Field Crops Research 156 (2014) 303–312

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

A simple model for simulating heat induced sterility in rice as a function of flowering time and transpirational cooling

P.A.J. van Oort[a,b,*], K. Saito[a], S.J. Zwart[a], S. Shrestha[a]

[a] Africa Rice Center (AfricaRice) 01 BP 2031 Cotonou, Benin
[b] Crop & Weed Ecology Group, Centre for Crop Systems Analysis, Wageningen University, PO Box 430, AK , 6700, Wageningen, The Netherlands

ARTICLE INFO

Article history:
Received 11 February 2013
Received in revised form
18 September 2013
Accepted 15 November 2013

Keywords:
Rice
Sterility
Heat
Climate change
Flowering
Crop modelling

ABSTRACT

Rice spikelets become sterile when exposed to high temperatures during flowering. Recent experimental studies have shown that transpirational cooling and flowering time (within the day) are important factors determining sterility. Extrapolation of the results from these experimental studies to other environments requires an integrated approach through incorporating such effects on spikelet fertility in a crop growth model. Here we review existing fertility functions (fertility as a function of panicle temperature) in different studies, and propose a simple new model that incorporates insights on diurnal patterns of temperature and relative humidity, recent studies on the relation between panicle temperature and sterility, and studies on how flowering time depends on environmental conditions. We illustrate the model for a typical arid and typical humid climate. There was a large difference between the existing fertility functions, and simulated fertility was very sensitive to differences in fertility functions, causing differences in simulated fertility of up to 59%. Ignoring transpirational cooling led to overestimation of sterility of 14–73%. Shifting flowering times from 12:00 to 9:00 led to a 7–35% reduction in sterility. Within day flowering duration had only a marginal impact (max 2%). We conclude that any climate change impact simulation is highly dependent on the choice of the fertility function, and identification of causes of differences between reported fertility functions deserves further investigation.

1. Introduction

Climate change will increase heat induced spikelet sterility in rice (Matthews et al., 1995, 1997; Wassmann et al., 2009; Krishnan et al., 2011). Already in the current climate sterility is in some parts of the world an issue of concern, especially when sowing outside recommended sowing windows (Dingkuhn et al., 1995; Chakrabarti et al., 2010; De Vries et al., 2011). Physiologically the effects of heat on sterility are quite well understood, based on research under controlled conditions in climate chambers and phytotrons (Horie, 1993; Matsui and Omasa, 2002; Matsui et al., 1999, 2000, 2001; Jagadish et al., 2007, 2008; Weerakoon et al., 2008; Rang et al., 2011). How to use their findings for prediction of sterility under field conditions remains a challenge. When researchers first used laboratory-derived temperature relations they found that predicted sterility was much higher than observed sterility. The main cause of this overestimation was that originally sterility was calculated with air temperature (Horie et al., 1995; Matthews et al., 1995, 1997). Since then researchers realised that it is spikelet (or panicle) temperature and not air temperature that determines sterility. Several researchers have since measured sterility as a function of panicle temperature (Abeysiriwardena et al., 2002; Matsui et al., 1997, 2007; Weerakoon et al., 2008; Yan et al., 2010, Julia, 2012). A comparison between these fertility functions has to date not been made.

Transpirational cooling is the main driver of the difference between air and panicle temperature and is greater at low relative humidity (*RH*) [i.e. due to a larger vapour pressure deficit (*VPD*)]. In semi-arid environments *RH* values during daytime can be as low as 20% and cause cooling of up to 7 °C (Matsui et al., 2007). In humid environments high *RH* and low wind speed restrict cooling and create sterility risk already at relatively low air temperatures (Tian et al., 2010 report a panicle temperatures of 0 to 4 °C higher than air temperature in an environment with *RH* 80% and wind speeds <1 m s^{-1}). Several studies have reported air temperature, panicle temperature and *RH* (Abeysiriwardena et al., 2002; Matsui et al., 2007; Weerakoon et al., 2008; Tian et al., 2010; Yan et al., 2010). Yoshimoto et al. (2005, 2011) developed a mechanistic model based on heat balance equations. Julia (2012) derived through linear regression an equation for panicle temperature as a function of several weather variables. Both these models require a high number of input variables, which are often not available.

---

[*] Corresponding author. Tel.: +31 317 481357; fax: +31 317 485572.
E-mail addresses: P.vanOort@cgiar.org, pepijn.vanoort@wur.nl (P.A.J. van Oort), K.Saito@cgiar.org (K. Saito), S.Zwart@cgiar.org (S.J. Zwart), S.Shrestha@cgiar.org (S. Shrestha).

0378-4290/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.fcr.2013.11.007

Air temperature increases during the day and along with increasing air temperature the *RH* drops. Spikelet temperature therefore also increases during the day, but less than air temperature. With increasing temperature during the day it is obvious that early morning flowering reduces exposure to heat induced spikelet sterility in rice and many efforts are underway to identify cultivars and QTLs for early morning flowering (Jagadish et al., 2008; Shivrain et al., 2009; Ishimaru et al., 2010, 2012; Thanh et al., 2010).

The importance of transpirational cooling and flowering time have been proven experimentally, as evidenced from the references above. Most existing crop growth models for quantifying heat induced sterility are too simple in the sense that they do not account for transpirational cooling and flowering time (e.g. the Horie (1993) and Horie et al. (1995) spikelet sterility model implemented in the ORYZA2000 model (Bouman et al., 2001) and also recently used by Yoshida and Horie, 2009). One mechanistic model simulates panicle temperature at different times of the day (Yoshimoto et al., 2011) but does not account for flowering time and does not include fertility functions (spikelet fertility versus temperature). The RIDEV2 model described in Julia (2012) does account for flowering time and transpirational cooling but requires many input parameters and several weather variables which are often not available.

Rice flowers in a field do not open at exactly the same time, but spread out over a period of mostly 2 to 4 h and it is during this period when the anthers are out in the open that heat induced sterility occurs. Since sterility changes non-linearly over time simulated fertility may be different depending on within flowering duration. If the effect is large then it needs to be included in further modelling studies and it would tell breeders that this an interesting trait to work on. A few studies have tested statistically if there is an effect of flowering duration, with mixed results (Jagadish et al., 2008). The drawback of empirical studies to test the effect of flowering duration is that such studies cannot consider extreme cases (very short or very long flowering duration) and that they are constrained by the peak flowering time, which cannot be controlled.

The objectives of this paper are (1) present a new simple model for simulating heat-induced sterility in rice, which can take accounts into flowering time, transpirational cooling and within-day flowering duration and (2) to present illustrations of the model to quantify how heat-induced sterility is affected by differences in fertility functions, flowering time, relative humidity and within day flowering duration. For objective (2), we consider a typical arid climate with low humidity and large diurnal temperature amplitude and a typical humid climate with high humidity and smaller diurnal temperature amplitude, both with the same daylength and daily average temperature.

2. Model description

Our model consists of five components discussed in the sections below. Parameters and variables are defined in Table 1. The model was implemented in MS Excel and can be obtained from the authors.

2.1. Diurnal temperature patterns

The diurnal pattern of air temperature as a function of daily minimum ($T_{\min}$) and maximum ($T_{\max}$) temperature and daylength (*DL*) is described by two equations, sinusoid during day (Eq. (1)) and exponential during night (Eq. (2)), often referred to as the sinus-exponential model. More on this model is found in Parton and Logan (1981), Goudriaan and van Laar (1994) and Ephrath et al. (1996). We follow the notation of Ephrath et al. (1996):

$$T_{\text{air}}(t) = T_{\min} + (T_{\max} - T_{\min}) \times \sin(\pi \times \frac{t - t_{\text{sunrise}}}{DL + 2 \times P}) \quad \text{for}\, t_{\text{sunrise}} < t < t_{\text{sunset}}(\text{daytime}) \tag{1}$$

$$T_{\text{air}}(t) = \frac{T_{\min} - T_s \times \exp(-\eta/\tau) + (T_s - T_{\min}) \times \exp(-(t - t_{\text{sunset}})/\tau)}{1 - \exp(-\eta/\tau)} \times \text{for} \quad t < t_{\text{sunrise}} \quad \text{and} \quad t > t_{\text{sunset}}(\text{night time}) \tag{2}$$

The temperature at sunset, T_s in Eq. (2), is obtained by filling in for time *t* in Eq. (1) the time of sunset. Night length η is calculated as 24-*DL* and τ is the nocturnal time coefficient. The sunrise time, sunset time and peak temperature time are calculated as:

$$t_{\text{sunrise}} = LSH - 0.5 \times DL \tag{3}$$

$$t_{\text{sunset}} = LSH + 0.5 \times DL \tag{4}$$

$$t_{\text{peaktemp}} = LSH + P \tag{5}$$

In these equations, *LSH* is the time at which sun is at its highest point. In solar time the sun is at its highest point at 12 h but local time zones and longitude can cause *LSH* to deviate markedly from 12 h. Changing the value of *LSH* shifts the whole temperate versus time graph to the left or right on the time axis but has no effect on the shape of the graph. Maximum temperature occurs some time after solar noon, cf. Ephrath et al. (1996) we assume this is $P = 1.5$ h. For any given day of the year and latitude, daylength *DL* can be calculated using standard astronomic equations which we will not discuss here. The fact that $T_{\min}$ and $T_{\max}$ values differ between days can be accounted for as follows. In Eq. (1) set $T_{\min}$ to $T_{\min(J+1)}$ for $t > t_{\text{peaktemp}}$, that is after peak temperature time we calculate with the $T_{\min}$ value of the next day $J+1$. In Eq. (2) for $0 < t < t_{\text{sunrise}}$ use $T_{\min}$ and the T_s of the previous day (based on $T_{\max(J-1)}$ and $T_{\min}$) and for $t_{\text{sunset}} < t < 24$ calculate using $T_{\min(J+1)}$ *and* the T_s of the current day (based on $T_{\max}$ and $T_{\min(J+1)}$).

Ephrath et al. (1996) also provide the equation for the diurnal pattern of relative humidity (*RH(t)*, 0 to 100%). It is calculated using the vapour pressure at dew point temperature (*VPA*) and *ES(t)*, the saturated vapour pressure (in hPa) at a given time *t* of the day:

$$VPA = 6.107 \times \exp\left(\frac{T_{d(\text{cal})} \times 17.4}{239 + T_{d(\text{cal})}}\right) \tag{6}$$

$$ES(t) = 6.107 \times \exp\left(\frac{T_{\text{air}}(t) \times 17.4}{239 + T_{\text{air}}(t)}\right) \tag{7}$$

$$RH(t) = 100\% \times \max\left(1, \frac{VPA}{ES(t)}\right) \tag{8}$$

In these equations the crucial parameter is the dew point temperature $T_{d(\text{cal})}$. Ephrath et al. (1996) experienced difficulties in estimating this parameter, finding that it was different between locations and in one location correlated with $T_{\max}$. Location specific hourly (US) and daily average (global) dew point temperatures from around the globe are nowadays freely available at http://cdo.ncdc.noaa.gov/cdo/info.html (Daly et al., 2000). Note that from the above equations the vapour pressure deficit *VPD*(*t*) can be calculated as $VPD(t) = \max(0, ES(t) - VPA)$.

2.2. Transpirational cooling

We conducted a meta-analysis of studies in which simultaneously air temperature, panicle temperature and relative humidity were observed (Table A1). The dataset covers a wide range of environments (*RH* 21 to 88%, T_{air} 28.0 to 37.2oC, $n = 42$). The