

CLIMATE CHANGE AND AGRICULTURE PAPER

Impact of high-temperature stress on rice plant and its traits related to tolerance

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SUMMARY

The predicted 2–4 °C increment in temperature by the end of the 21st Century poses a threat to rice production. The impact of high temperatures at night is more devastating than day-time or mean daily temperatures. Booting and flowering are the stages most sensitive to high temperature, which may sometimes lead to complete sterility. Humidity also plays a vital role in increasing the spikelet sterility at increased temperature. Significant variation exists among rice germplasms in response to temperature stress. Flowering at cooler times of day, more pollen viability, larger anthers, longer basal dehiscence and presence of long basal pores are some of the phenotypic markers for high-temperature tolerance. Protection of structural proteins, enzymes and membranes and expression of heat shock proteins (HSPs) are some of the biochemical processes that can impart thermo-tolerance. All these traits should be actively exploited in future breeding programmes for developing heat-resistant cultivars. Replacement of heat-sensitive cultivars with heat-tolerant ones, adjustment of sowing time, choice of varieties with a growth duration allowing avoidance of peak stress periods, and exogenous application of plant hormones are some of the adaptive measures that will help in the mitigation of forecast yield reduction due to global warming.

INTRODUCTION

By the end of the 21st Century, the earth's climate is predicted to warm by an average of 2–4 °C (IPCC 2007), due to both anthropogenic and natural factors (Eitzinger *et al.* 2010). Emission of green house gases (GHG) such as carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) from agricultural systems is one of the major sources contributing to this global increase of temperature (Maraseni *et al.* 2009; Smith & Olesen 2010). Studies have shown that the annual mean maximum and minimum temperatures have increased by 0.35 and 1.13 °C, respectively, for the period 1979–2003 at the International Rice Research Institute, Manila, Philippines (Peng *et al.* 2004). This

increase in temperature has exposed most of the world's crops to heat stress during some stages of their life cycle. The difficulty in precise prediction of the projected agricultural impacts of climate change further adds to the uncertainty (Watanabe & Kume 2009). Rice (*Oryza sativa* and *Oryza glaberrima*) is one of the important cereals grown across the world. Although it has been used as a model plant for many years, the growth responses of rice to high temperature are still poorly understood (Nagai & Makino 2009).

Most rice is currently grown in regions where current temperatures are already close to optimum for rice production. Therefore, any further increases in mean temperatures or of short episodes of high temperatures during sensitive stages, may be supra-optimal and reduce grain yield. Yields of rice have been estimated to be reduced by 41% by the end of the 21st Century (Ceccarelli *et al.* 2010). There is sufficient

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evidence that increasing night-time temperature has been the main cause of increases in global mean temperatures since the middle of the 20th Century, and is thus the main factor contributing to the yield decrease (Kukla & Karl 1993; Ziska & Manalo 1996; Peng *et al.* 2004; Sheehy *et al.* 2005).

Conversely, in some areas temperature increase would improve the crop establishment of rice, for example in Mediterranean areas, where cool weather usually causes poor crop establishment (Nakagawa *et al.* 2003). But the negative effects associated with temperature increment heavily outweigh the positive. And thus, while some countries in the temperate zone may reap some benefit from climate change, many countries in the tropical and subtropical zones appear more vulnerable to the potential impacts of global warming (Rosenzweig & Parry 1994).

The objective of the present review is to summarize recent important research findings on the responses of rice to high temperature, with special emphasis on genotypic variation and morphological characteristics of rice in relation to high temperature, and also to gain an insight into the mechanisms of high-temperature stress tolerance. Some of the strategies that will help in mitigating heat stress are also discussed.

HIGH TEMPERATURE IN RELATION TO GROWTH AND DEVELOPMENT OF THE RICE PLANT

Temperature, along with photoperiod, is the main driving force for crop development (Kropff *et al.* 1995). The optimum temperature for the normal development of rice ranges from 27 to 32 °C (Yin *et al.* 1996). High temperature affects almost all the growth stages of rice, i.e. from emergence to ripening and harvesting (Table 1). The developmental stage at which the plant is exposed to heat stress determines the severity of the possible damage to the crop (Wahid *et al.* 2007).

However, flowering (anthesis and fertilization) and to a lesser extent the preceding stage booting (microsporogenesis) are considered to be the stages of development most susceptible to temperature in rice (Satake & Yoshida 1978; Farrell *et al.* 2006). Exposure to 41 °C for 4 h at flowering caused irreversible damage and plants became completely sterile (IRRI 1976), whereas this high temperature (41 °C) had no effect on spikelet fertility at 1 day before or after flowering (Yoshida *et al.* 1981). In the same study, it was also found that pollination of heat-stressed stigmas with unstressed pollen as well as self-pollination at 1 h before heat stress application did not affect spikelet fertility. These analyses delineated the heat-sensitive stage of spikelets to 1 h before and after flowering. A temperature increase of 1 °C shortened the number of days from sowing to heading by *c.* 4–5 days for some genotypes (Nakagawa *et al.*

Table 1. *Symptoms of heat stress in rice plants*

Growth stage	Threshold temperature (°C)	Symptoms	References
Emergence	40	Delay and decrease in emergence	Yoshida (1978), Akman (2009)
Seedling	35	Poor growth of the seedling	Yoshida (1981)
Tillering	32	Reduced tillering and height	Yoshida (1978)
Booting	–	Decreased number of pollen grains	Shimazaki <i>et al.</i> (1964)
Anthesis	33·7	Poor anther dehiscence and sterility	Jagadish <i>et al.</i> (2007)
Flowering	35	Floret sterility	Satake & Yoshida (1978)
Grain formation	34	Yield reduction	Morita <i>et al.</i> (2004)
Grain ripening	29	Reduced grain filling	Yoshida (1981)

2001). There is genotypic variation in spikelet sterility at high temperature in both the sub-species of *O. sativa*, *indica* and *japonica* (Matsui *et al.* 2001; Prasad *et al.* 2006), which can be defined by different temperature thresholds (Nakagawa *et al.* 2003). However, in general, *indica* is more tolerant to higher temperatures than *japonica* (Satake & Yoshida 1978).

HIGH TEMPERATURE AND SPIKELET STERILITY

Temperatures higher than the optimum induced floret sterility and thus decreased rice yield (Nakagawa *et al.* 2003). Spikelet sterility was greatly increased at temperatures higher than 35 °C (Matsui *et al.* 1997a). In greenhouse experiments with both *indica* and *japonica* genotypes, Jagadish *et al.* (2007) found that less than 1 h of exposure to temperatures above 33·7 °C was sufficient to induce sterility. Enhanced CO₂ levels may further aggravate this problem, possibly because of reduced transpirational cooling (Matsui *et al.* 1997a).

Mechanism of heat-induced floret sterility

Ecophysiological analysis has revealed the mechanism responsible for heat-induced floret sterility (Matsui

et al. 2007). A key mechanism of high-temperature-induced floret sterility in rice is the decreased ability of the pollen grains to swell, resulting in poor thecae dehiscence (Matsui *et al.* 2000). This swelling of pollen grains in the locules is the driving force for anther dehiscence (Matsui *et al.* 1999a). Endo *et al.* (2009) found that although high-temperature-treated pollen showed a normal round shape, some of the tapetum functions such as pollen adhesion to the stigma and its subsequent germination were negatively affected. Endo *et al.* (2009) also identified some temperature-responsive genes in the anther by clustering of microarray data. Some other possible reasons discussed by researchers for decreasing spikelet fertility at high temperature are altered hormonal balance in the floret (Michael & Beringer 1980), disturbance in the availability and transport of photosynthates to the kernel (Afuakwa *et al.* 1984), lack of ability of the floral buds to mobilize carbohydrates under heat stress (Dinar & Rudich 1985) and changes in the activities of starch and sugar biosynthesis enzymes (Keeling *et al.* 1994; Singletary *et al.* 1994).

Significant genotypic variations in high-temperature-induced floret sterility exist. Matsui *et al.* (2001) found a 3 °C variation of temperatures causing sterility of 0.5 between the most tolerant and most susceptible cultivars among nine *japonica* cultivars. Similarly, Sheehy *et al.* (2005) reported altered responses of rice genotypes in terms of spikelet fertility to different levels of temperature increases. Greater increments in temperature resulted in higher proportions of sterility. Exogenous application of growth regulators has been shown recently to have some positive effects on the spikelet fertility and pollination (Mohammed & Tarpley 2009a). In fact, their exogenous application increased the level of endogenous antioxidants and thus prevented the oxidative damage to the membranes in rice (Mohammed & Tarpley 2009b).

Pollination in relation to spikelet fertility at high temperature

Pollination contributing factors (pollen production, viability and reception) play a dominant role in productivity of the crop. Generally, male reproductive development in rice is known to be more sensitive to heat stress (Wassmann *et al.* 2009a). Prasad *et al.* (2006) reported that high-temperature stress during rice flowering led to decreased pollen production and pollen shed. The probable reasons were the inhibition of swelling of pollen grains, indehiscence of anthers and poor release of pollen grains (Matsui *et al.* 2000, 2005), and thus fewer numbers of pollen grains were available to be intercepted by the stigma. Mackill *et al.* (1982) stated that the proportional fertility was positively correlated with the number of pollen grains shed on the stigma under both high and ambient temperatures. Physiologically, the decreased

production of pollens at elevated temperatures may be attributable to impaired cell division of the microspore mother cells (Takeoka *et al.* 1992). Similarly, high temperatures at anthesis or soon after can cause poor pollen germination and retarded pollen tube growth, along with poor anther dehiscence. Different reasons have been discussed for variation of these traits among tolerant and susceptible cultivars. For example, Matsui *et al.* (2001) stated that the occurrence of well-developed cavities in anthers, and thick locule walls which enable easy rupture of the septa in response to swelling of pollen, resulted in better anther dehiscence and pollen shed in tolerant cultivars.

Exposure of pollen grains to high temperature resulted in a loss of pollen viability within 10 min (Song *et al.* 2001) and it was essential that more than 10 pollen grains germinated on the stigmata to ensure successful fertilization of a rice floret (Satake & Yoshida 1978). Given that *c.* 0.50 of the pollen grains on a stigma germinate, there must be over 20 pollen grains on a stigma to ensure fertilization (Matsui & Kagata 2003a). Along with this, exposure to high temperature for a few hours can reduce pollen viability greatly and therefore causes yield loss (Wassmann & Dobermann 2007). The stigma is less sensitive to heat than the anther and pollination of the stigma with unstressed pollen generally restores the spikelet fertility (Yoshida *et al.* 1981). The decrease in spikelet fertility can be termed a phenotypic character of rice plant under high temperature, while the decrease in pollen germination and activity can be considered as the physiological factors responsible for this decrease (Tang *et al.* 2008). Thus, all these traits, which somehow ensure normal pollination, are also vital for the thermo-tolerance capabilities of various genotypes.

Role of humidity in spikelet sterility at high temperature

Humidity also plays an important role in rice yield, as higher relative humidity (RH) at the flowering stage under increased temperature affects spikelet fertility negatively (Yan *et al.* 2010). Field observations in some high-yielding rice areas with a drier climate and high temperatures (e.g. New South Wales and Southern Iran) suggested no significant increase in spikelet sterility even at temperatures >40 °C (Wassmann & Dobermann 2007). Prior to this, a decrease in the fertility of spikelets at high air temperatures with increased humidity was reported by Matsui *et al.* (1997b) who suggested that humidity modified the impact of high temperature on spikelet fertility. An RH of 85–90% at the heading stage induced almost complete grain sterility in rice at a day/night temperature of 35/30 °C (Abeyisiriwardena *et al.* 2002). Heavy water loss from florets might impede one of the major processes of pollination, such as swelling

Table 2. Fertile spikelet ratio of different varieties of indica and japonica rice exposed to different daytime air temperatures and RH levels

Fertile spikelets ratio						
Variety	36/30 °C		34/30 °C		32/24 °C	30/24 °C
	RH (85%)	RH (60%)	RH (85%)	RH (60%)	RH (80%)	RH (80%)
IR 36	11.4	61.0	66.9	80.6	77.5	94.4
IR 24	22.6	66.4	39.2	65.1	76.5	94.3
Hinohikari	23.3	69.2	67.3	85.4	85.7	94.6
Yumehikari	44.4	80.8	59.4	78.4	76.5	98.2
Average	25.4	69.4	58.2	77.4	79.0	95.4

Adapted from Weerakoon *et al.* (2008).

of the pollen grains (Matsui *et al.* 1999b). Weerakoon *et al.* (2008) reported that spikelet fertility was not always inhibited by high humidity, because at low temperature (> 30 °C) the fertility was *c.* 0.9. They also observed that with increased RH, pollen shedding on stigma was reduced at high temperature, while no such reduction with increased RH was noted at lower air temperatures (Table 2). These observations suggest that the shedding of pollen on the stigma and the subsequent spikelet sterility are affected by RH along with temperature. Nishiyama & Satake (1981) also showed that the dehiscence of the anther, which plays an important role in the fertility of the spikelet, was promoted by dry air. The temperature inside the spikelet decreases with a reduction in RH, possibly due to the enhancement of transpiration at low RH (Weerakoon *et al.* 2008). This reduction in temperature inside the spikelet increases the viability of pollen grains. Viable pollen grains absorb moisture and swell at moderate to high RH levels and create the required pressure for the rupture of the septum, which helps in the deposition of pollen on stigma and thus produces a fertilized spikelet (Weerakoon *et al.* 2008).

PHYSIOLOGICAL AND BIOCHEMICAL MECHANISMS OF HEAT TOLERANCE

Heat tolerance is generally defined as the ability of the plant to grow and produce economic yield under high temperature (Wahid *et al.* 2007). As plants cannot move, the only option they have to defend themselves from various stresses is to make metabolic and structural adjustments (Yamanouchi *et al.* 2002). Rice tolerance classically comprises elements of escape or avoidance, i.e. the timing of panicle emergence and spikelet/floret opening relative to the occurrence of the stress, and the absolute tolerance of key processes, such as anther dehiscence, to the stress. The ability of a variety to decrease its spikelet

temperature with reduced RH can be considered as an avoidance mechanism, while the variability among the varieties in spikelet sterility at a given spikelet temperature could be considered as true tolerance (Weerakoon *et al.* 2008). True heat tolerance at sensitive stages might be conferred by protecting structural proteins, enzymes and membranes from heat damage. The role of heat shock proteins (HSPs) and other stabilizing factors is crucial in these processes (Maestri *et al.* 2002). Relatively little is known about stress avoidance and true tolerance mechanisms in rice. For phenotyping and modelling, it is required that these two mechanisms, as well as the effects of temperature on the fertility of spikelets, are clearly understood and investigated further.

Acquired or induced thermo-tolerance is the ability induced by a sub-lethal heat stress to overcome subsequent exposure to lethal high temperatures (Burke *et al.* 2000). This type of tolerance is a cell autonomous phenomenon that results from an exposure to a short period of sub-lethal temperature or other moderate stress treatment (Larkindale & Vierling 2008). It depends mainly on the induction of specific pathways during the acclimation period and subsequent acquisition of thermo-tolerance (Klueva *et al.* 2001).

Basal or inherent thermo-tolerance is the measure of the inherent capacity of an organism to tolerate high temperature (Lee *et al.* 1995). Quantitative trait loci (QTL) studies have shown that heat tolerance of rice during flowering is under polygenic control (Zhang *et al.* 2009), which makes it more difficult to study.

Role of HSPs in inducing thermo-tolerance

High temperatures generally induce the expression of HSPs and suppress, at least in part, the synthesis of normal cellular proteins. Such a response allows

organisms to become tolerant to lethal high temperatures (Chang *et al.* 2007). HSPs are not only induced in response to short-term stress but their production is also vital for heat acclimation (Timperio *et al.* 2008). The rapid accumulation of HSPs in the sensitive organs can play an important role in the protection of the metabolic apparatus of the cell, thereby acting as a key factor for plants' adaptation to, and survival under, heat stress (Wahid *et al.* 2007). The HSPs produced in eukaryotes can be grouped into six different families/classes: HSP100, HSP90, HSP70, HSP60, sHSPs (small HSPs) and the Ubiquitin HSP8.5 group (Efeoglu 2009). Apart from heat shock, HSPs are also produced in response to various abiotic stresses including water stress, chilling stress, salinity stress and anoxic conditions (Pareek *et al.* 1995). These HSPs can help in coping with heat stress by improving photosynthesis, partitioning of assimilate, nutrient and water use efficiency and membrane thermal stability (Wahid *et al.* 2007). A positive relationship has been documented in many plant species between HSPs and heat tolerance of the whole plant (Huang & Xu 2008). Also, a relationship between HSPs and reactive oxygen species (ROS) has been proposed which corroborates the hypothesis that during the course of evolution plants were able to suppress ROS and now plants are using these ROS as signalling molecules to induce HSPs (Timperio *et al.* 2008). Better acclimation was reported when the high-temperature stress occurs gradually instead of through a sudden change in temperature (Larkindale & Vierling 2008).

Considering the crucial role of HSP in imparting thermo-tolerance, Katiyar-Agarwal *et al.* (2003) developed transgenic rice by the introduction of HSP101 from *Arabidopsis thaliana* cDNA into the *indica* rice variety Pusa Basmati 1. Overall, this transgenic rice showed normal growth and development, and it also performed significantly better in the recovery after heat stress when compared with the untransformed rice. Similarly, the over-expression of rice *OsHSF7* gene in *A. thaliana* has very recently been reported to increase the thermo-tolerance by increasing the proportion of plants surviving 42 °C for 16 h, from 0.22 to 0.52 (Liu *et al.* 2009). On the other hand, expression of a member of rice heat stress transcription factors (*OsHsfA2e*) has been reported to enhance tolerance to environmental stresses such as high temperature and salt stress in *Arabidopsis* (Yokotani *et al.* 2008).

Factors other than HSPs contributing to thermo-tolerance

A complex network of changes is involved in plant acclimation to heat stress. Research findings have shown that pathways other than HSPs induction also play a vital role in thermo-tolerance of plants

(Larkindale & Vierling 2008). Disruption of some plant growth hormones such as ethylene, salicylic acid, abscisic acid, calcium and hydrogen peroxide through mutation affected the thermo-tolerance capability of the plants, although the levels of accumulated HSPs did not vary from their wild types in these mutated plants (Larkindale *et al.* 2005). When applied exogenously, these chemicals can enhance thermo-tolerance without an accompanying accumulation of HSPs (Larkindale & Knight 2002), mainly through increased antioxidant capacity and membrane thermal stability which can reduce the extent of damage caused by ROS (Mohammed & Tarpley 2009b). Another prominent alteration produced at the molecular level to counteract the high-temperature stress in plant cells is the modification of antioxidant enzymes, and alteration of membrane composition and structure (Stone 2001). The ability of some cultivars to undergo evaporative cooling can also impart tolerance to high-temperature stress, especially when availability of irrigation water is ensured under sufficient vapour pressure deficit between the canopy and atmosphere.

TRAITS RELATED TO TOLERANCE OF HIGH TEMPERATURE STRESS

Below is a brief description of some morphological characteristics that can alter the response of crops towards heat stress.

Plant architecture

Plant architecture can play an important role in high-temperature stress tolerance. Thus, developing plant varieties with appropriate architecture will help to cope with the increase in temperature. For example, if the plant morphology is such that the panicle is surrounded by many leaves, the plant will be able to withstand high-temperature stress due to increased transpirational cooling and by preventing evaporation from the anther due to its shading by the leaves. The reduced evaporation from the anther will ensure swelling of the pollen grains, an important trait for anther dehiscence. The newly developed semi-dwarf improved varieties may prove quite useful in this regard due to their improved canopy architecture (Wassmann *et al.* 2009a). The reduced height may also enhance resistance to lodging, thus giving more resilience to the crop against indirect stresses such as floods, which will become more frequent due to global warming.

Time of flowering and anthesis

The occurrence of flowering early in the morning was discussed many years ago as a useful phenomenon imparting heat tolerance to rice genotypes

(IRRI 1977). In addition, early flowering is considered a relatively simple trait that can be used easily in breeding (Yoshida 1981). Nishiyama & Blanco (1981) conducted a series of experiments on the probability of controlling flower opening time during the day and on the mechanism of flower opening in rice plants. They found that a dark treatment lasting 1 h prior to the natural flower opening advanced the flower opening time by up to 2 h in some cases. This advancement was, however, accompanied by some anther indehiscence. The day–night change of (29/21 °C) temperature was more effective in advancing the opening time than the constant temperature (25/25 °C) in their experiments. Longer or shorter durations of dark treatments were also effective, but to a lesser extent.

Flowering and anthesis in most *O. sativa* genotypes of rice occur over a 5-day period, with most spikelets reaching anthesis between 10:00 h and 12:00 h (Nishiyama & Blanco 1980; Prasad *et al.* 2006). A rice floret emerges from the sheath of the flag leaf just before anthesis and opens for about 1 h in the morning (Matsui & Kagata 2003b). Avoidance mechanisms also include: (i) cooling of the spikelet at flowering, (ii) asynchronous tiller and panicle development, (iii) asynchronous flowering time of spikelets within each panicle and (iv) anthesis and pollination taking place within the same spikelet (self-pollination). The latter was considered as one of the major difference between heat-tolerant (N22) and susceptible varieties (Yoshida 1981). Yield depression resulting from exposure to high temperatures during critical developmental stages is mitigated to some extent within a crop because it is composed of individuals whose tillers are not of the same age. This means that the panicles produced pass through their vulnerable stages at different times and some might therefore escape heat damage. However, breeders and growers do not want crops to be unreasonably asynchronous as this extends the ripening period and increases the risk of crop loss due to other factors.

The anthesis time during the day is important because spikelet sterility is induced by high temperature during or soon after anthesis (1–3 h after anthesis in rice, Satake & Yoshida 1978), but not after fertilization is completed. Sheehy *et al.* (2001) showed that a large variation exists in time-of-day of flowering among rice cultivars. Identification of genes responsible for controlling the time of day when flowering commences would be crucial for this stress avoidance mechanism (Sheehy *et al.* 2005).

Although *indica* and *japonica* genotypes of *O. sativa* have similar patterns of flowering, it is worth noting that *O. glaberrima* genotypes flower much earlier in the day, with more than 0.90 of spikelets reaching anthesis by 09:00 h (Nishiyama & Blanco 1980; Prasad *et al.* 2006). This is a potentially useful trait that should be incorporated into *O. sativa* now that interspecific crosses can be made (Jones *et al.* 1997).

While phenotyping for heat tolerance, it is essential that high temperature (or other stress) is timed to coincide with the peak period and that escape is taken into account (Jagadish *et al.* 2007). Developing some techniques to ensure that the process of anthesis completely occurs within the same spikelet will help the plant to avoid heat stress successfully. In this regard, the application of methyl jasmonate (MeJA) has been proved to significantly induce opening of rice floret within about 30 min, with the most rapid induction occurring just 6 min after treatment (Zeng *et al.* 1999). The results indicated that MeJA-induced opening of rice florets significantly. In addition, exogenous application of MeJA in *A. thaliana* has been reported to confer basal thermo-tolerance and protect it against heat shock (Clarke *et al.* 2009).

Length of anther

It has been suggested that cultivars with large anthers are tolerant of high temperature at the flowering stage (Matsui & Omasa 2002). As the direct cause of temperature stress is the reduction in the number of pollen grains that germinate on the stigmata (Satake & Yoshida 1978), it can be assumed that cultivars with large anthers are tolerant to temperature stress because they have a large number of pollen grains per anther, which compensates for the reduction in the number of pollen grains that germinate under high temperature (Matsui & Omasa 2002).

Size of basal pore

Basal pores are located just above the stigmata and at the bottom of the theca, and open at the time of flower opening when the anthers stand erect. Therefore, pollen grains in the anthers with large basal pores would readily drop out of the basal pores on to the stigmata. In contrast, most of the pollen grains in anthers with small basal pores would remain in the anthers at the time of floret opening (Matsui & Kagata 2003a). Thus, this trait, along with the length of the anther, increases the chances of pollination (a process generally perturbed under high-temperature stress as discussed earlier), mainly by facilitating pollen release from the anther. As these characters can be easily identified compared with some other morphological traits, they can be used easily in breeding and as screening tool for selection of rice germplasm for high-temperature resistance.

Length of basal dehiscence of anther

Anther dehiscence is the final step of anther development and results in the release of pollen grains to enable pollination, fertilization and seed set (Goldberg *et al.* 1993). In *O. sativa*, filaments begin to elongate at the beginning of anthesis and pollen

grains swell rapidly. The increased pressure from the swollen pollen grain causes the locule to bulge, resulting in rupture of the septum, which has been weakened by hydrolytic enzyme action (Keijzer *et al.* 1996; Matsui *et al.* 1999a). For successful anther dehiscence and pollination, a series of developmental events leading to the breakage of the stomium and release of pollen grains must synchronize with other developmental processes that occur within both the anther and the floret (Zhu *et al.* 2004).

Matsui & Omasa (2002) showed that some high-temperature-tolerant cultivars with spikelet fertility of >0.80 under a day temperature of 37.5 °C, have well-developed lacuna for the anther dehiscence between the septum and stomium of theca. The well-developed lacuna may weaken the septum and promote theca dehiscence, thus increasing the tolerance of pollination to high temperatures (Matsui & Omasa 2002). The well-developed lacuna, however, is not an appropriate marker for exploration of genetic resources and breeding of high-temperature tolerant cultivars because the lacuna is not visible from the outside of the anther and it is time consuming to observe it. For efficient selection in a breeding programme, visible markers of high-temperature tolerance are required. Matsui & Kagata (2003a), using *japonica* rice cultivars in Japan, reported that long basal dehiscence of theca for pollen dispersal increased the stability and certainty of pollen transport to the stigmata under normal conditions. Genetic improvement for large basal dehiscence may increase the certainty of pollen shedding, by compensating for the decrease of theca dehiscence and delay of the pollen release, thereby increasing tolerance to high temperatures. It is easy to measure the dehiscence size. Under severe high temperature, the swelling of the pollen grains is inhibited, which leads to indehiscence of the theca (Matsui *et al.* 2000), while moderately high temperatures usually result in failure of pollen release (Matsui *et al.* 2005).

In another experiment, Matsui (2005) found that the long basal dehiscence of the theca helps the pollen grains to fall from the theca onto the stigmata and increases the stability of the pollination under hot and humid conditions as well as in normal conditions. He concluded that under normal conditions the tolerance of a variety to high temperature can be estimated by measuring the length of basal dehiscence. And as genotypes with large basal dehiscence under normal temperatures will also have greater basal dehiscence under high temperature, thus it can be easily estimated for high temperature from that under normal conditions (Matsui *et al.* 2005). It shows that this character is expressed stably both under normal and high temperatures. The length of basal dehiscence of thecae has been reported to be under strong genetic control (Matsui *et al.* 2005). Later, the experiments of Matsui *et al.* (2007) also suggested that the external

environment also has some effect on the basal dehiscence as it was longer at the edge of the rice canopy than inside the community and tended to be longer on the second day than on the first day. If such variation in the size of the basal dehiscence among cultivars from different origins correlates with the viability of pollination in a wide range of genotypes, the size of the basal dehiscence could be a useful morphological marker of pollen viability.

INTERACTIVE EFFECT OF TEMPERATURE WITH OTHER CLIMATIC FACTORS ON RICE

The atmospheric CO₂ level is projected to increase in the future, which will have significant effects on various plants. As a C₃ plant, rice will certainly benefit from this increase in CO₂, mainly through reduced photorespiration. A positive role of CO₂ enrichment has also been shown for biomass accumulation, tillering, panicles per plant and grain yield of rice (Baker *et al.* 1990, 1992; Ziska & Teramura 1992). Higher CO₂ levels will influence stomatal behaviour beneficially by reducing water loss through transpiration, thus increasing water use efficiency (Wassmann *et al.* 2009b). So the projected rise in CO₂ concentration will be advantageous in some ways for rice growth and development. However, the overall effect is negative when increases in both CO₂ and temperature are taken into account simultaneously (Moya *et al.* 1998; Wassmann *et al.* 2009a). The rising CO₂ level may exacerbate future scenarios for rice production in the long run, as it will further increase the global temperature. Furthermore, research on the interactive effect of these two climatic components has revealed that the canopy temperature increases with an increase in CO₂ level due to closure of stomata, which in turn, may also reduce the critical air temperature for spikelet sterility (Matsui *et al.* 1997a).

The global rise in temperature will also increase the severity of other environmental stresses such as floods and drought. It may alter the whole hydrological cycle and will bring more unpredictability and intensity in terms of precipitation. Probably, the wet places will become wetter and the dry will get drier. The variation in rainfall will lead to more frequent floods and droughts, which are the most important constraints for deep water and aerobic cropping systems, respectively. Both these extreme conditions (drought and flood), if exceed certain critical period, will have substantial consequences on rice and may lead to complete failure of the rice crop when occur at sensitive stages either in the form of water shortage or excessive submergence. And thus, the changing climate may enforce a shift in the cropping pattern in most parts of the world most probably making rice the most suitable choice for areas with increased water

availability but becoming less appropriate for farmers in areas with decreased wetness. So there is a need to adopt a multi-faceted approach while studying the impact of high-temperature stress, also focusing on other environmental stresses, which may be equally detrimental for rice productivity. In addition to these abiotic stresses, rice plants will become more and more susceptible to biotic stresses such as insect pest infestation with the changes in temperature and other climatic factors.

MITIGATING STRATEGIES FOR THE FORTHCOMING WARMER CLIMATE

The availability of high-density genetic and physical maps, expressed sequence tags (ESTs), genomic sequences and mutant stocks such as T-DNA insertional mutants (Jeon *et al.* 2000) have established rice as an excellent model plant for the study of heat tolerance among cereals. And the high level of synteny and homology within the Poaceae family will facilitate transfer of identified QTLs and candidate genes from rice to other cereals (Maestri *et al.* 2002). Some of the strategies that may help to cope with the threats of changing climate are outlined below.

Breeding perspective

Progress in rice breeding has rapidly accelerated due to the availability of the full rice genome sequence (IRGSP 2005) and intensive QTLs mapping efforts for a wide range of traits (Ismail *et al.* 2007). Some of the breeding options which, if adapted, will help to mitigate the problem of rising temperature can be briefly summarized as follows.

The fertility of spikelets at high temperature can be used as a screening tool for high-temperature tolerance during the reproductive phase. Selection for heat tolerance should be done for those breeding materials which can tolerate temperatures higher than 38 °C (Satake & Yoshida 1978). Some cultivars that are not so sensitive to relatively higher temperatures, e.g. N22, have already been identified, so in the case of breeding for high-temperature stress only these materials should be used as genetic donors. For efficient selection in a breeding programme, visible markers of high-temperature tolerance are required. In this regard, the length of the anther and the size of its basal pore are some of the morphological traits that can be easily identified and can be used in breeding and as screening tool for selection of rice germplasm for high-temperature resistance. Genetic modification of the male reproductive organ should be targeted in future breeding programmes as it is more sensitive to high temperature.

Exploiting the existing genotypic variation in flowering time (especially the wild-type) serves as a useful mitigation option for rising temperature as it

is a relatively simple trait that needs to be focused in breeding programmes. Introgression of the early morning flowering gene from *Oryza officinalis* into *O. sativa* has recently been shown to have positive effect on reducing the spikelet fertility (Ishimaru *et al.* 2010).

QTL mapping, along with associated genetic studies focusing on the relationship between the phenotype of a trait and its genetic markers, should provide an opportunity to relate specific alleles to trait variation and thus to identify candidate genes (Cardon & Bell 2001). Breeding of cultivars with asynchronous tillers and panicles will increase the likelihood that critical processes of growth and development may occur at a cooler time in some tillers, but this phenomenon also has some other complications. The production of high-temperature tolerant transgenic rice cultivars would provide a stability advantage and will improve its overall performance under temperature stress.

More research on the inheritance of tolerance related traits and genotype-by-environment interaction ($G \times E$) is needed. The targeted $G \times E$ -based findings will not only help to understand the relationship of production environment and genotypic characteristics of rice, but (as an immediate solution for the problem) will also help to select better genotypes suitable for particular environments (Krishnan & Rao 2005). Variation in response of cultivars to CO₂ enrichment has already been reported (Ziska *et al.* 1996), so additional research is needed to identify or develop cultivars that can maintain higher yield at high temperatures along with high CO₂.

Future research activities should be aimed at identification and breeding of heat tolerant germplasm exploiting the variation in both genotypic and morphological characters. Several approaches should be actively exploited to improve heat tolerance in current cultivars, including discovery and exploitation of new genes and alleles, improved breeding efficiency, marker-assisted selection and genetic modification.

Management Options

Wide variability in response to temperature exists in the current rice genetic resource. Replacement of the sensitive cultivars by tolerant cultivars in the fields will increase the global rice production. From the management point of view, it is essential to adjust the duration of varieties such that they avoid peak stress periods. And for this purpose, the development of varieties with suitable growth durations and tolerance of altered sowing times can play a vital role. Site-specific adjustments in cropping systems may be needed because the effect of these changes in climatic factors varies with the region. The inherent diversity in rice agronomic systems, such as aerobic and flooded rice,

may be quite effective for this targeted adaptation. Similarly, a shift in the cropping pattern from flooded to aerobic rice is expected in the near future. Keeping the field wet but not flooded and with added organic matter reduces the global warming potential from rice fields without a decrease in yield (Yu *et al.* 2004). Management practices such as saturated soil culture (SSC), alternate wetting and drying (AWD) and aerobic rice cultivation in the case of drought stress, while growing improved varieties containing the *sub1* gene in flooded soils, offer some adaptive options for the indirect stresses related to temperature increase. AWD of the irrigated rice fields may also help indirectly, as it reduces methane emission (a significant contributor to global warming). Similarly, the no-tillage system is also an effective management strategy to reduce GHGs from rice fields (Ahmad *et al.* 2009). The use of some growth regulators like MeJA (for advancing the flowering time to early morning), salicylic acid and glycine betaine (for increasing the percent pollen germination and spikelet fertility) will be also useful in mitigating the yield

reduction threats. MeJA has recently been shown to cause an increase in spikelet sterility (although it enhanced flowering time), possibly due to indehiscence and poor pollination (Kobayasi & Atsuta 2010). However, the use of these regulators needs more experimental verification since literature on this topic is scarce. Growing rice varieties with higher yield potential reduces GHG emissions by actively channeling carbon from the atmosphere to the grains. The utmost care should be taken such that any improvement in tolerance to high-temperature stress of rice plant will not have a negative effect on qualitative traits.

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