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Countermeasures for heat damage in rice grain quality under climate change

Satoshi Morita^a, Hiroshi Wada^a and Yuji Matsue^b

^aNARO Kyushu Okinawa Agricultural Research Center (KARC), Fukuoka, Japan; ^bFaculty of Agriculture, Kyushu University, Fukuoka, Japan

ABSTRACT

Climate change has been an increasingly significant factor behind fluctuations in the vield and quality of rice (Oryza sativa L.), particularly regarding chalky (white-back, basal-white, and milkywhite) grain, immature thin grain, and cracked grain. The development and use of heat-tolerant varieties is an effective way to reduce each type of grain damage based on the existence of each varietal difference. Cultivation methods that increase the available assimilate supply per grain, such as deep-flood irrigation, are effective for diminishing the occurrence of milky-white grains under high temperature and low solar radiation conditions. The application of sufficient nitrogen during the reproductive stage is important to reduce the occurrence of most heat damage with the exception of milky-white grain. In regard to developing measures for heat-induced poor palatability of cooked rice, a sensory parameter, the hardness/adhesion ratio may be useful as an indicator of palatability within a relatively wide air-temperature range during ripening. Methods for heat damage to rice can be classified as either avoidance or tolerance measures. The timing of the measures is further divided into preventive and prompt types. The use of heat-tolerant varieties and late transplanting are preventive measures, whereas the application of sufficient nitrogen as a top dressing and irrigation techniques during the reproductive stage are prompt types which may function to lower the canopy temperature by enhancing evapotranspiration. Trials combining the different types of techniques will contribute towards obtaining more efficient and steady countermeasures against heat damage under conditions of climate change.

Over the past decades, rice has become one of the largest food crops worldwide (FAOSTAT, 2015) because of the rapid increase in the populations in both Asia and Africa who consume rice as a staple food. However, climate change (IPCC, 2013) has become an increasingly significant factor behind fluctuations in the grain yield (Lobell & Gourdji, 2012) and guality (Lanning et al., 2011; Lyman et al., 2013; Zhao & Fitzgerald, 2013) of rice because the rice average season temperature is recently above optimum. In Japan, frequent extremely high temperatures during ripening have led to the deterioration of grain quality, especially after about the year 2000 (Morita, 2008, 2011; Terashima et al., 2001). Also when rice is exposed to high temperatures over a certain threshold during ripening, there is a decrease in the palatability of cooked rice (Matsue, 2012: Okamoto, 1994). Furthermore, when air temperatures at flowering time exceed around 35 °C under chamber experiment, heat-induced spikelet sterility occurs (Kim et al., 1996; Satake & Yoshida, 1978). Although actual damage in the open field had rarely been reported, the record heat

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reaching 40 °C in 2007 at the Kanto and Tokai regions in Japan induced substantial sterility (Hasegawa et al., 2011), also around 35 °C in summer of 2006 with high humid and low wind conditions induced spikelet sterility in hybrid rice grown at Jianghan Basin in China (Tian et al., 2010). Given that global warming is expected to continue (IPCC, 2013), the powerful methods for preventing heat-induced poor grain quality and yield loss are therefore required.

In this paper, we focus on the heat damage on rice grain quality which has recently become a serious problem in Japan, and first review their incidences and the corresponding studies in Japan. Then, we identify the common countermeasures based on the mechanisms of different forms of rice heat damage, such as chalky grains including milky-white induced by hot and dry wind condition, fissured grains, immature thin grains with deep creases related to grain yield decline, and poor palatability of cocked rice. We also review crop model approach. Finally, we discuss the strategies for countermeasures including future research.

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CONTACT Satoshi Morita 🖾 moritas@affrc.go.jp

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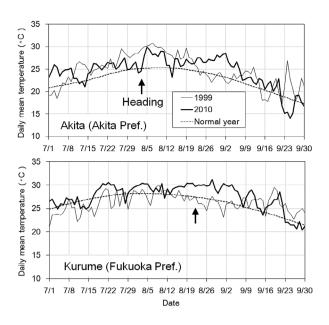


Figure 1. Daily mean temperature trends in the summer of 1999, 2010, and normal year at 1981–2010 each representative site. Site name in each graph shows AMeDAS point in the prefecture shown in parentheses. The arrowhead indicates heading date obtained from MAFF (2014).

Changes in the occurrence of rice heat damage in Japan, and related studies

Nagato and Ebata (1965) described that the quality of Japanese rice had decreased around 1960, because of the elevated temperature during ripening; this, in turn, was caused by the earlier heading dates from the increased early planting cultivation. Thus, the research on the heat damage, such as the heat-shade interaction (Matsushima et al., 1957), the classification of damaged rice (Nagato & Ebata, 1965), heat sensitive stages and organs (Sato, 1979), varietal differences (Yoshida & Hara, 1977), heat-induced sterility (Satake & Yoshida, 1978) was advanced during this period, through the 1970's.

The recent frequency of heat damage affecting rice guality was considered to be due to the increase in the frequency of extremely high temperatures that has been recorded from the beginning of the 1990's (JMA, 2015), as well as the earlier heading dates caused by the spread of early maturing varieties, such as Koshihikari, and the change in the planting date to earlier in the year, between late April and early May (Matsumura, 2005). Extremely high temperatures after heading recorded in 1999, induced a widespread deterioration of rice quality (Terashima et al., 2001). Furthermore, both the level and the duration of increased air temperature after the heading period in 2010 exceeded those recorded in most regions in 1999, with the exception of northern regions, such as Akita of Tohoku district (Figure 1). Consequently, rice quality deterioration was much more severe in 2010 than in 1999, in most regions, except for the Tohoku district (Figure 2).

Countermeasures based on the mechanism behind heat damage in rice

Chalky grain

Conditions leading to chalky grain

One of the most prominent forms of the damage due to high temperature exposure during ripening is chalky grain. Examinations via optical (del Rosario et al., 1968) or scanning electron micrographs (Tashiro & Ebata, 1975; Tashiro & Wardlaw, 1991; Zakaria et al., 2002) revealed that the starch granules of chalky endosperm cells are loosely packed, while those of normal translucent endosperm are tightly packed; the numerous air

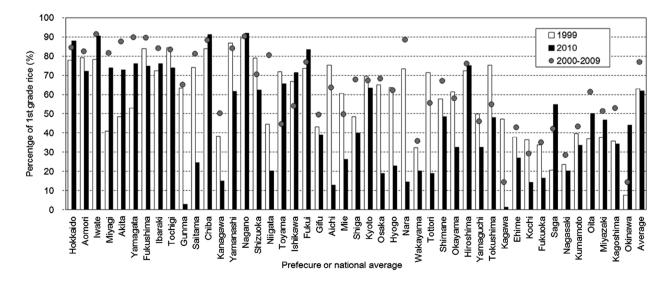


Figure 2. Percentage of the first grade rice by inspection in 1999, 2010, and the 10 years mean from 2000 to 2009 of each prefecture and the national average in Japan. Data of 1999, 2010, and 2000–2009 were obtained from Terashima et al. (2001), MAFF (2011, 2015), respectively.

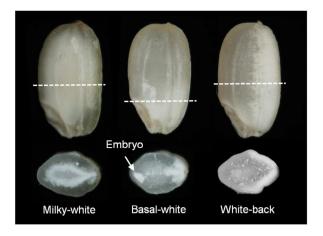


Figure 3. Major types of chalky grains induced by heat damage. The photos below are the transverse sections.

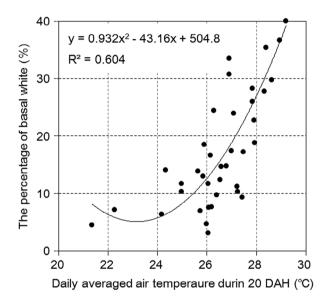


Figure 4. Relationship between the ratio of chalky grain and the air temperature during 20 DAH using var. 'Koshihikari' cultivated at 15 experimental stations in Japan in 2004. The graph was adopted from Figure 5 in Morita (2005).

spaces between starch granules cause random light reflections to create a chalky appearance. It has been suggested that the occurrence of chalky grains caused by high temperature exposure is due to a lack of starch substrates in the endosperm (Kobata et al., 2004), the down-regulation of some starch synthesis-related genes (Yamakawa et al., 2007), and up-regulation of starch degrading α -amylase-encoding genes (Hakata et al., 2012; Yamakawa et al., 2007). The translucence conferred by starch accumulation in the developing rice endosperm moves outwards from the center of the grains (Nagato & Kobayashi, 1959). Consequently, when starch accumulation is disturbed by environmental stresses, the chalkiness often emerges at a site corresponding to the progression of translucence development in the endosperm (Nagato & Kobayashi, 1959).

The chalky grain defect is classified into several types based on the position of chalkiness in the grain. The major types induced by high temperature exposure are milkywhite, basal-white, and white-back grain (Nagato & Ebata, 1965) (Figure 3). Masutomi et al. (2015) quantified the critical air temperature during 30 d after heading (DAH) at which chalky rice began to occur (T_{cr}), as well as the sensitivity of chalky grain incidence to air temperature changes above the T_{cr} (S_t), using the heat sensitive cultivar 'Sainokagayaki.' They clarified that basal-white grains have both a lower T_{cr} (25.1 °C) and a higher S_t (10.3% °C⁻¹). In addition, whole chalky grains begin to occur at about 24 °C on average during 20 DAH in Koshihikari (Morita, 2005; Figure 4) with the slope about 10% per 1 °C from 28 to 29 °C.

Countermeasures against heat damage focusing on each type of chalky grain

The dominant types of chalky grain differ, depending on the weather conditions during ripening. The occurrence of milky-white grains increases under high temperatures coupled with low solar radiation, but decreases when spikelet numbers are reduced by plant thinning (Kobata et al., 2004) and panicle-clipping (Tsukaguchi & lida, 2008), suggesting that source ability per grain would be a significant factor affecting the occurrence of milky-white grains. Varietal differences in the occurrence of milky-white grains under high temperature conditions were also explained by the amount of starch substrates per grain (Tsukaguchi et al., 2011). Thus, it can be suggested that the development of varieties and cultivation methods that increase the available assimilate supply per grain are an effective means of diminishing the occurrence of milky-white grains at high temperatures and low solar radiation. In fact, it is indicated that the heat-tolerant variety Nikomaru (Sakai et al., 2007) features a large amount of non-structural carbohydrate content in the stem at full heading (NSCh), which is translocated to the panicle during ripening, in turn contributing improved ripening performance at high temperatures and low solar radiation (Morita & Nakano, 2011; Morita et al., 2008). Chiba et al. (2013) proposed the deep-flood irrigation, as it can increase the source ability (NSCh, nitrogen of leaf blade at full heading and the leaf area at ripening) per grain to decrease the production of milky-white grains under heat condition in spite of the higher number of grains per panicle.

Based on the regularity of starch accumulation as described in the above section (Nagato & Kobayashi, 1959), the appearance of dehulled grains can be objectively evaluated using a chalky rice grain predictor that is capable of determining the number of milky-white grains by analyzing scanned images of sliced grains harvested between 7 and 10 d prior to the harvest (Morita, 2011). This predictor is now commercially available.

The occurrence of basal-white (Morita et al., 2005a) and white-back (Wakamatsu et al., 2008) grains increases under high temperatures and when the nitrogen concentration in plants is lower, but is not related to low radiation and grain number per area (sink size). A recent study using a Free-Air CO₂ enrichment showed that elevated CO₂ concentration reduces grain protein content through enhancement of dry matter production and substantially exacerbates heat-induced basal-white grains (Usui et al., 2015). Thus, the application of sufficient nitrogen during the panicle initiation stage or later is an effective means of diminishing the occurrence of these types of chalky grains. However, it is not easy to optimize the nitrogen application concentration to achieve a good balance among yield, grain quality, and palatability. This is because, these characteristics are all influenced by nitrogen application at the reproductive stage through the upregulation of yield (increase in grain number and photosynthetic rates) and increases in quality (decrease in the occurrence of white-back and basal-white grains, especially under high temperatures) or decreases in quality (increase in the occurrence of milkywhite grains, especially at high temperatures coupled with low solar radiation) and palatability (increase in protein content in rice), as well as yield loss in some cases (increase in lodging risk). There are some methods available for overcoming this difficulty, such as the use of delayed-release fertilizers as topdressing (Sakata et al., 2008; Tanaka et al., 2010). It was also suggested that deeper tillage and organic matter application are effective ways for increasing rice grain guality through the maintenance of leaf color (Matsumura & Chiba, 2006). Shiraya et al. (2015) demonstrated that 15-20 cm is a suitable root zone depth for achieving high and stable grain quality when air temperatures are high during ripening, in Niigata prefecture. Furthermore, it was suggested that the expansion of root zone may contribute to a decrease in chalky grains induced by low root/shoot ratio due to high temperature before heading (Wada et al., 2010).

Because the optimal amount of top dressing depends on both weather conditions and nitrogen status of plants during the time when the top dressing is applied, a weather-adaptive top dressing technique, which includes an adjustment of the amount of top dressing to be used, based on the weather forecast and the leaf color (SPAD), is being developed (Morita, 2011; Morita et al., 2015).

The use of heat-tolerant varieties is an effective way for diminishing basal-white and white-back grains because of the existence of their varietal differences (Nagato & Ebata, 1965; Wakamatsu et al., 2008). The QTLs associated with the occurrence of white-back and basal-white grain were identified using recombinant inbred lines (Kobayashi et al., 2007; Tabata et al., 2007; Wada et al. 2015) and verified the effects of QTLs for white-back grain using near-isogenic lines (Kobayashi et al., 2013; Wada et al. 2015). These findings will accelerate development of heat-tolerant variety to decrease white-back and basal-white grains under high temperature. It is also suggested that the heat-tolerant varieties would diminish these types of chalky grain generated by an increase in CO₂ concentration (Usui et al., 2014).

Chalky grain induced by hot and dry wind – mechanisms and countermeasures

It has been long recognized that the deterioration of rice appearance is often caused by typhoon/foehn-induced high-speed dry wind (Ishihara et al., 2005; Nagato et al., 1955). Also, it has been widely recognized that foehn (dry high-speed wind) causes an excessive cuticular transpiration from the panicle that subjects the plants to the short-term shoot water deficit, resulting in spikelet sterility (Ishihara et al., 1990; Muramatsu, 1982; O'Toole et al., 1984). Aside from the spikelet sterility at flowering, dry wind occurred during the ripening substantially increases ring-shaped chalky kernels, called milky-white rice, and contrastingly lowers perfect rice (Ishihara et al., 2005; Wada et al., 2011). It is also known that rice plants during the middle ripening stage are particularly vulnerable to wind-induced water deficit, compared with other ripening stages (Oya & Yoshida, 2008). Ishihara et al. (2005) pointed out that there is a close relation between the occurrence of milky-white rice and the extent of foehn-induced water deficit during ripening.

Recently, the direct turgor measurements using a cell pressure probe have further extended the understanding of dry wind-induced chalky ring formation at moderately low water potential (Wada et al., 2011, 2014). It has been shown that the inner endosperm cells, where a high frequency of chalky ring was observed, maintained endosperm cell turgor by osmotic adjustment under shortterm dry wind conditions prior to the chalky formation, which sustains the kernel development (Wada et al., 2011). And, a temporal reduction in starch biosynthesis with no starch degradation also occurred at osmotic adjustment during short-term dry wind conditions (Wada et al., 2014).

Varietal differences on the foehn resistance were reported by several investigators and breeders (Kang et al., 2003; Oya and Yoshida, 2008; Uehara, 2008), but unfortunately information is limited. Oya and Yoshida (2008) found that there was a clear varietal difference on chalky formation among varieties under the wind treatments. Interestingly, they documented that varietal difference for water stress is to some extent similar to high temperature, but what causes the similarity has remained unclear. More efforts are required to investigate further foehn-induced dry wind resistance on grain quality in the view of breeding science. A pump-up pressure chamber,

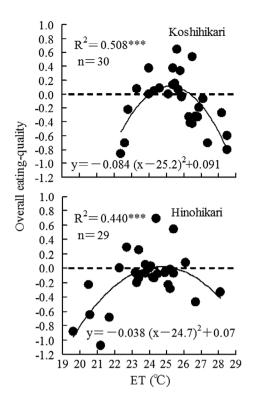


Figure 5. Relationship between overall eating-quality and environmental temperature during the ripening period (ET). The reference cultivar for sensory test was newly cropped Koshihikari transplanted mid-June. ***: Significant at p < .001.

known as a rapid and portable pressure chamber (see Kirkham, 2004), may be a useful device even under the field conditions when studying the foehn resistance with rice varieties in the future study.

As the practical countermeasures to foehn-induced water deficit, first, the paddy fields need to be flooded by irrigation in advance when foehn is expected to occur, so that the effect of water stress can be minimized. Also, cultural management to increase root activity, such as deeper tillage and improving of soil physical properties may have advantage to reduce the risk of short-term water deficit.

Cracked grain and immature thin grain with deep creases

Cracked grain, a serious damage causing the breakage of rice during milling, is induced by the physical stress built up in the endosperm by the unequal swelling resulting from the uneven absorption of water (Nagato et al. 1964). Recently, it has been reported that high temperatures occurring at the earlier ripening stage (Takahashi et al., 2002), especially in the daytime (Nagata et al., 2004), are a critical factor driving the formation of cracked grain. It is indicated that continuous irrigation with running water, which lowers the water and soil temperatures (Nagata et al., 2005), and increases the nitrogen status of the plants contributes to decreases in the occurrence of cracked grain (Takahashi et al., 2002). Prediction methods are also proposed using the above findings (Takahashi et al., 2002). Recently, the existence of varietal differences in the occurrence of cracked grain in response to high air temperature was reported (Nagata et al., 2013). 'Hananomai,''Hanaechizen,''Nikomaru,''Himenomai,' and 'Yan Xuang 203' have been found to have a tolerance to the development of cracked grain. Thus, these varieties would be useful to develop crack-tolerant varieties in the future works.

The formation of immature thin grain with deep creases is also a serious issue, because it can both lower grain quality by decreasing milling efficiency, and lower grain yield by reducing grain weight (Morita et al., 2005b). Recently, using a new method for evaluation of the crease depth based on image analysis (Morita, 2009; Yonemaru & Morita, 2012), it was indicated that high temperatures during ripening promoted creasing, and that the creases on the grain surfaces of the heat-tolerant variety 'Nikomaru' were shallower than those of the heat sensitive variety 'Hinohikari,' when the air temperature during ripening was high (Yonemaru & Morita, 2012). The prevalence of immature thin grains with a deep creases increases under low nitrogen conditions (Morita et al., 2005a). These observations suggest that uses of heat-tolerant varieties and the application of sufficient nitrogen are effective means of decreasing the incidence of deep crease in rice under heat stress.

The effect of weather conditions on the palatability of cooked rice

Although the variety is a major factor of rice palatability (Shigyo & Ono, 1991), air temperature during ripening would be most effective to the palatability among weather condition. Previous reports indicated that the higher the temperature within the range below 26 °C, the better the physicochemical properties of rice (Inatsu, 1988; Matsue et al., 1991), suggesting that the palatability seems to increase as the temperature rises within this range of temperature.

Although there is a negative correlation between rice protein content and its palatability irrespective of the temperature during ripening (Inatsu, 1988; Juliano et al., 1965; Matsue et al., 1991), there is no correlation between temperature above 26 °C and rice protein content (Okamoto, 1994; Matsue, 2012). So, the rice protein content does not mediate the high temperature-induced poor palatability. Amylose content showed a negative correlation with the temperature during ripening irrespective of the level of temperature (Asaoka et al., 1985; Inatsu, 1988; Matsue et al., 1991) and with the palatability under the temperature within the range below 26 °C (Inatsu, 1988; Matsue et al., 1991), but no correlation with the palatability under the temperature above 26 °C (Matsue, 2012; Okamoto, 1994). This means that the rice amylose content does not mediate the high temperature-induced poor palatability. The amylographic characteristics (maximum viscosity and breakdown value) had a positive correlation with temperature during ripening (Matsue et al., 1991; Suzuki et al., 1959). However, the amylographic characteristics do not necessarily correlate with palatability when the temperature during ripening was high above around 26 °C (Matsue, 2012; Okamoto, 1994).

On the other hand, Okamoto (1994) found a quadratic relationship between the stickiness evaluated by a sensory test of Koshihikari and daily mean temperature during 30 DAH, and that the stickiness was the highest when the temperature was 25.3 °C. Also, Matsue (2012) clarified that the palatability (overall eating quality by a sensory test) had a quadric correlation with the temperature during ripening showing a peak at 25.2 and 24.7 °C in Koshihikari and Hinohikari, respectively (Figure 5), and that the hardness (H)/ adhesion (-H) ratio, which showed a negative correlation with the palatability, also had a quadric correlation with the temperature during ripening showing a peak at 24.4 and 24.1 °C in Koshihikari and Hinohikari, respectively. The H/–H ratio would be useful as an indicator of palatability even when the temperature during ripening was above 26 °C.

Regarding the relationship between the palatability and the grain appearance quality under heat stress, it was reported that the palatability decreases by chalkiness under heat stress (Chun et al., 2009; Ishizuki et al., 2013b), especially by the addition of milky-white rice (Wakamatsu et al., 2007). But it was estimated that the basal-white grain induced by high temperature in 2010 does not cause the poor palatability (Ishizuki et al., 2013a). Further studies will be required to clarify the adverse effect of high temperature on the rice palatability.

Crop model approach

Crop growth simulation models are helpful for understanding the complex interactions among the different environmental variables that influence the growth and yields of crops, and are useful decision-making tools (Krishnan et al., 2011) not only at the local level (e.g., selection of crop management methods), but also at the global level. Numerous works have been carried out in the past several decades to assess the climate change impacts on crop production with process-based crop models such as ORYZA1 model (Kropff et al., 1995) and SIMRIW model (Horie et al., 1995).

As Easterling et al. (2007) reviewed, these models suggested that the elevated CO₂ concentration will attenuate the yield reduction resulting from increasing temperatures by promoting biomass production via an increase in photosynthesis. However, uncertainties associated with crop models still remain to be quantified. The Agricultural Model Intercomparison and Improvement Project, known as AgMip, was launched in 2010 to assess the impacts of climate change on agricultural production and food security using thousands of simulated crop yield data, and also has efforts to quantify the sources of uncertainty in crop yield prediction (Rosenzweig et al., 2013). Recently, Li et al. (2015) evaluated 13 rice models at four sites with the diverse climatic conditions in Asia including Shizukuishi, Japan and reported that the individual models did not consistently reproduce both experimental and regional yields well, and the uncertainty was larger at both the warmest and coolest sites. However, the mean of predictions of all crop models reproduced experimental data, with an uncertainty of less than 10% of measured yields. Furthermore, Makowski et al. (2015) used a meta-model, a statistical analysis of ensembles of process-based models (Li et al., 2015) to show that the rice in Shizukuishi would require a temperature increase of 5 °C with a CO₂ concentration increase of 180 ppm, before experiencing a yield loss.

To our knowledge, there are only a limited number of studies available addressing model-based rice quality predictions. Wakiyama et al. (2010) developed a process-based empirical model for both milky-white and basal-white grain occurrences, on a field scale. In addition, Okada et al. (2009) developed a prediction model for chalky grain occurrence using a statistical model with air temperature and radiation as variables on a regional scale. More recently, Cappelli et al. (2014) have developed a web-based software library of existing knowledge of rice quality prediction.

Conclusions and perspectives – strategies for countermeasures

The countermeasure technique should be a robust method suitable for long-term and systematic approaches because of the increasing frequency and intensity of heat stress due to climate change (IPCC, 2013). Here, we categorize the available approaches to summarize the future areas of research.

As shown in Figure 6 (Morita, 2011), the available countermeasures that can be applied to rice production under conditions leading to heat damage can be classified as either (1) avoidance or (2) tolerance types. The former involves avoiding exposure to high temperatures during the reproductive stage, and the latter requires changes in

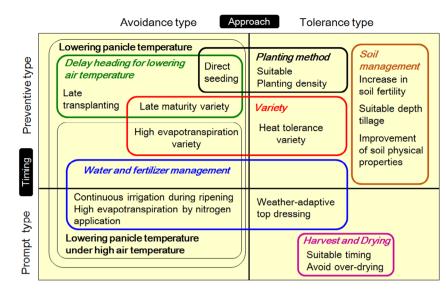


Figure 6. Conceivable measures to meet heat damage categorizing based on two aspects. Generated as a revision of Morita (2011).

genetics or cultivation methods to make rice more tolerant to high temperatures, as described in the previous chapter. The timing of countermeasures can also be classified into two types, (1) preventive and (2) prompt measures. The former involves interventions, such as the selection of varieties and selecting a transplanting date in the spring when the weather from flowering through ripening cannot be predicted. The latter involves interventions such as top dressing technique and water management protocols that are implemented during periods of high temperature, or when high temperatures can be predicted.

Late transplanting, which is a typical avoidance and preventive-type countermeasure, has been implemented widely in Japan in recent years. However, because the effect of this measure is often confounded by extreme weather conditions including typhoons, it is important to find an appropriate transplanting period that can reduce the risk of poor ripening due to every possible weather condition. Also, the combination of late transplanting and other techniques (Kawatsu et al., 2007), such as less basal nitrogen fertilizer (Tanaka et al., 2010) and higher planting density (Morita et al., 2012), are proposed to enhance these effects. Inoue (2012) suggested that the combination of late transplanting and delayed-release fertilizers with sigmoidal release curves was an effective means of reducing heat damage in Fukui prefecture, even in an extremely hot year, 2010 (Figure 2).

In Japan, continuous irrigation with running water has also been proposed as an effective method to avoid heat damage (Nagata et al., 2005), but few farmers can afford to irrigate abundantly, especially in hot years with less precipitation. Therefore, an alternate management method using less water has recently been proposed (Shiraya et al., 2015). Furthermore, transpirational cooling is an important factor to reduce both chalk (Zhao and Fitzgerald, 2013) and heat-induced spikelet sterility (Matsui et al., 2007, 2014) by keeping their canopy cool because the panicle is the organ most sensitive to heat damage that impacts rice guality and yield (Morita et al., 2004; Sato & Inaba, 1973; Satake & Yoshida, 1978). In this view, a canopy-temperature-based irrigation scheduling procedure (Wanjura & Upchurch, 1997) may contribute to the reduction of heat damage in rice. In addition, it has been indicated that the use of nitrogen application with a heat-tolerant variety is a highly effective means of decreasing heat damage via lowering of the canopy temperature by enhancing evapotranspiration (Xiong et al., 2015). Also, it would be effective to use varieties which have a higher transpiration conductance and/or lower temperature of flowering rice panicle (Fukuoka et al., 2012; Maruyama et al., 2013) for diminishing heat damage.

As described above, some trials combining the different types of techniques to obtain more efficient and steady countermeasure techniques have already begun. By promoting those trials, it is expected that the optimal countermeasure techniques corresponding to each situation will be developed to enhance rice production in the face of further climate change.

Abbreviations

ET, environmental temperature during the ripening period H, hardness

-H, adhesion

NSCh, non-structural carbohydrate content in stem at full heading

Disclosure statement

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Notes on contributors

Satoshi Morita, PhD, is a leader of measures for rice heat damage project at NARO (National Agriculture and Food Research Organization), Japan. He is currently researching weather-adaptive top dressing technique, which includes an adjustment of the amount of top dressing to be used, based on the weather forecast and the leaf color.

Hiroshi Wada, PhD, is a senior researcher at NARO, Japan. He is an environmental plant physiologist interested in understanding how crop plants interact with abiotic and biotic stress environments under climate change. He is currently working on plant water relations and cell metabolomics in rice plants.

Yuji Matsue, PhD, is a professor of faculty of agriculture at Kyushu University, Japan. He conducts researches into the influence of a high temperature during the ripening period on the yield, appearance quality and palatability of rice.

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