Field survey on rice spikelet sterility in an extremely hot summer of 2018 in Japan

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Abstract

In rice (*Oryza sativa* L.), heat-induced spikelet sterility (HISS) has long been recognized a major threat in the production, and currently the potential risk of yield reduction is likely to be increasing under global warming. However, there have been few studies on HISS conducted under field conditions. In recent years in Japan, extremely high temperatures have frequently recorded in the daytime during the summer. In 2018, heat wave lasted from mid-July to late August, which overlapped the typical rice heading period from eastern to western Honshu and raised a concern about HISS during flowering. To examine this possibility, we surveyed rice sterility in eight prefectures in the Kanto, Tokai, and Kinki regions. During surveys in 2018 and 2019, we collected field data on the sterility of ‘Koshihikari’, the most popular rice variety in Japan, and the sterility ranged from 3.7 to 15.4% in paddy fields. The sterility tended to be higher in the paddy fields where heading occurred during the heat wave. We modeled the sterility rate using the heat dose based on daytime mean panicle temperature, with a threshold for HISS at 33°C. The model estimates based on meteorological data showed that HISS can be induced even under current climatic conditions, depending on the timing of heading. Considering the projected global warming, this study raises an issue that rice plants would face a risk of HISS under the temperate climate in Japan.

Key words: Heat dose, Heat-induced spikelet sterility, Heat wave, *Oryza sativa* L., Panicle temperature

1. Introduction

Global warming and the resulting increased frequency of heat waves will likely reduce rice yields due to the effects of heat stress (Wassmann *et al.*, 2009; Horie, 2019). One of the major concerns in heat stresses in rice is heat-induced spikelet sterility (HISS) at flowering. Satake and Yoshida (1978) showed that anthesis (flowering) is the most heat-sensitive process during the reproductive stage, since high temperatures at this time can lead to failure of grain setting. Previous studies using chamber experiments have shown that HISS begins when the daily maximum air temperature exceeds a certain threshold, such as 35°C, and that a rapid decline in fertility occurs within 4 to 5°C above this threshold (Kim *et al.*, 1996; Maruyama *et al.*, 2013).

However, when the results of the chamber experiments were applied to open fields, the estimated sterility rate was much higher than the observed rate (Hasegawa *et al.*, 2011). One main reason for this overestimation is the gap between the temperature of plant organs and the air temperature; this gap results from transpirational

cooling in paddy fields. Matsui *et al.* (2014) reported that the sterility rate was much lower than expected at extremely high temperatures, exceeding 40°C, in a semi-arid Australian environment. The dry and windy climate stimulated transpirational cooling of the plant canopy, which reduced the panicle temperature by as much as 6°C, resulting in stable pollination even under extremely hot conditions. On the other hand, Tian *et al.* (2010) reported that the panicle temperature can exceed the air temperature by 4°C in the Jiangnan Basin, China, where the humid conditions and low wind speed reduced transpirational cooling of the plant canopy, resulting in high sterility despite a moderate daily maximum air temperature of approximately 35°C. These cases showed the effectiveness of panicle temperature, but not air temperature, to predict HISS in paddy fields.

Previously, researchers have focused on quality deterioration as the effect of heat stress in Japanese rice, since the percentages of white immature grains (i.e., chalky rice) were increased by high temperatures during the ripening period (Mitsui *et al.*, 2016). This deterioration has already become noticeable for farmers and researchers and was predicted by models that used appropriate temperature variables (e.g., Masutomi *et al.*, 2015; Ishigooka *et al.*, 2021). To mitigate this damage, adaptation measures are already taken, such as the development of heat-tolerant varieties and improved cultivation methods (Morita *et al.*, 2016).

However, little research has been conducted on HISS in Japan because researchers have been confident that the problem is not apparent so far, and not serious under Japan’s current climatic

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conditions. Hasegawa *et al.* (2011) conducted a pioneering survey of rice sterility in paddy fields in five prefectures in Japan during the record-breaking hot summer in 2007, when an unprecedented temperature of 40.9°C was recorded in mid-August in Kumagaya, Saitama Prefecture, in the Kanto region, and in Tajimi, Gifu Prefecture, in the Tokai region. Under such extremely high temperature conditions with heat wave (the temperature remained significantly higher than normal for a certain period), higher sterility rates were observed compared with the normal year, 2008. This indicated that HISS that had previously been observed in controlled environments, could also occur in Japanese paddy fields. The sterility rate was, however, smaller than that estimated from the daily maximum air temperature based on the findings of the chamber experiments. One explanation for this may be that the panicle temperature during flowering was lower than the daily maximum air temperature (Yoshimoto *et al.*, 2011). In addition, on a regional or prefectural scale, flowering of many rice crops did not coincide with the heat wave, resulting in no obvious yield losses due to HISS. However, there has been no other research on the actual situation of HISS in paddy fields in Japan, and little data exists on sterility rates compared to the larger body of research on rice yield and quality collected annually during Japan's national Crop Survey. Therefore, there is considerable uncertainty in predicting HISS under present and future environments, and how it will affect yield remains to be studied. First of all, it is necessary to understand the actual status of HISS in the field and to identify its explanatory variables. Only when this knowledge allows us to quantify HISS in terms of environmental variables, will we be able to understand the process by which HISS influences yield.

In recent years, Japan has experienced frequent heat waves during the summer. In 2018, the summer was extremely hot, with temperatures occasionally surpassing the high temperature record in the 2007 survey, and the air temperature reached a record

high of 41.1°C on July 23 in Kumagaya, Saitama Prefecture. In addition, the heat wave lasted from mid-July to late-August, which includes the typical rice heading period in eastern to western Honshu, which raised concerns about the possibility of HISS during flowering. To examine this possibility, we conducted a sterility survey in eight prefectures in the Kanto, Tokai, and Kinki regions that experienced high temperatures in 2018, according to the 2007 survey protocol. For comparison, we also conducted the same survey in 2019, which had more normal temperatures.

Our objectives were (1) to determine the occurrence of the HISS in 2018, an extremely hot year; (2) to determine the relationship between the sterility rate and thermal variables such as the air and panicle temperatures; and (3) to estimate the risk of HISS induction in 2018 and 2019 under the current climate conditions from meteorological data using the relationship determined in (2). Our ultimate goal is to estimate the impact on yield through HISS in the current and future climates. To achieve this goal, however, this study intended to first accumulate quantitative data of HISS, the actual status of which in paddy fields has not yet been clarified. This will reduce the uncertainty in yield impact assessment by determining the HISS using the appropriate environmental variables under current and future climatic conditions and contribute to the development of adaptation measures for HISS.

2. Materials and Methods

2.1 Study sites

We selected eight prefectures that had high temperatures in the summer of 2018 as our study sites (Table 1), and repeated the survey at the same sites in 2019. The study sites were in Ibaraki, Chiba, Gunma, and Saitama Prefectures in the Kanto region (in eastern Honshu), and in Gifu, Aichi, and Mie Prefectures in the Tokai region and Kyoto Prefecture in the Kinki region (in central and western Honshu). The study sites were mostly paddy

Table 1. Locations of the study sites.

Prefecture	Municipality	Location	Latitude (°N)	Longitude (°E)	Elevation (m)	Number of fields (<i>n</i>)	
Kanto region							
Ibaraki	Mito city	Ibaraki Agricultural Center	36.44	140.45	35	3 (2)	2 (2)
Ibaraki	Ryugasaki city	Ibaraki Agricultural Center	35.89	140.21	5	3 (2)	3 (2)
Ibaraki	Tsukubamirai city	On-farm	35.97	139.99	10	3 (3)	4 (3)
Chiba	Chiba city	Chiba Prefectural Agriculture and Forestry Research Center	35.55	140.16	7	2 (3)	1 (3)
Chiba	Sanbu county, Yokoshibahikari town	On-farm	35.70	140.48	5	1 (3)	
Gunma	Tatebayashi city	Gunma Agricultural Technology Center	36.25	139.57	18	2 (2)	1 (3)
Gunma	Oura county, Itakura town	On-farm	36.20	139.63	15	3 (3)	4 (3)
Saitama	Kumagaya city	Saitama Prefectural Agriculture and Forestry Research Center	36.17	139.35	37	1 (2)	1 (2)
Tokai and Kinki regions							
Gifu	Gifu city	Gifu Prefectural Agricultural Technology Center	35.44	136.70	15	1 (1*)	1 (3)
Gifu	Ibi county, Ono town	On-farm	35.48	136.64	33	2 (1*)	
Aichi	Nagakute city	Aichi Agricultural Research Center	35.17	137.06	95	4 (1*)	2 (2)
Mie	Iga city	Mie Prefecture Agricultural Research Institute	34.71	136.14	158	3 (3)	3 (2)
Mie	Matsusaka city	Mie Prefecture Agricultural Research Institute	34.64	136.50	6	4 (1*)	1 (2)
Kyoto	Kameoka city	Kyoto Prefectural Agriculture, Forestry and Fisheries Technology Center	35.01	135.56	102	1 (2)	2 (2)

n means the number of replicates of the paddy fields at the public experiment stations or the number of sampling areas from one paddy field in the farmlands. A superscripted * mark on the number *n* indicates that samples were only obtained from one plot as replicate or area (*n*=1) due to few paddy fields available for survey as we initiated the survey urgently in 2018.

fields at public experiment stations, but in some prefectures, we included farm paddy fields.

We selected ‘Koshihikari’, the most popular rice variety in Japan (Kobayashi *et al.*, 2018), as the target variety for our study, and collected rice samples from paddy fields at the study sites. The basic cultivation information, such as the planting density; the amounts and timing of fertilizer application; and the dates of sowing, transplanting, and heading, were recorded in the paddy fields at the public experiment stations. We collected the same information for the farm paddy fields through interviews. The cropping season was almost typical for each prefecture, with sowing dates ranging from March 12 to May 11, transplanting dates from April 10 to June 1, and heading dates from July 11 to August 9. The amount of nitrogen (N) fertilizer applied ranged from 4 to 10 g m⁻² in paddy fields with basal application only. While in paddy fields where top-dressing was applied, the amounts of N fertilizer ranged from 2 to 6 g m⁻² of basal application and from 0.85 to 5.2 g m⁻² of top-dressing, with a total from 3.8 to 10.8 g m⁻², and top-dressing was applied once or twice in the range of from 31 to 6 days before the respective heading date. Thus, all paddy fields were cultivated under conventional range of typical fertilizer, with no special cultivation conditions such as extremely low fertilizer application, which tended to increase the sterility rate (Hasegawa *et al.*, 2011). Cultivation was done by pest control and water management conventional for each paddy field.

2.2 Sampling and measurements

We harvested five consecutive hills in the same row adjacent to the yield survey area in the paddy fields from two or more replicates at the public experiment stations. In the farm paddy fields, which were not experimental fields, three locations were set along a diagonal line of one paddy field as sampling areas representative of the paddy field as an alternative of replicates, from which we respectively harvested five consecutive hills in the same row that avoided the edge of the paddy field. The rice samples were air-dried and threshed. The spikelets were then water-screened and separated into submerged (fertile) spikelets and floating spikelets. After drying, the floating spikelets were soaked in an 80% ethanol solution to decolor the hull, after which the degree of ovary growth was examined by touch and by light penetration (Kobata *et al.*, 2010). Spikelets that were totally empty and that had ovary growth less than half of the length of the spikelet were defined as sterile spikelets, and the floating spikelets that were not sterile were defined as stunted spikelets. We counted the number of spikelets in each category (sterile, stunted, and fertile) and calculated their percentages of the total number of spikelets.

2.3 Meteorological data

To get the overview of the two-year weather conditions of the eight target prefectures, we used weather data from the Japanese Weather Office or an AMeDAS station near the study sites. For detail analysis of the relationship between the sterility rate and weather conditions in each surveyed paddy field, the values of climate parameters were calculated using the 1-km grid-point meteorology data developed by NIAES (Seino, 1993; Ishigooka *et al.*, 2017) at the point nearest to the respective site. We focused on the daily maximum air temperature (T_{amax})

and the daytime mean panicle temperature based on the 6-hour average from 09:00 to 15:00 (T_{pd}) as explanatory variables for the sterility rate. Daily maximum air temperature has often been used as an explanatory variable for the sterility rate (e.g., Nakagawa *et al.*, 2003; Hasegawa *et al.*, 2011) because of the easy availability of data. The hourly panicle temperature was calculated using the heat balance model, IM²PACT (Yoshimoto *et al.*, 2011). Setting the actual flowering hours during the day at each study site as the time for calculating the average panicle temperature may provide the optimal explanatory variable for sterility rate. In this study, however, we chose the period from 09:00 to 15:00 for the averaging, which covers the entire flower opening time for ‘Koshihikari’ (Ishimaru *et al.* 2010).

The thermal variables were calculated by averaging (T_{amax} and T_{pd}) or by calculating the heat dose (HD) over 5 days around the heading date according to the method of Hasegawa *et al.* (2011). We calculated HD_c for temperatures above the threshold temperature (c) based on the daytime mean panicle temperature (T_{pd}) as follows:

$$HD_c = \sum_{i=a-2}^{a+2} \max(T_i - c, 0) \quad (1)$$

where T_i is the T_{pd} value on day i , and a is the center date of the 5-day accumulation period.

3. Results

3.1 Climate in 2018 and 2019

Since August 16, 2007, when the record high temperature of 40.9°C was recorded at that time in Kumagaya, Saitama Prefecture and Tajimi, Gifu Prefecture, Japan has experienced hot summers and the record high temperature has been updated. In 2018, the record high temperatures were updated in many places, with 41.1°C recorded in Kumagaya, Saitama Prefecture on July 23, and 41.0°C in Kanayama, Gifu Prefecture on August 6 and in Mino, Gifu Prefecture on August 8. In 2019, no location had recorded a high temperature reaching 41.0°C. The frequent extreme high temperatures from July to August in 2018 overlapped the typical heading season for rice in Japan. Table 2 shows the climatic condition in the heading seasons of 2018 and 2019. The seasonal average daily mean air temperature was more than 2°C higher than normal in all eight prefectures of the study site, and up to 3.5°C higher in Gifu, Aichi, and Saitama Prefectures. In 2019, this temperature was slightly higher than normal, with a difference of 0.4 to 1.1°C.

In 2018, the seasonal average daily solar radiation was more than 3 MJ m⁻² d⁻¹ higher and the seasonal precipitation was much lower than normal in all eight prefectures (Table 2). In contrast, the solar radiation in 2019 was normal or slightly lower than normal in Tokai and Kinki regions, and the precipitation was higher than in 2018, especially in Gifu and Aichi Prefectures, where the difference was much larger. In summary, 2018 was a year of extremely high air temperature, with high radiation and low rainfall, whereas 2019 had a slightly warmer air temperature than normal, with normal radiation and higher rainfall than in 2018.

3.2 Spikelet sterility in eight prefectures

The measured sterile and stunted rates for the eight prefectures were plotted against the respective 50% heading dates along with

Table 2. Seasonal means of daily mean air temperature, solar radiation, and seasonal precipitation in the heading seasons for 32 days from July 10 to August 10 in 2018 and 2019 at eight prefectures. Weather data were obtained from the Japanese Weather Office or an AMeDAS station near the study site. Normal values are averaged over the 30-year period from 1981 to 2010.

Prefecture (name of Japanese Weather Office/AMeDAS station near the study site)	Daily mean air temperature (°C)			Solar radiation (MJ m ⁻² d ⁻¹)			Precipitation (mm)		
	(Normal)	2018	2019	(Normal)	2018	2019	(Normal)	2018	2019
Kanto region									
Ibaraki (Tateno)	(24.9)	27.8	26.0	(16.2)	20.4	17.3	(124)	110	120
Chiba (Chiba)	(26.1)	28.6	26.6	(17.1)	20.3	17.4	(120)	87	136
Gunma (Tatebayashi)	(26.4)	29.5	27.1	(15.0)	20.2	16.6	(151)	73	89
Saitama (Kumagaya)	(26.3)	29.7	27.2	(16.0)	20.7	16.6	(163)	73	121
Tokai and Kinki regions									
Gifu (Gifu)	(27.5)	31.1	28.1	(17.7)	24.2	17.8	(212)	21	350
Aichi (Nagoya)	(27.3)	30.8	27.7	(17.7)	23.5	17.4	(174)	6	236
Mie (Ueno)	(26.1)	28.8	26.9	(17.3)	22.6	17.0	(184)	105	186
Kyoto (Kyoto)	(27.8)	30.7	28.3	(16.8)	21.6	16.2	(190)	26	193

Fig. 1. Seasonal variation of daily maximum air temperature (lines) and the sterile or stunted rates (dots) plotted against the date of 50% heading in a paddy field in (a, b) 2018 and (c, d) 2019. The upper graphs (a, c) show data from the Kanto region and the lower graphs (b, d) show data from the Tokai and Kinki regions. Weather data were obtained from the Japanese Weather Office or an AMeDAS station near the study site. Values for the sterile and stunted rates are the mean $\pm$ SE for each paddy field.

the daily maximum air temperature (Fig. 1). In 2018, the Kanto region experienced several heat waves in mid- to late July, early August, mid-August, and late August, with daily maximum air temperatures well above 35°C (Fig. 1a). The heat was especially severe in Gunma and Saitama. The Tokai and Kinki regions also experienced heat waves in mid- to late July and early August (Fig. 1b). The mean sterility rate (averaged over replicates) ranged from 3.7 to 15.4% in 2018, with a particularly high sterility rate observed in paddy fields in the Kanto region, where panicles emerged around the time of the heat wave in late July.

In 2019, temperatures were low due to the long rainy season before late July, but high temperatures prevailed from late July to

early August, with the daily maximum air temperatures exceeding 35°C, especially in Gunma and Saitama in the Kanto region (Fig. 1c, d). The mean sterility rate ranged from 3.7 to 10.5% in 2019, lower than in 2018, but tended to increase in paddy fields where panicles emerged during the high-temperature period.

The percentage of stunted spikelets in two-years (all eight prefectures combined) ranged from 2.8 to 20.8%, with a mean value of $9.7\% \pm 0.51\%$ S.E. The stunted spikelets rate was significantly higher in paddy fields in the Kanto region in 2018 than others (ANOVA, $P < 0.001$), and the high percentages of sterile and stunted spikelets sometimes reduced the fertility rate below 70%.

Fig. 2. Relationships between the sterility rate and the thermal variables (a) daily maximum air temperature (T_{amax}) and (b) daytime 6-hour mean panicle temperature from 09:00 to 15:00 (T_{pd}). The thermal variables were averaged over a 5-day period centered on the 50% heading date. Thermal variables were calculated using the 1-km grid-point meteorology data developed by NIAES (Seino, 1993; Ishigooka *et al.*, 2017) at the point nearest to each paddy field, and the hourly panicle temperature was calculated using the heat balance model, IM²PACT (Yoshimoto *et al.*, 2011). Values for the sterility rate are the mean $\pm$ SE for each paddy field.

3.3 Relationship between spikelet sterility and thermal variables

We plotted the sterility rate against the thermal variables (T_{amax} and T_{pd}) averaged over a 5-day period centered on the 50% heading date (Fig. 2). The sterility rate was significantly related to the average values of both T_{amax} and T_{pd} over the 5 days of the heading period, but the difference in the response curves between years was slightly smaller when the T_{pd} was used as the temperature index, where the response curves in 2018 and 2019 were consistent.

Fig. 3. Coefficient of determination (R^2) for the linear relationship between the sterility rate and the daytime panicle temperature (T_{pd}) or the corresponding heat dose (HD). The numbers in the HD variable names represent the threshold temperature for T_{pd} . X-axis represents the center point of the 5-day period used to calculate the average temperature or HD in days after heading. Data are from both years of 2018 and 2019 ($n=58$). The horizontal solid line indicates the R^2 level above which the regression is significant at the 0.01% level.

Figure 3 shows the distribution of the coefficient of determination (R^2) of the linear relationship between the sterility rate and the T_{pd} and the corresponding HD relative to the center point of the 5-day period used to calculate T_{pd} or HD . The R^2 value peaked when the center of the 5-day period was set at the 50% heading date (days after heading = 0). The peak value of R^2 was larger when using HD based on T_{pd} than when using T_{pd} itself as the independent variable for linear regression, and it was the largest when the HD threshold was about 33 to 34°C. The peak value of R^2 was largest (0.57) when the HD threshold was 34°C, but Figure 2b shows that there were few cases when T_{pd} exceeded 34°C. The number of non-zero HD_{34} data was therefore greatly reduced, resulting in a larger R^2 value.

Fig. 4. Relationship between the sterility rate and the heat dose with a 33°C threshold (HD_{33}) based on the daytime mean panicle temperature. Values for the sterility rate are the mean $\pm$ SE for each paddy field.

Therefore, we adopted the HD value with a threshold of 33°C (HD_{33}) as a more representative estimate, and used that value to investigate the relationship with the sterility rate (Fig. 4). The relationship between the sterility rate and HD_{33} based on T_{pd} was approximated by the following exponential equation:

$$\text{Sterility rate (\%)} = 5.32 \exp(0.0973 HD_{33}), \quad (2)$$

where the coefficient of determination (R^2) was 0.51.

3.4 Distributions of possible spikelet sterility in the summers of 2018 and 2019

We used equation 2 to estimate the distribution of possible spikelet sterility at the study sites in the summers of 2018 and 2019. Specifically, we assumed that each day from July 1 to September 10 represented a potential 50% heading date, and then calculated the HD_{33} for the 5 days centered on each of those days to obtain the sterility rate using equation 2. We classified the calculated sterility rates by season and region, and plotted their distributions as box-and-whisker plots (Fig. 5).

In 2018, sterility could most possibly occur in mid-July in all regions. In Kanto region and in the Tokai and Kinki regions, the median sterility rates were 6.6% and 9.0%, respectively, and the maximum values were 12.7% and 15.5%, respectively. In this survey, the number of samples from paddy fields that headed in mid-July in the Tokai and Kinki regions was smaller than in the Kanto region (Fig. 1b), and the maximum overall sterility rate was observed in mid-July in the Kanto region (15.4%), but the risk of sterility would have been higher in the Tokai and Kinki regions than in the Kanto region if heading occurred during this period. Sterility

could have been occurring in later periods as well. The sterility rate could reach a maximum of 11.7% and 10.3% in late July, and 10.7% and 9.5% in early August, in the Kanto region and in the Tokai and Kinki regions, respectively. In late August, the risk of sterility increased in the Kanto region, with a maximum value of 8.5%.

In 2019, the likelihood of induced sterility was lower than in 2018, except in the Kanto region in early August, with a median sterility rate of 8.3% and a maximum value of 14.4%, which were comparable to the predicted sterility under the heat wave in mid-July in 2018. In early August in 2019, the risk of sterility increased also in the Tokai and Kinki regions, with a maximum value of 9.0%.

4. Discussion

‘Koshihikari’ is the most popular rice variety and is widely cultivated in Japan. It is moderately tolerant to HISS (Matsui *et al.*, 2005). During our survey in 2018 and 2019, we were able to collect data on the sterility of ‘Koshihikari’, and sterility ranged from 3.7 to 15.4% in paddy fields under conventional cultivation practices with standard fertilizer application. Throughout both years, there was a tendency for higher sterility in paddy fields where the heading occurred during heat waves with a daily maximum air temperature exceeding 35°C . This was consistent with the results of the 2007 survey (Hasegawa *et al.* 2011), although the degree of sterility induction cannot be directly compared with this earlier study because Hasegawa *et al.* (2011) survey included experimental paddies with different nitrogen treatments or varieties with different heat tolerance.

The thermal variables averaged over the 5 days of the heading

Fig. 5. Distributions of the possible sterility rate in Kanto region (stripe) and in Tokai and Kinki regions (black fill) in the summers of 2018 and 2019, estimated by using equation 2. The heat dose with a threshold temperature of 33°C (HD_{33}) was calculated for assumed 50% heading dates between July 1 and September 10 at all the studied sites. The hourly panicle temperature was calculated by using the heat balance model, IM²PACT (Yoshimoto *et al.*, 2011) using the 1-km grid-point meteorology data at the nearest point in the grid. Horizontal lines represent the medians, boxes represent the 25% to 75% interval, whiskers represent the 95% confidence interval, and any values outside of this range, outliers, are displayed by dots.

period that all the surveyed paddy fields encountered ranged from 28.7 to 37.3°C for T_{amax} and ranged from 27.5 to 34.6°C for T_{pd} (Fig. 2). T_{pd} was 0 to 3.1°C lower than T_{amax} , and the difference increased with increasing T_{amax} . On days with high T_{amax} , the relative humidity was lower, and this would have stimulated transpirational cooling of the plant canopy, resulting in a lower panicle temperature. This heat balance structure resembles that described by Matsui *et al.* (2014) in Australia, although the cooling effect in our study was not as extreme.

More of the paddy fields encountered higher temperatures in 2018 based on T_{amax} , where data for temperatures above 35°C accounted for 33% of the total data in 2018, versus 12% (only three data points) in 2019 (Fig. 2a). However, the distribution of T_{pd} was similar between the two years, with the maximum T_{pd} of 34.6°C in 2018 and 34.1°C in 2019 (Fig. 2b). This is because the difference between T_{amax} and T_{pd} tended to be smaller in 2019 due to the higher humidity in that year, whereas 2018 had high solar radiation and drier environmental conditions. By using T_{pd} instead of T_{amax} as an index, the sterility model could be slightly improved, thereby obtaining a relationship with sterility rate that varied less between years.

In the present study, the threshold at which sterility started to be induced was about 33°C for both T_{amax} and T_{pd} (Fig. 2). In the Hasegawa *et al.* (2011) survey in paddy fields, the data for three *japonica* rice varieties, including ‘Koshihikari’, showed that the threshold was either 33°C or 34°C for T_{amax} . In the experiment by Maruyama *et al.* (2013) using temperature-gradient chambers, the threshold for ‘Koshihikari’ was about 35°C at the daily maximum air temperature, and was estimated to be about 33 to 34°C at the panicle temperature because it was observed 1 to 2°C lower than the air temperature in their environment. The present results are consistent with these findings on temperature thresholds.

Based on the relationship between the sterility rate and HD_{33} (Fig. 4), the rate of increase in sterility above the threshold was about 7% per 8 (°C-days) increase in HD_{33} based on the cumulative 5-day HD , which represents a mean increase of 4.4% per 1°C increase in T_{pd} . This rate is much smaller than previous findings from chamber experiments (e.g., 12% per 1°C in Horie, 2019; 16% per 1°C in Kim *et al.*, 1996; 19% per 1°C in Maruyama *et al.*, 2013). One reason for this, of course, is that the rate in a chamber experiment is evaluated based on the level of a single panicle, whereas in a paddy field, the community of panicles or plants has a temporal and spatial distribution of flowering, with different temperature exposures for each panicle during flowering. Although there are still few field-scale studies to support sterility modeling, Julia and Dingkuhn (2013) modeled sterility with the calculated panicle temperature based on data compiled for four cultivars at three sites with widely different climates, and found an increase of 7.6% per 1°C elevation of panicle temperature. The increase rate of 4.4% per 1°C in the present study is still smaller, but this may be because the sterility ranged up to 15% in the present study, and we only examined the onset of increasing sterility in a non-linear relationship. In addition, there are likely to be inter-varietal differences in the heat resilience.

Estimating the distribution of possible spikelet sterility with the model as a function of HD_{33} based on panicle temperature (Fig. 5) suggests that even in 2019, with nearly normal climatic conditions,

the sterility was comparable to that during the heat waves of 2018, when high temperatures occurred in early August in 2019. This suggests that HISS may be already occurring under current climatic conditions in temperate Japan, depending on the timing of heading, and that the risk will increase further with global warming.

The stunted spikelet rate tended to be higher in paddy fields where panicles headed in mid- to late July of 2018 in the Kanto region (Fig. 1a). Its overall average for all sites in 2018 and 2019 reached about 10%, and together with the occurrence of sterility, the occurrence of stunted spikelets will further reduce the percentage of fertile grains that can be used for food, so elucidating and modeling the mechanism responsible for the stunting will be an important research challenge for the future. In addition, it has not been clarified yet how the increase in the sterility rate will affect yield. Rice yield is controlled by the sink size as the yield capacity and the source size as the amount of the photo assimilation product to be located to the sinks (e.g., Lubis *et al.*, 2003). Under source-limited conditions, for instance, the failure of fertility due to HISS or other abiotic stresses may not be proportional to the reduction in yield because other factors become more important. Furthermore, the occurrence of sterility may influence on the source–sink balance, which leads to compensatory effects, such as changing the grain size distribution. It has been also reported that the late-emerging panicles can compensate for the failure to fertility of the early-emerging panicles, resulting in no reduction of the yield (e.g., Maruyama *et al.*, 2015). Conversely, this means that even if HISS increases due to global warming and the resulting increasingly frequent heat waves, its effects on rice yield would not be directly detected by yield monitoring such as the monitoring that is done under Japan’s national Crop Survey. In fact, according to the Japan’s national Crop Survey, the rice crop index in the eight prefectures surveyed in this study was almost normal ranging from 97 to 102 in the extremely hot year of 2018, which was rather slightly higher than in the normal year of 2019 ranging from 95 to 98. In the surveyed paddy field in Saitama Prefecture, where the highest sterility rate (15.4%) was observed in this study in 2018, the spikelets number per unit area was 30% larger than normal because high temperatures in the early growing stage promoted tillering, but the yield was only 7% higher than normal (Saitama Prefectural Agriculture and Forestry Research Center, 2018). The reasons why the higher spikelets number per unit area did not proportionally lead the increase in yield could be due to HISS or lack of sources, and detailed identification of the factors is needed. Therefore, it is necessary to accumulate more detailed data on sterility through fertility surveys in paddy fields such as those in the present study, and to examine the relationship between sterility and yield components to support more accurate predictions of HISS and its effect on rice yield.

5. Conclusion

Our wide-area survey of paddy fields used to cultivate ‘Koshihikari’, the most popular variety of rice in Japan, revealed that HISS may be induced even under current climatic conditions in temperate Japan, depending on the timing of heading. Using the daytime mean panicle temperature as an index, it may be possible to estimate the risk of HISS under global warming, where the timing and intensity of the heat waves responsible for this damage will vary among years and among regions. On the other hand, we still do not

know how HISS affects yield, and yield monitoring cannot detect the occurrence of HISS due to ongoing global warming. It will be necessary to carry out fertility surveys using samples collected from paddy fields to accumulate more detailed data on sterility and to examine the relationship between sterility and yield components. This knowledge will reduce the uncertainties in predicting HISS and will support the development of effective adaptation measures to mitigate the HISS associated with global warming.

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