

## Does susceptibility to heat stress confound screening for drought tolerance in rice?

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**Abstract.** Drought affected rice areas are predicted to double by the end of this century, demanding greater tolerance in widely adapted mega-varieties. Progress on incorporating better drought tolerance has been slow due to lack of appropriate phenotyping protocols. Furthermore, existing protocols do not consider the effect of drought and heat interactions, especially during the critical flowering stage, which could lead to false conclusion about drought tolerance. Screening germplasm and mapping-populations to identify quantitative trait loci (QTL)/candidate genes for drought tolerance is usually conducted in hot dry seasons where water supply can be controlled. Hence, results from dry season drought screening in the field could be confounded by heat stress, either directly on heat sensitive processes such as pollination or indirectly by raising tissue temperature through reducing transpirational cooling under water deficit conditions. Drought-tolerant entries or drought-responsive candidate genes/QTL identified from germplasm highly susceptible to heat stress during anthesis/flowering have to be interpreted with caution. During drought screening, germplasm tolerant to water stress but highly susceptible to heat stress has to be excluded during dry and hot season screening. Responses to drought and heat stress in rice are compared and results from field and controlled environment experiments studying drought and heat tolerance and their interaction are discussed.

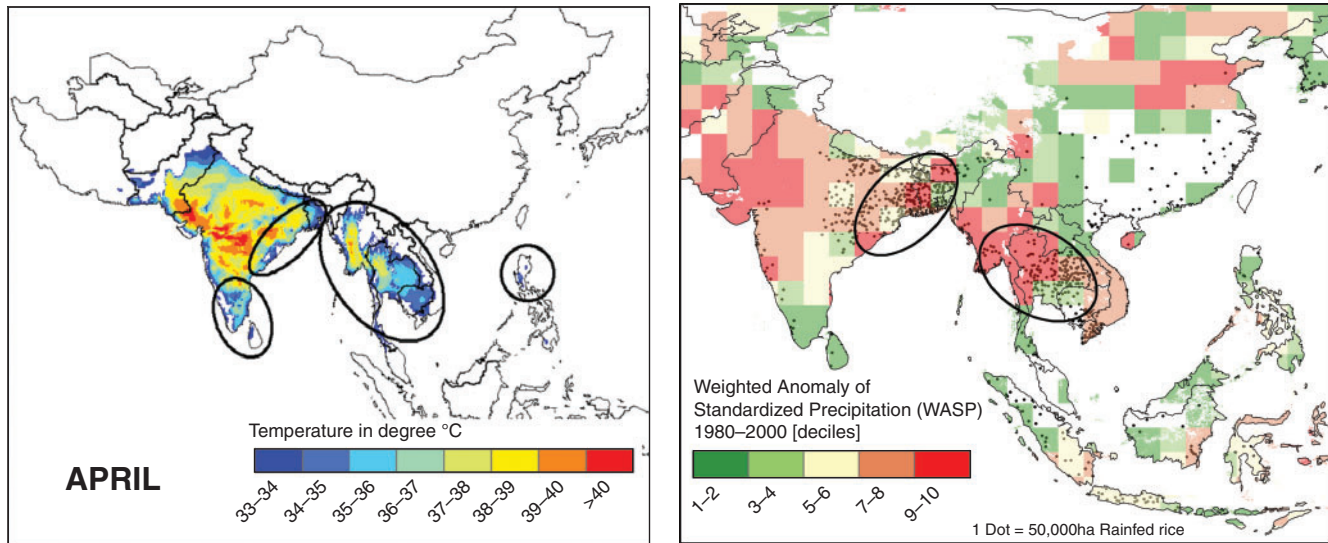
**Additional keywords:** flowering, heat, spikelet fertility, tissue temperature.

### Introduction

Drought – defined as a condition where available soil water or moisture is insufficient to support average crop production – affects 23 million ha of rice regularly (Pandey *et al.* 2007). Anticipated changes in climate in future are likely to double the area affected by drought, especially in the tropical and subtropical regions of the world (IPCC 2007). Developing improved drought-tolerant rice (*Oryza sativa* L.) germplasm for drought prone areas is a major focus of many agricultural research programs (Virk *et al.* 2003; Atlin *et al.* 2006; Ouk *et al.* 2006; Pinheiro *et al.* 2006; Bernier *et al.* 2007; Steele *et al.* 2007; Venuprasad *et al.* 2007, 2008; Kumar *et al.* 2008; Verulkar *et al.* 2010). Drought most often occurs during dry, hot periods with limited or no precipitation. Moreover, drought seldom occurs in isolation; often interacting with other abiotic and biotic stresses (Ceccarelli *et al.* 2004); most commonly with heat stress (Rizhsky *et al.* 2002, 2004; Mittler 2006). Heat stress is associated with temperatures rising above an optimum, which may adversely affect the physiological activities (for e.g. photosynthesis; Vani

*et al.* 2001) and lead to an altered path of development (e.g. reduced grain quality; Kobata and Uemuki 2004). Further, general circulation models also predict an increase in mean global temperatures by 2.0–4.5°C with increased variability over the mean by the end of the century (IPCC 2007), greatly exacerbating drought and heat stress interactions.

Using spatial techniques and cropping pattern data from the rice almanac (Maclean *et al.* 2003; Siddiq 2006), Wassmann *et al.* (2009) examined the occurrence of drought and heat stress experienced by the rice crop in Asia. They reported that high-temperature stress during the susceptible/critical flowering to early grain filling period would coincide with drought stress in Bangladesh, eastern India, southern Myanmar, and northern Thailand (Fig. 1). For example, in Bangladesh, rice is grown in large areas during the ‘boro’ season (dry season, December–April) with temperatures ranging from 36–40°C during the critical flowering stage. Hence, with the frequency of high temperatures during crop growing seasons predicted to increase in many areas, drought exacerbated by heat stress



**Fig. 1.** Geographic illustration of Asia's rice-producing regions highlighting maximum temperatures  $>33^{\circ}\text{C}$  (monthly averages) and (a) ellipsis depict high-temperature regions where rice crop is at flowering and/or ripening stage in April. For a similar analysis during the other months of the year see Wassmann *et al.* (2009). (b) The weighted anomaly standardised precipitation (WASP) index, which is based on average monthly precipitation data from 1980 to 2000 at a resolution of  $2.5^{\circ}$ . Both these maps show regions which could be potentially vulnerable to combined high temperatures and drought stress under current climates and more so during future warmer and drier climates. Reprinted from *Advances in Agronomy* 102, Wassmann R, Jagadish SVK, Sumfleth K, Pathak H, Howell G, Ismail A, Serraj R, Redoña E, Singh RK, Heuer S. Regional Vulnerability of Climate Change Impacts on Asian Rice Production and Scope for Adaptation. 91–133, Copyright (2011), with permission from Elsevier.

(Battisti and Naylor 2009) will have serious implications for future rice production in drought prone areas.

### Effect of temperature and drought on fertility

The effects of high temperature and drought at various stages of floral development leading to spikelet sterility are compared in Table 1, and as described below, these effects are broadly similar at all stages except flowering responses and early grain-filling. High temperatures during the reproductive stage (booting/meiosis, anthesis; pollination and post-fertilisation) in rice has a strong negative effect on yield, with the maximum yield depression occurring when high temperatures occur during anthesis, pollination and pollen germination (i.e. flowering) (Yoshida *et al.* 1981; Prasad *et al.* 2006; Jagadish *et al.* 2007, 2008, 2010a, 2010b). High temperatures before flowering, during booting which coincides with microsporogenesis, also affects fertility but to a lesser extent compared with flowering. There is genetic variation in the critical temperature thresholds at which spikelet fertility falls below 50% (Yoshida *et al.* 1981). The tolerant cv. N22 has a critical temperature of  $36.5^{\circ}\text{C}$  compared with  $32^{\circ}\text{C}$  in a susceptible entry IR747B-2-6. In rice, high temperatures (up to  $41^{\circ}\text{C}$ ) 1 hour after pollination has no effect on spikelet fertility. Critical temperatures have also been measured for other reproductive stages/processes and in peanut (*Arachis hypogea* L.) for example, the critical temperature varies from  $33^{\circ}\text{C}$  during meiosis, pollination and fertilisation (Vara Prasad *et al.* 2001) to  $36^{\circ}\text{C}$  for fruit-set (Vara Prasad *et al.* 2000). Likewise, in 21 peanut genotypes average temperature thresholds for pollen germination and pollen tube growth were  $30.1$  and  $34.4^{\circ}\text{C}$ , respectively (Kakani *et al.* 2002).

In rice, spikelet sterility at high temperatures is closely associated with abnormal anther dehiscence (Matsui *et al.* 2000; Jagadish *et al.* 2010a), resulting in less pollen and germinated pollen on the stigma (Yoshida *et al.* 1981). Pollen tube growth may also be reduced causing sterility (Jagadish *et al.* 2010a). Heat tolerant genotypes are able to deposit sufficient (10–20) viable pollen grains on the stigma to ensure successful fertilisation.

The largest reduction in yield occurs when drought stress coincides with the flowering stage (Cruz and O'Toole 1984; Boonjung and Fukai 1996). Water stress at panicle initiation (~35 days before flowering) and more so at heading reduces peduncle elongation, thereby inhibiting complete exertion of the panicle out of the flag leaf sheath, which, in turn, reduces fertility because spikelets that remain within the leaf sheath have lower fertility (Cruz and O'Toole 1984). Further, rice plants exposed to drought or heat stress 3 days before heading had peduncle lengths reduced by 24 and 8%, respectively, which resulted in a significantly higher number of spikelets trapped in the leaf sheath but only with drought stress (Rang *et al.* 2011). Drought stress at panicle initiation also reduces the number of spikelet primordia (Boonjung and Fukai 1996; Mackill *et al.* 1996).

### Effect of drought and $[\text{CO}_2]$ on tissue/canopy temperature

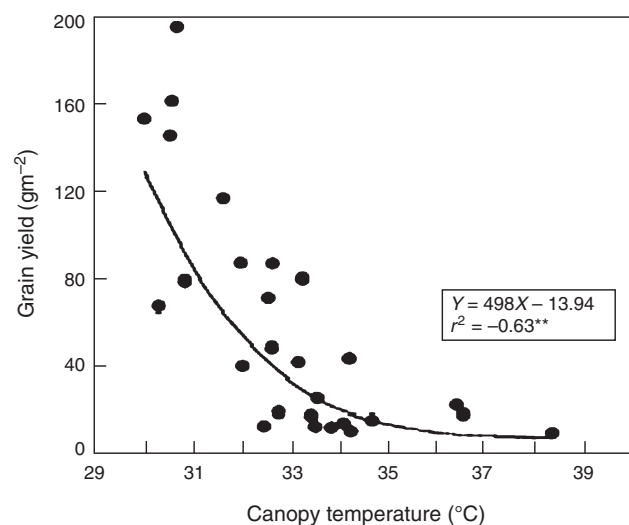
An immediate response to drought stress is the reduction of transpiration (through partial stomatal closure), which, in turn, increases canopy and tissue temperatures (Rizhsky *et al.* 2002, 2004) due to less transpiration cooling. Using infrared thermometry during 1981 and 1982 dry-season drought

**Table 1. Physiological impacts of high temperature and drought stress on different developmental stages in rice**

Developmental stage	High temperature stress	Drought stress	References
Seedling	Thylakoid structure disorganised, significant loss in PSII activity	Reduced leaf expansion growth and photosynthesis	Vani <i>et al.</i> (2001) <sup>A</sup> ; Singh <i>et al.</i> (1996) <sup>B</sup> ; Boonlertnirun <i>et al.</i> (2007) <sup>B</sup>
Panicle initiation	–	Reduced spikelet number	Allah <i>et al.</i> (2010) <sup>B</sup>
Booting/microsporogenesis	Drastic reduction in pollen production and impaired cell division of microspore mother cells	Reduced number of viable pollen; pollen abortion; dead microspores	Prasad <i>et al.</i> (2006) <sup>A</sup> ; Takeoka <i>et al.</i> (1992) <sup>A</sup> ; Sheoran and Saini (1996) <sup>B</sup> ; Nguyen <i>et al.</i> (2009) <sup>B</sup>
Pollen development	Decreased pollen volume and diameter; reduced starch accumulation; stamen hypoplasia	Inhibition of starch accumulation; stamen hypoplasia and abnormal organogenesis	Takeoka <i>et al.</i> (1991) <sup>A</sup> ; Matsui <i>et al.</i> (2000) <sup>A</sup> ; Sheoran and Saini (1996) <sup>B</sup> ; Liu and Bennett (2010) <sup>B</sup>
Pistil development	Pistil hyperplasia	–	Takeoka <i>et al.</i> (1991) <sup>A</sup>
Flowering	Reduction in days to flowering; earlier time peak flowering; shorter flowering period	Days to flowering extended; flowering rate reduced; extended flowering duration	Ishimaru <i>et al.</i> (2010) <sup>A</sup> ; Jagadish <i>et al.</i> (2008) <sup>A</sup> ; Prasad <i>et al.</i> (2006) <sup>A</sup> ; Pantuwan <i>et al.</i> (2002b) <sup>B</sup> ; Jongdee <i>et al.</i> (2006) <sup>B</sup> ; Rang <i>et al.</i> (2011) <sup>A,B</sup>
Anther dehiscence and pollination	Abnormal anther dehiscence; low or no pollen count on stigma; asynchronous pollination	Incomplete panicle exertion and peduncle elongation; reduced anther dehiscence; spikelet abortion	Matsui and Omasa (2002) <sup>A</sup> ; Matsui <i>et al.</i> (1997) <sup>bA</sup> ; Yoshida <i>et al.</i> (1981) <sup>A</sup> ; Jagadish <i>et al.</i> (2010) <sup>A</sup> ; Rang <i>et al.</i> (2011) <sup>A,B</sup> ; Liu <i>et al.</i> (2006) <sup>B</sup>
Pollen germination and fertilisation	Reduced pollen viability and rate of pollen tube growth, spikelet sterility	Viability and pollen tube growth rate reduced; spikelet sterility	Yoshida <i>et al.</i> (1981) <sup>A</sup> ; Prasad <i>et al.</i> (2006) <sup>A</sup> ; Jagadish <i>et al.</i> (2010b) <sup>A</sup> ; Liu <i>et al.</i> (2006) <sup>B</sup> ; Rang <i>et al.</i> (2011) <sup>A,B</sup>
Early grain filling	Chalkiness; shorter grain filling period; reduced grain weight	Grain abortion and chaffiness	Fitzgerald <i>et al.</i> (2009a), (2009b) <sup>A</sup> ; Kobata and Uemuki (2004) <sup>A</sup> ; O'Toole and Namuku (1983) <sup>B</sup>

<sup>A</sup>High temperature studies.<sup>B</sup>Drought stress studies.

screenings at IRRI Garrity and O'Toole (1995) recorded a canopy temperature increase from 28 to 37°C during drought stress (after accounting for cloud cover, wind speed, and minimising solar angle interactions). Furthermore, there was a significant negative relationship ( $r^2 = -0.63$ ,  $P < 0.05$ ) between yield and midday canopy temperature on the day of 50% flowering with complete sterility when midday temperatures were  $\geq 34^\circ\text{C}$  (Fig. 2). They concluded that entries with lower canopy temperature or higher canopy: air difference were better drought avoiders, similarly capable of avoiding combined drought and heat stress. Fischer *et al.* (1989) in maize (*Zea mays* L.) recorded a significantly negative relationship ( $r = -0.73$ ,  $P < 0.01$ ) between canopy temperature and yield under severe water stress. Similar increase in relative leaf temperature of 4.4–5.4°C has also been observed in cotton (*Gossypium barbadense* L. cv. PF-15) 6 days after drought stress was imposed (Cohen *et al.* 2005). The soil moisture content ranging from 25 to 175%, resulted in corresponding variation in canopy temperature of rice, with lower soil moisture recording a higher canopy temperature (Zhang *et al.* 2007). Evapotranspiration and energy-exchange studies in flooded and aerobic rice have shown that under aerobic conditions, a large proportion of the available net radiation



**Fig. 2.** Relationship between rice grain yield and canopy temperature in 27 cultivars on the date of 50% flowering during 1982 dry-season drought screening at IRRI. (Garrity and O'Toole 1995; reprinted with permission from The American Society of Agronomy).

was used for sensible heat transfer that warmed the surrounding ambient air temperature (Alberto *et al.* 2009). With the predicted doubling ( $\sim 700 \mu\text{mol mol}^{-1}$ ) of  $[\text{CO}_2]$  by the end of the century (IPCC 2007), grain yields may increase at lower temperatures due to the  $\text{CO}_2$  fertilisation effect (Long and Ort, 2010) but at higher temperatures yields will be severely affected by  $[\text{CO}_2] \times$  temperature interactions, such as in rice (Matsui *et al.* 1997a) and sorghum (*Sorghum bicolor* (L.) Moench, Vara Prasad *et al.* 2006). This has been attributed to higher canopy temperature at elevated  $[\text{CO}_2]$  due to stomatal closure and reduced transpirational cooling. For example, Vara Prasad *et al.* (2006) recorded a canopy temperature increase of 1.3–2.7°C at  $700 \mu\text{mol mol}^{-1} \text{CO}_2$  in temperature regimes of 32/22°C to 44/34°C in sorghum. Furthermore, Matsui *et al.* (1997a) recorded a 1°C reduction in the critical air temperature induced spikelet sterility with elevated  $[\text{CO}_2]$ . Hence, in future climates with increasing frequency and intensity of droughts combined with increased  $[\text{CO}_2]$ , the adverse influence of warmer temperatures leading to higher canopy temperatures that exceed critical levels are likely to adversely affect yield formation processes in rice and other crop species.

### Combined drought and heat stress

Relatively little is known about the interaction between drought and heat stress in rice (Moffat 2002; Shah and Paulsen 2003). In tobacco (*Nicotiana tabacum* L. cv. Xanthi-nc NN), heat stress caused stomata to open, whereas, under drought stress or combined drought and heat stress, stomata remained closed, resulting in a 2–3°C increase in leaf temperature relative to leaves subjected to heat stress only (Rizhsky *et al.* 2002).

The effects of drought and heat stress could be additive (Barnabás *et al.* 2008), with the combined effect of both stresses shown to be greater than that of each stress individually in sorghum (Craufurd and Peacock 1993) and barley (*Hordeum vulgare* L., Savin and Nicolas 1996). Recently, Rang *et al.* (2011) studied the effect of heat and drought independently and in combination at flowering in five rice genotypes with known levels of tolerance/susceptibility to either heat or drought. The heat tolerant cultivar N22 had high spikelet fertility under heat, drought and the combined stress. Conversely, the heat-sensitive and drought-tolerant cultivars Apo and Moroberekan were on par with N22 under drought stress but recorded the lowest spikelet fertility under combined stresses, suggesting a negative interaction between heat and drought, wherein susceptibility to heat stress dominated the interaction.

One drought tolerance strategy is to maintain turgor in both the male and female reproductive organs to ensure normal reproductive processes during anthesis (Saini and Aspinall 1982). In rice, the lemma and palea, to a certain extent, protect the heat-sensitive reproductive organs (anthers, stigmas) from direct radiative heating effects before anthesis. However, at anthesis, the spikelet is open for  $\sim 45$  min (Ekanayake *et al.* 1989), with both anthers and stigma exposed directly to high ambient air temperatures and high transpirational demand. When severe drought coincides with anthesis, canopy temperature is known to increase beyond critical levels (Garrity and O'Toole 1995). This results in increased transpiration from the spikelets

and a loss of moisture needed for pollen swelling, in turn, reducing anther dehiscence (Matsui *et al.* 2000), and, thus, affecting the succeeding processes involved in grain formation. It is, therefore, essential to test putatively drought tolerant lines for their heat tolerance, and not to ascribe tolerance or susceptibility to drought only.

### Screening for drought tolerance

One major limitation to the improvement of rice for drought-prone areas has been the lack of appropriate screening methods to routinely and reliably impose drought in order to select tolerant lines: both true tolerance and those exhibiting plasticity. Breeders have tried several methods including late-sown wet-season reproductive-stage screening (Jongdee *et al.* 2002; Pantuwan *et al.* 2002a; Kumar *et al.* 2008), line-source sprinkler screening (Garrity and O'Toole 1994), rain-out shelter screening (Lilley and Fukai 1994), and dry-season reproductive-stage screening (Atlin and Lafitte 2002; Kumar *et al.* 2008). Field trials are often conducted during the dry season, in which both drought stress and water supply can be managed artificially through irrigation. Managed field drought-screening protocols for reproductive-stage stress tolerance generally fall into the following three categories, depending on the objectives of the drought screen; stress being imposed (i) as a cyclic drought stress (Bernier *et al.* 2007; Venuprasad *et al.* 2007, 2008); (ii) at panicle initiation till panicle emergence/heading, followed by re-watering at flowering to study the impact of drought on pollen meiosis and spikelet sterility (Saini and Aspinall 1982); or (iii) to expose the most sensitive flowering stage to drought stress. To account for differences in phenology while using the second and third protocols, either staggered planting or drip irrigation at plot level is followed (Lafitte *et al.* 2002, 2004). The remaining part of this paper concentrates mainly on studies using the first or third screening protocol, provided severe drought stress coincided with flowering.

Although interactions between drought and high temperature have been observed (Rang *et al.* 2011), drought tolerance does not necessarily confer heat tolerance; indeed, many drought-tolerant cultivars have been shown to be highly sensitive to heat stress (Jagadish *et al.* 2007, 2008, 2010a, 2010b; see also Craufurd *et al.* 2003 for peanut). Moreover, the rice gene pool has large genotypic variation for tolerance of heat stress (Jagadish *et al.* 2008); thus, although all accessions in a drought screen experience similar exposure to high temperature at flowering, tolerance of heat stress varies among the accessions. Unless experiments are designed to account for combined tolerance of drought and heat stress, the interpretation of results from dry-season drought screens in the field will be confounded by the influence of heat stress.

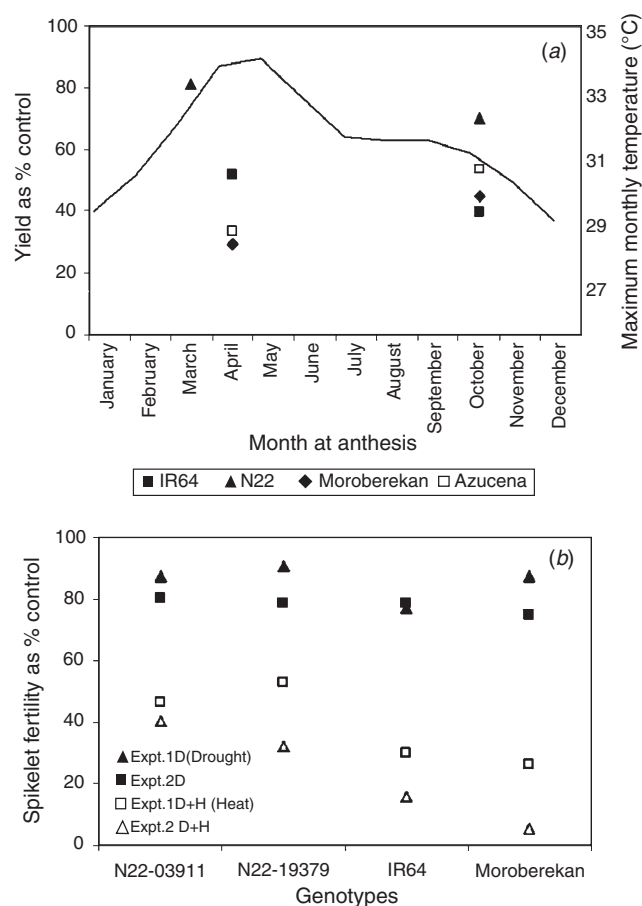
Case studies involving drought screening at International Rice Research Institute (IRRI) and India are considered for addressing the hypothesis of heat stress influencing dry season drought screening. A large proportion of drought screening at the IRRI in Los Baños, Philippines (14°10'N, 121°15'E), is conducted during the dry season, which runs from January to mid-May. The flowering period in these experiments is generally from March to April (Lafitte *et al.* 2004; Venuprasad *et al.* 2007, 2008; Kumar *et al.* 2008), when rainfall is minimal, allowing

efficient application of drought stress. IRRI experimental farm weather records from 1979 to 2008 show average maximum temperatures of 32 and 34°C and high RH of 80 and 78% in March and April, respectively. Since the weather data provides a measure of ambient air temperature 2 m above the crop canopy, with progressive drought, canopy and tissue temperatures can rise much higher than the ambient temperature, as discussed previously (Fig. 2; Garrity and O'Toole 1995).

There are several rice cultivars that have been studied extensively, for which the extent of drought and heat tolerance are known. These include N22 (heat and drought tolerant: Selote and Chopra 2004; Prasad *et al.* 2006; Jagadish *et al.* 2008), Moroberekan and Azucena (drought tolerant but susceptible to heat stress; Champoux *et al.* 1995; Babu *et al.* 2001; Sharma *et al.* 2002; Hittalmani *et al.* 2004; Jagadish *et al.* 2007, 2008, 2010a), and IR64 (moderate heat tolerant, sensitive to drought stress; Liu *et al.* 2006; Jagadish *et al.* 2008). The percentage reduction in grain yield of Moroberekan and Azucena, N22 and IR64 in field experiments conducted in the dry season (2005) and wet season (2008) at IRRI and the average maximum monthly temperature are shown in (Fig. 3a). Although the intensity and duration of stress varied between seasons, the drought-sensitive and moderately heat tolerant check IR64 (Jagadish *et al.* 2008) provides an indication of the level of stress. Drought-tolerant checks Moroberekan and Azucena had a greater reduction in grain yield under drought stress in the dry season relative to IR64, but this trend was reversed in the wet season. Other studies with Moroberekan show similar effects in wet and dry seasons (Babu *et al.* 2001; Hittalmani *et al.* 2004; Liu *et al.* 2006; Table 2). We hypothesise that this is due to higher temperatures rather than drought stress, as Moroberekan and Azucena are extremely sensitive to heat stress (Jagadish *et al.* 2008, 2010a). Across both seasons, N22 had a significantly lower yield decline than the other entries, indicating better heat and drought tolerance (Yoshida *et al.* 1981; Prasad *et al.* 2006; Jagadish *et al.* 2008). Recently, we have also shown under controlled drought at anthesis (~50% flag leaf RWC) that the spikelet fertility of Moroberekan was not significantly different from N22. However, under combined heat and drought stress at anthesis spikelet fertility was significantly reduced ( $P < 0.01$ ) in Moroberekan compared with N22 (Fig. 3b; Rang *et al.* 2011). The ability to tolerate drought with an efficient antioxidant defence mechanism in N22 panicles has been reported by Selote and Chopra (2004).

Although many other factors such as difference in the severity of the stress, management, and genotype  $\times$  environment interactions may have also contributed to the differences in yield, the better performance of other drought-tolerant checks indicates that they may be good heat avoiders (i.e. low canopy temperature; Garrity and O'Toole 1995), possess development traits contributing to heat escape (i.e. early morning flowering; Sheehy *et al.* 2005) or have true heat tolerance (Yoshida *et al.* 1981; Jagadish *et al.* 2008; Weerakoon *et al.* 2008). In peanut, some of the most drought tolerant lines also possess good heat tolerance (Craufurd *et al.* 2003).

The co-location or otherwise of quantitative trait loci (QTL) for heat and drought tolerance also provide some insight into these heat and drought interactions. Azucena, which is drought tolerant but susceptible to heat stress (Jagadish *et al.* 2008), has been used in developing several mapping populations used for studying



**Fig. 3.** (a) Mean percentage reduction in rice grain yield under water stress relative to well watered plots is presented for varieties IR64 (drought-sensitive check), N22, Moroberekan (drought-tolerant check) and Azucena. Each data point is an average of four replications of 1 linear meter (J. E. Cairns and R. Lafitte, unpubl. data). Dry-season experiments were sown in January 2005, with flowering in March and April. Drought stress was imposed at flowering using a drip irrigation system. Wet-season experiments were sown between June and August 2007. After establishment in the drought treatments, plants relied on rainfall. Only plots in which flowering coincided with a period of natural drought stress were included. Temperature data was obtained from the IRRI Climate Unit and collected from the IRRI lowland agro-meteorological weather station during 1979–2008. (b) Two independent experiments with flowering in rice exposed to drought (closed symbols) and combined high temperature and drought stress (open symbols) with the duration of high temperature differing from 2–4 days between the first and second experiments, respectively. N22 was the most tolerant to both stresses even with longer duration of high temperature stress while Moroberekan performed equally well under mild drought stress but recorded close to complete sterility with four days of high temperature stress at flowering (Rang *et al.* 2011).

drought tolerance in particular. For example, in the Bala/Azucena mapping population, QTL for root traits conferring drought tolerance and grain yield were co-located in wet season experiments in southern India (Gomez *et al.* 2006), but poorly co-located under drought stress in the dry season at IRRI (Lafitte *et al.* 2004). More recently, Jagadish *et al.* (2010b) identified QTL for heat tolerance during anthesis in the same mapping population. They found the most significant and consistent QTL for spikelet fertility under heat stress,

**Table 2. Performance of (rice) Moroberekan and drought tolerant checks during dry season drought screening at IRRI, Philippines and wet season screening at Raipur, India respectively during 2008**  
Grain yield reduction was calculated as a percent of stress/non-stress

Season	Temperature (°C)	Entry	Grain yield (t ha <sup>-1</sup> )		Percent reduction
			Non-stress	Stress	
Dry season	24–34	Moroberekan	2.36	0.44	81.5
		check – IR77298-14-1-2-10	4.90	1.75	64.0
		SE	0.52	0.33	–
Wet season	24–30	Moroberekan	3.33	1.55	53.0
		check – IR42253	5.50	2.61	53.0
		SE	0.77	0.46	–

accounting for nearly 18% of the phenotypic variation, on chromosome 1. There was, however, no co-location between QTL for spikelet fertility under ambient and heat stress conditions. The QTL for heat stress was in the same physical location on the rice genome as drought and other stress QTL (e.g. Kumar *et al.* 2007; Jagadish *et al.* 2010b). Similarly, Pinto *et al.* (2010) using Seri × Babax wheat (*Triticum aestivum* L.) mapping population identified QTL for cooler canopy temperature co-localising for both drought and heat stress under field conditions.

Transcript profiling in tobacco and *Arabidopsis* (*Arabidopsis thaliana* (L.) Heynh cv. Columbia) showed lower expression of dehydrins (stress proteins involved in protection against dehydration; Allagulova *et al.* 2003) under combined heat and drought stress than with drought stress only, whereas heat shock proteins had greater expression under combined heat and drought stress than with either heat or drought stress alone (Rizhsky *et al.* 2002, 2004). A similar response has been observed in the desert legume *Retama raetam* (White Broom; Pnueli *et al.* 2002), indicating comparative responses across species. Recently, a comprehensive compilation of transcripts and metabolic changes to combined drought and heat stress showed >770 transcripts and unique metabolites, especially sugars, altered under combined stress that were not altered by either drought or heat stress (Mittler 2006). Using ‘the stress matrix’, Mittler (2006) emphasised the study of abiotic stress combinations as a new state of abiotic stress rather than just a sum of two different stresses.

These QTL and molecular analyses suggests that certain chromosomal regions, genes and metabolic pathways are responsive to both companions of stresses, with a certain proportion being particularly responsive to either of these two stresses. Most importantly, these studies highlight the interaction of heat and drought stress during the dry-season screening and raise important questions for future drought research. The hidden effects of high temperatures during flowering-stage drought screening can lead to confounding results and screening outputs (germplasm, QTL and candidate genes), which may not translate into gains in drought tolerance in the target environment.

## Conclusions

Managed drought screens in the dry season are often exposed to high-temperature stress, confounding drought screening. Hence, caution should be exercised in interpreting cultivars or candidate

QTL or genes from these trials, as drought-tolerant entries highly susceptible to heat stress during anthesis or flowering could be discarded. Potential drought tolerant material should be further tested under cooler wet season to identify true drought tolerant varieties. Conversely, dry season screening may also involve selecting for heat tolerance, which will be needed as global temperatures are predicted to increase. Further physiological and molecular analysis using well planned controlled environment and field studies are needed to understand the impact of the combined heat and drought stress on rice growth and productivity. Furthermore, to ensure developing crops that can cope with the rapidly changing climate, stress-tolerant germplasm has to be evaluated for stress defence and yield potential under multiple abiotic stresses occurring in farmers fields before release for commercial cultivation.

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