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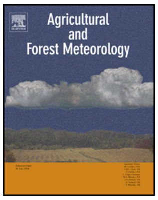

Temperature thresholds for spikelet sterility and associated warming impacts for sub-tropical rice

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ABSTRACT

Identifying a reliable and robust temperature threshold inducing rice spikelet sterility under field conditions involving cultivars with highly varying phenology has been a major limitation. This challenge has been a consistent bottleneck in devising a phenotyping strategy for rice breeders and to accurately estimate heat stress impacts by the climate and crop modeling communities. In an attempt to address this challenge, we used 292 diverse indica cultivars, recorded 15 min air temperature data during the key flowering period across wet season and two consecutive dry (summer) seasons. We identified 33 °C as the critical threshold beyond which large sterility increases were observed. This is the first report that demonstrates the need to consider cultivar and seasonal fixed effects in a regression model framework to derive meaningful temperature thresholds. We find that an additional growing degree hour (*GDH*) above 33 °C is associated with a 0.26 percentage point increase in sterility. The average and maximum exposures above this threshold in the sample data are 13.0 and 46.5 h, respectively, corresponding to a 3.4 and 12.0 percentage point increase in sterility. We simulate warming impacts between 0.5–2.0 °C increase in daily temperatures, which increases sterility between 2.9–13.1 percentage points for the dry summer season and 0.2–3.2 percentage points for the wet season. Evidence for threshold heterogeneity across different sterility classes – low, medium and high sterility cultivar groups is tested and we find limited evidence for this extension of the model. The identified threshold can be utilized by breeders to test contrasting cultivars or segregating mapping populations in an unbiased set up and for precise heat stress impact modeling exercises. Heat sensitivity analysis indicated substantial genetic variability for heat induced spikelet sterility, providing ample evidence for producer adaptation to a warming climate by developing and switching to more heat stress resilient cultivars.

1. Introduction

Mean global temperatures are predicted to increase by up to 2 °C between 2046 and 2065, and will likely be accompanied by an increase in frequency and intensity of extreme heat events (IPCC, 2013). Although typically short in duration, when these events coincide with the highly temperature-sensitive flowering stage in rice they can induce spikelet sterility and yield reductions (Bahuguna et al., 2015; Jagadish et al., 2007). As an example, a heat event in 2003 along the Yangtze River in China resulted in daytime temperatures above 38 °C and lasted more than 20 days. The timing coincided with the flowering stage of local rice, damaging an estimated three million hectares of rice, and resulted in approximately 5.18 million tons of paddy rice loss (Li et al., 2004). Similar losses were recorded in the same region as a result of heat events during the 2006 and 2007 growing seasons (Zou et al., 2009). A 2007 heat event in the Kanto and Tokai areas of Japan had temperature reaching 40 °C and coincided with flowering, resulting in 25% reduction in paddy rice yield (Hasegawa et al., 2011).

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Predicting the impact of increased frequency and intensity of heat events under climate change during critical rice-growth stages is an important and evolving science. Of key interest is the temperature range used to define extreme heat. Climate model predictions from Gourdji et al. (2013) focused on the rice reproduction phase by utilizing a threshold of 36 °C. Their findings suggest that the percentage increase in rice growing area exposed to a minimum of 5 days of temperatures above this threshold will increase spikelet sterility from 8% in the 2000s to 16% by 2030 and 27% by 2050. A similar exercise focusing more generally on a collection of agricultural crops (maize, wetland rice, soybean), used 35 °C as the threshold (Teixeira et al., 2013). Laborte et al. (2012) used a fixed 10 day flowering period interval and a threshold of 35 °C in their effort to identify vulnerable rice growing regions.

Flowering has been identified as the most sensitive stage to high temperature stress, and prevailing ambient temperatures during anthesis (flower opening) have been causally linked to reproductive outcomes (Jagadish et al., 2007; Yoshida et al., 1981). Rice flowers open for approximately 45 min, during which a series of heat stress sensitive processes such as anther dehiscence, a process through which pollen is released from the anthers; pollination, wherein pollen grains are deposited onto the stigmatic surface (Jagadish et al., 2010; Matsui et al., 2001), pollen germination and pollen tube growth occur. Fertilization is typically completed within 1.5 to 4 h after anthesis (Cho, 1956).

Controlled environments have been extensively used to determine the mechanistic responses of rice cultivars to high temperature stress during the flowering stage under a range of high temperature exposures (Jagadish et al., 2007, 2008, 2010; Matsui and Omasa, 2002; Yoshida et al., 1981). A threshold of 35 °C has been proposed for heat susceptible cultivars while a threshold of 38 °C is considered more appropriate for identifying true heat tolerant varieties (Yoshida et al., 1981). Nakagawa et al. (2002) drew on several controlled environmental studies using phytotrons or temperature gradient chambers, and posited a threshold of 33 °C, beyond which a linear decline in spikelet fertility was proposed. Thus, these studies provide a wide range of temperature thresholds and reflect the lack of consensus in the literature.

Although controlled environments are useful in quantifying biological responses to well-defined temperature exposures, their main shortcoming lies in their inability to realistically replicate actual growing conditions. This is especially challenging as temperature, precipitation, light intensity, and wind speed all play important roles in plant growth and fertility. Plant exposure to these variables varies spatially and temporally both within and across growing seasons, and the outcomes themselves at any one point in time are often correlated (e.g. low precipitation and high temperature often occur together). In addition, physical space constraints often limit the number of cultivars that can be included in the experimental design (Jagadish et al., 2008; Prasad et al., 2006).

In light of the above, the current literature on rice heat stress is characterized by a lack of consensus on the appropriate threshold used to define extreme heat (Rezaei et al., 2015; Sánchez et al., 2014). We address this issue here by utilizing recent statistical advances for identifying such thresholds using regression analysis, combined with a balanced panel of rice sterility outcomes from field-trials conducted in Tamil Nadu, India. Using such data allows us to overcome the main short-comings associated with controlled environments as we included 292 cultivars in each of three growing seasons. On the ground weather stations allowed us to directly link temperature outcomes to the test plot with readings taken every 15 min. In principle, an extreme heat threshold should be determined by the exposure-level above which large yield losses begin to accumulate. A strong driver of such losses is heat stress induced spikelet sterility during the flowering stage of development and is thus the focus of our study.

2. Materials and methods

2.1. Data

The data were collected at Coimbatore, Tamil Nadu (11.1176° N, 76.9944° E) in India for the 2012 wet season (July–November), and the 2013 and 2014 dry seasons (February–June). The data were collected on 292 different rice cultivars that were planted under a randomized design in each of three seasons. The panel includes 252 indica, 12 japonica, 9 landraces, 7 breeding lines and 12 improved rice cultivars. The diversity panel (292 cultivars) used in this study was assembled through a major effort involving entries representing major tropical rice growing regions, as a part of the GRISP – Global Rice Phenotyping Network (http://ricephenonetwork.irri.org) and are not biased to any specific geographic region. The pooled data is thus a balanced panel of 876 observations. Each cultivar was grown in a plot size of 2.4 m (length) × 1.4 m (width) with a spacing of 20 × 20 cm, accommodating 8 rows. Observations were recorded from the middle 6 rows to overcome border row effect. For crop establishment standard recommended package of practice for rice (150:50:50 kg NPK/ha) was followed as per crop production guide 2012, TNAU, Coimbatore (http://agritech.tnau.ac.in/agriculture/agricropproduction cereals rice tranpudlow.html). Nitrogen (N) and potassium (K) fertilizers were applied in splits while the 50 kg of phosphorus (P) fertilizer was applied as basal dose. First split was added a day before transplanting (16.6 kg/ha K), second split at active tillering stage (50 kg/ha N), third split at panicle initiation stage (50 kg/ha N and 16.7 kg/ha K) and fourth split at heading (50 kg/ha N and 16.7 kg/ha K). In all three seasons, about 5–10 panicles on the main tillers that were at the same developmental stage were tagged at the start of heading, for each of the 292 cultivars. The day on which a particular cultivar had its first spikelet flowered (anthers visible to the outside), and when 50% and 100% plants flowered in the plot were recorded as first, 50% and 100% (complete) flowering, respectively. The flowering period is defined as the number of days (duration) from the first spikelet opening to 50% of plants in the plot undergoing flowering. Since the main tiller panicles were meticulously targeted (as they emerged early among all tillers), the days from the start (i.e. first flower opening) to 50% flowering at the plot level were considered for the analysis. This approach allowed capturing the duration within which the targeted (tagged) main tiller panicles completed their flowering. Once the plants reached physiological maturity, the tagged panicles were harvested separately and spikelet fertility was estimated following Mohammed and Tarpley (2009) and Prasad et al. (2006).

Many studies attempting to assess the effect of climatic change have defined temperature variables in growing degree hours (*GDH*) and used these to identify thresholds above which temperatures have a detrimental effect on yields. We followed, Schlenker and Roberts (2009) piecewise linear approach, but focused on one threshold since our range of observed temperatures (21–37 °C) are smaller than theirs (0–39 °C). Unlike Welch et al. (2010), which focused on the effects of minimum and maximum observed temperatures, we are interested in determining a threshold at which large effects begin to materialize. In addition, it has been well documented that rice flowering begins at around 0900 h and ends before noon on any given flowering day (Ishimaru et al., 2010; Yoshida et al., 1981). We extended this window from 0900 h to 1400 h to accommodate any late flowering spikelets and to account for the damaging impact of temperatures during the fertilization and initial embryo formation.

An automatic weather station (Vantage Pro2^{TM} Davis) was placed just beside the experimental plot and all weather parameters were recorded at 2 m from the ground surface once every 15 min. Temperature observations measured at 15 min intervals between 0900 h to 1400 h (Indian standard time scale) were used