r(P)$ four functions were considered:

$$r(P) \begin{cases} 1 & \text{for } P \leq P_0 \\ 1 - \delta(P - P_0) & \text{for } P > P_0 \end{cases} \quad (2)$$

$$r(P) = \left[\left(\frac{P - P_b}{P_0 - P_b} \right) \left(\frac{P_c - P}{P_c - P_b} \right)^{\frac{(P_c - P_0)}{(P_0 - P_b)}} \right]^\beta \quad (3)$$

$$r(P) = \begin{cases} 1 & \text{for } P \leq P_0 \\ \frac{1}{1 + \gamma(P - P_0)} & \text{for } P > P_0 \end{cases} \quad (4)$$

$$r(P) = \begin{cases} 1 & \text{for } P \leq P_0 \\ \exp(k(P - P_0)) & \text{for } P > P_0 \end{cases} \quad (5)$$

Yin et al. (1997c) analysed a large data-set of cultivars and found a large genotypic variation in the PP-sensitivity parameters, whereas, the genotypic variation in optimum photoperiod (P_0) was relatively small. The estimated value of P_0 was very close to the widely used value i.e. 10 h d^{-1} (Vergara and Chang, 1985). In this study, the P_0 was therefore fixed to 10 h d^{-1} as this also helped to reduce the number of parameters to be estimated.

The PP-sensitivity parameters δ , β , γ and k were estimated such that $r(10) = 1$ and the best fit through the three data points (10 h d^{-1} , 12.5 h d^{-1} and 15 h d^{-1}) was obtained. Note that Eq. (2) shows a linear response; whereas the response is non-linear in Eqs. (3)–(5) (see the Results section for the shape of these equations fitted to experimental data). Eq. (3) is the beta function where P_b and P_c are the base and ceiling photoperiods, set to 0 h d^{-1} and 24 h d^{-1} , respectively (Yin and Kropff, 1996).

From the first step we derived, for each genotype, the values of θ_1 and θ_2 and the $r(P)$ function and its parameters. With these parameters fixed, we moved to step 2 where we estimated the remaining temperature parameters and f_0 (d). Temperature response was assumed to be the same for all developmental phases. First a bilinear temperature response model was used (Eq. (6)):

$$g(T_h) = \begin{cases} \frac{T_h - \text{TBD}}{\text{TOD} - \text{TBD}} & \text{TBD} < T_h < \text{TOD} \\ \frac{\text{TMD} - T_h}{\text{TMD} - \text{TOD}} & \text{TOD} < T_h < \text{TMD} \end{cases} \quad (6)$$

where TBD (°C) is the base temperature, TOD (°C) the optimum and TMD (°C) the maximum temperature and T_h the hourly temperature. We included the bilinear temperature model (6) because it is the most commonly used approach in existing crop growth models like ORYZA2000 (Matthews et al., 1995; van Oort et al., 2011;

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