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Temperature thresholds and crop production: a review

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Abstract Temperature thresholds for a range of crops from cereal crops to horticultural crops and to legum crops were identified through an extensive literature review. Identification of temperature thresholds provides a basis for quantifying the probability of exceeding temperature thresholds which is a very important aspect of climate change risk assessment. The effects of extreme temperatures on yield and yield components were then reviewed and summarised. Through these processes, critical phenophases were defined based on the sensitivity of crop yield and/or yield components to extreme high temperatures which were imposed on various phenophases. Information on the direction and degree of the impact of extreme temperature on yield/yield components can contribute to the improvement of crop models in which the effects of extreme temperature on crop production have not been adequately represented at this stage. Identification of critical phenophases at which crops yield and/or other economic characteristics are sensitive to extreme temperatures will help scoping appropriate adaptation options.

1 Introduction

Temperature (T) is one of the major environment factors affecting the growth, development and yields of crops especially the rate of development. On one hand, crops have basic requirement for T to complete a specific phenophase or the whole life cycle. On the other hand, extremely high and low Ts can have detrimental effects on crop growth, development and yield particularly at critical phenophases such as

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anthesis. Wheeler et al. (2000) pointed out that the effects of hot T episodes close to the time of anthesis were of more importance to the yield of many crops than the effects of the increase in mean seasonal T of about 2°C. Cardinal T (i.e. base T (Tbase), optimum T (Topt1 and Topt2), and failure point T (Tfp)) and lethal T (e.g. lethal minimum T (Tlmin) and lethal maximum T (Tlmax)) are typical Ts associated with crop production. Crops grow and develop ideally within the range of Topts and at a slower rate beyond the range (the so-called sub/supra-Topt). It was found that the rate of many development processes is a positive linear function of T between Tbase and Topt and a negative linear function of T between Topt2 and Tfp (Roberts and Summerfield 1987; Wheeler et al. 2000). Figure 1 depicts the relative position of these temperatures. Tfp represents failure (ceiling) T at which grain yield fails to zero yield (Hatfield et al. 2008). The difference between lethal Ts and cardinal Ts is that recovery of function is possible within the range of cardinal Ts but is irrecoverably lost beyond the lethal limits (Porter and Gawith 1999). Cardinal T and lethal T are associated with thresholds. What they relate to climate change risk assessment is how often and much T thresholds will be crossed and what the effects of exceeding those T thresholds might be in relation to crop yield and yield components including impact direction and magnitude. Under global warming scenarios, the chances and extent of crossing T thresholds may be higher and more than those under current temperature regime.

It seems that there is an urgent need to identify temperature thresholds and the effects of extreme temperature on crop production. Identification of temperature thresholds will provide a starting point for assessing extreme temperature related risks and this will provide a pathway toward to exploring adaptation options. Identification of the effects of extreme temperature on crop production across various phenophases will help to define critical phenophases so that impact assessment and adaptation evaluation/implementation are focus-oriented. Information on the effects of extreme temperature on crop production under various field/controlled environmental conditions can be used to improve crop models for accurate quantification of the impacts of temperature change on crop production at regional level. The impacts of mean T on crop production were represented in some crop models by growing degree days (GDD). However, the effect of extreme Ts on crop production is lacking in many models which may bias the projection of the impacts of climate

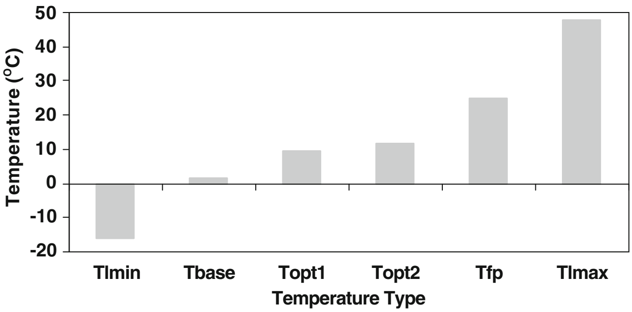

Fig. 1 Relative position of temperature types. Data source: Porter and Gawith (1999). The cardinal temperatures (Tbase, Topt and Tmax) are associated with terminal spikelet initiation stage

change on crop production. This indicates that crop models need to be improved to accommodate the effects of extreme T on crop production.

From what argued above, this paper aims to identify temperature thresholds and the effects of exceeding temperature thresholds on crop yield and yield components for various phenological stages and across a range of crops from cereal crops to legume crops and to horticultural crops based on an extensive literature review and to identify the key phenophases which are most sensitive to the exceedance of temperature thresholds. This kind of information will be very useful for assessing temperature change impacts and for scoping appropriate adaptation options either for a specific industry or for a specific region where a range of crops grow.

2 Temperature thresholds

2.1 Cereal crops

Wheat Temperature thresholds in relation to wheat were well defined. Porter and Gawith (1999) extensively reviewed temperature thresholds across different components (root, leaf, culm) and phenophases based on worldwide experimental studies. Key findings from that literature were given in Table 1. It is found that cardinal temperatures increase as wheat growth and development progress (Porter and Gawith 1999; Slafer and Rawson 1995). This was demonstrated in Fig. 2.

Barley Prasil et al. (2007) evaluated the tolerance of 39 barley cultivars and breeding lines to low temperature by using four direct methods in the Czech Republic: (1) field survival after five winters 1999–2004; (2) winter survival in a provocation pot test under natural conditions; (3) lethal temperature (LT50) of plants taken from a field in winter; and (4) LT50 of plants grown and hardened in a growth chamber. It was found that barley has a Tlmin50 (at which 50% of samples are killed) of $-17.3 \sim -12.9$°C across 20 cultivars which is close to the Tlmin ($-18 \sim -16$°C) of wheat as given in Table 1.

Maize Several studies found that temperatures of above 35°C are lethal to maize pollen viability (Herrero and Johnson 1980; Schoper et al. 1987; Dupuis and Dumas 1990). Leaf photosynthesis rate of maize has a high Topt of 33°C to 38°C (Crafts-Brandner and Salvucci (2002).

Rice The response of rice to temperature has been well studied. Leaf-appearance rate increases with temperature from a Tbase of 8°C, until reaching 36–40°C, the thermal threshold of survival (Alocilja and Ritchie 1991; Baker et al. 1995) with biomass increasing up to 33°C (Matsushima et al. 1964). However, the Topt for grain formation and yield is lower (25°C) (Baker et al. 1995). High percentages of rice spikelet sterility occur if temperatures exceed 35°C at anthesis and last for more than 1 h (Yoshida 1981).

Sorghum The vegetative development of sorghum has a Tbase of 8°C and Topt of 34°C (Alagarswamy and Ritchie 1991) while reproductive development of sorghum has a Topt of 31°C (Prasad et al. 2006). Maiti (1996) reported that sorghum vegetative growth has a Topt of $26 \sim 34$°C while reproductive growth has a Topt of $25 \sim 28$°C.

Table 1 Temperature thresholds (°C) for wheat

Temperatures		Components			Phenophases				
	Lethal limits	Leaf initiation	Shoot growth	Root growth	Sowing to emergence	Vernalization	Terminal spikelet	Anthesis	Grain filling
Tl_{min}	−17.2 (1.2)[a]			−20					
Tl_{max}	47.5 (0.5)[a]								
T_{base}		−1.0 (1.1)	3.0 (0.4)	2.0[b]	3.5 (1.1)	−1.3 (1.5)	1.5 (1.5)	9.5 (0.1)	9.2 (1.5)
T_{opt}		22.0 (0.4)	20.3 (0.3)	<16.3[b] (3.7)	22.0 (1.6)	4.9 (1.1)	10.6 (1.3)	21.0 (1.7)	20.7 (1.4)
T_{max}		24.0 (1.0)	>20.9 (0.2)	>25.0[b] (5.0)	32.7 (0.9)	15.7 (2.6)	>20.0	31.0	35.4 (2.0)

Porter and Gawith (1999)

[a] Information in the brackets is standard error from a range of samples

[b] Soil temperature

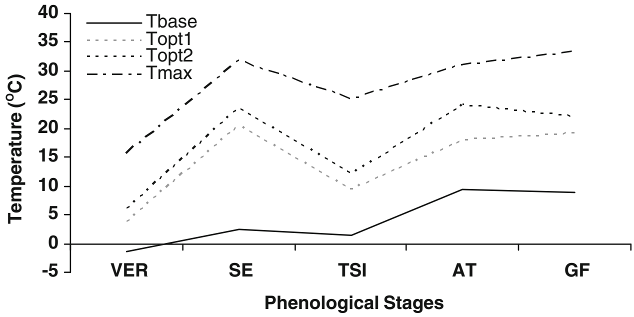

Fig. 2 Evolution of cardinal temperatures for wheat from vernalisation to grain filling (data source: Porter and Gawith (1999)). *VER* vernalisation, *SE* sowing to emergence, *TSI* terminal spikelet initiation, *AT* anthesis, *GF* grain filling

Downs (1972) found that grain yield and maximum dry matter production have a Topt of 27/22°C. A recent study by Prasad et al. (2006) found that grain yield, harvest index, pollen viability and percent seed-set have a Topt of 32/22°C and a Tfp of 40/30°C, and that vegetative biomass, photosynthesis and seed size has a Topt of 40/30°C, 44/34°C and 36/26°C respectively.

Summer cereal crops such as maize, rice and sorghum have relatively higher Topt for crop growth and development compared with that of winter cereal crops such as wheat. Reproductive stage of summer crops has relatively lower Topt compared with vegetative stage.

2.2 Horticultural crops

Broccoli Tan et al. (1999) quantified and assessed the effects of a range of sub zero Ts for a short period at different stages of crop development on the mortality, yield and quality of broccoli. Whole plants in pots or in the field were subjected to sub-zero T regimes from −1 to −19°C. It was found that lethal T for pot-grown broccoli was between −5 ∼ −3°C, whereas the lethal T for field-grown broccoli was between −9 ∼ −7°C. This study also found that the floral initiation is more sensitive to freezing Ts than at florescence buttoning stage. Tan et al. (2000) estimated Tbase and Topt for broccoli based on experimental studies in southeast Queensland. Three cultivars (Fiesta, Greenbelt and Marathon) were sown on eight dates from 11 Mar. to 22 May 1997 and grew under natural and extended (16 h) photoperiods under non-limiting conditions of water and nutrient supply. This study found that broccoli has a Tbase of 0°C and a Top of 20°C during the entire growing cycle. Unlike wheat, cardinal Ts do not increase with the progression of broccoli life cycle.

Citrus Rosenzweig et al. (1996) summarized Topt ranges for different phenophases of citrus. It was reported that dormancy stage has a Topt range of −4°C to 14°C. This stage includes two sub-stages: hardening and pre-bloom. Their corresponding Topt is −4°C to 8°C and 0°C to 14°C respectively. Flowering time has a Topt of 10–27°C. Fruit set has a Topt of 22–27°C and fruit growth has a Topt of 20–33°C. Similar to wheat crops Topt increases with the progression of citrus growth and development.

It was also reported that maturation has a Topt of 13–27°C for the development of soluble sugars and 8–18°C for the development of colour. Maximum temperature of 35°C and minimum temperature of 2°C were identified as the temperature thresholds for citrus across its growing season (Tahir Khurshid, pers. comm.).

Tomato Adams et al. (2001) reported that the rate of leaf appearance, rate of truss appearance and rate of progress to anthesis for tomato has a Tbase of 7°C and a Topt of 22°C, the rate of fruit development and maturation has a Tbase of 5.7°C and a Topt of 26°C, the rate of individual fruit growth has a Topt of 22 $\sim$ 25°C and the rate for fruit-set has a Topt at or lower than 26°C. Fruit size has a Topt of 17 $\sim$ 18°C (Adams et al. 2001; De Koning 1996). It was reported that leaf photosynthesis has a Tbase of 6 $\sim$ 8°C (Duchowski and Brazaityte 2001) and a Topt of about 30°C (Bunce 2000).

2.3 Legume crops

Dry bean/common bean Prasad et al. (2002) reported that dry bean seed yield has a Topt of 23°C and a Tfp of 32°C. A study by Laing et al. (1984) stated that bean yield has a Topt of 24°C.

Peanut/groundnut The Tbase for peanut leaf appearance rate and onset of anthesis is 10°C and 11°C respectively (Ong 1986). The Topt for leaf appearance rate is above 30°C while the Topt for rate of vegetative development to anthesis is between 29°C and 33°C (Bolhuis and deGroot 1959). Leaf photosynthesis has a fairly high Topt of 36°C. Pollen viability and percent seed-set have a Topt of <31°C and a Tfp of 44/34°C (Prasad et al. 2003). Percent fruit-set has a Topt of <33°C (bud temperature) and a Tfp of 43°C (bud temperature) (Prasad et al. 2001). Cox (1979) observed that single pod growth rate and pod size has a Topt of 24°C. Williams et al. (1975) found that peanut yield has a Topt of 20°C. Hatfield et al. (2008) summarised that Topt for pod yield, seed yield, pod harvest index and seed size is in the range of 23 $\sim$ 24°C and with a Tfp of 40°C based on Prasad et al. (2003).

Soybean Reproductive development (time to anthesis) in soybean has a Tbase of 6°C and a Topt of 26°C (Boote et al. 1998). The post-anthesis phase has a lower Topt of 23°C (Egli and Wardlaw 1980; Baker et al. 1989; Pan 1996; Thomas 2001; Boote et al. 2005) compared with that of reproductive development. Pan (1996) and Thomas (2001) found that mean temperature of 39°C is lethal to soybean yield production. Averaged over many cultivars the cardinal temperatures (Tbase, Topt, and Tfp) were 13.2°C, 30.2°C and 47.2°C for pollen germination and 12.1°C, 36.1°C and 47.0°C for pollen tube growth (Hatfield et al. 2008).

2.4 Other crops

It was reported that cotton vegetative development has a Tbase of 14°C and a Topt of 37°C (Reddy et al. 1999 and 2005) which is higher than that of other crops due to its higher adaptability to higher temperature environment (Hatfield et al. 2008). However, cotton reproductive progression has a lower Topt of 28 $\sim$ 30°C (Reddy et al. 1997 and 1999). Reddy et al. (2005) found that growth rate per boll has a Topt

Table 2 Temperature thresholds (°C) for other crops

Crops	Tlmin	Tbase	Topt	Tfp	References
Barley	−17.3 ∼ −12.9				Prasil et al. (2007)
Maize			33 ∼ 38 (LPR)	35 (TLmean, PV)	LPR: Crafts-Brandner and Salvucci (2002)
					PV: Herrero and Johnson (1980), Schoper et al. (1987), Dupuis and Dumas (1990)
Rice		8 (leaf)	36–40 (leaf)		Leaf: Alocilja and Ritchie (1991), Baker et al. (1995);
			33 (biomass)	40 (maxT for PV and PP)	Biomass: Matsushima et al. (1964); Yield (Topt):
			25 (yield)	35 (yield)	Baker et al. (1995); Yield (Tfp): Yoshida (1981); PV and PP: Kim et al. (1996)
Sorghum		8 (VD)	34 (VD)		Alagarswamy and Ritchie (1991)
			26 ∼ 34 (VG)		Maiti (1996)
			31 (RD)		Prasad et al. (2006)
			25 ∼ 28 (RG)		Maiti (1996)
			27/22 (yield and DMP),		Downs (1972)
			32/22 (yield, HI, PV, SS%)	40/30 (yield, HI, PV,SS%)	Prasad et al. (2006)
			40/30 (veg. biomass)	44/34 (panicle)	As above
			44/34 (photosynthesis)		As above
			36/26 (seed size)		As above
Broccoli	−9 to −7 (field)	0[a]	20[a]	35[b](maxT, IF, FI)	Tlmin: Tan et al. (1999)
	−5 to −3 (pot)				Tbase and Topt: Tan et al. (2000),
					Tfp: Bjorkman and Pearson (1998)
Citrus	2[a] (VG)	13(VG)	10 ∼ 27 (AT)	35[a](maxT, VG)	Topt: Rosenzweig et al. (1996)
			22 ∼ 27 (FS)		
			20 ∼ 33 (FG)		
Tomato		7 (LAR, TAR, PAR)	22 (LAR, TAR, PAR)		Adams et al. (2001)
		6–8 (LP)	30 (LP)		LP-Tbase: Duchowski and Brazaityte (2001), LP-Topt: Bunce (2000)
		5.7 (FDMR)	26 (FDMR)		Adams et al. (2001)
			22 ∼ 25 (IFGR)		As above
			17 ∼ 18 (fruit size)		Adams et al. (2001), De Koning (1996)
			<= 26 (FSR)		Adams et al. (2001)

Table 2 (continued)

Crops	Tlmin	Tbase	Topt	Tfp	References
Dry bean			23 ∼ 24 (yield)	32 (yield)	Prasad et al. (2002), Laing et al. (1984)
Peanut		10 (LAR)	>30 (LAR)		Tbase: Ong (1986), Topt for LAR and
		11 (onset of anthesis)	29 ∼ 33 (VD)		VD: Bolhuis and deGroot (1959)
			36 (photosynthesis)		As above
			<31 (PV and seed set%)	39 ∼ 40 (PV and seed set)	Prasad et al. (2003)
			<33 (bud T, fruit-set)	43 (bud T, fruit-set)	Prasad et al. (2001)
			24 (SPGR and pod size)		Cox (1979)
			20 (peanut yield)	40 (yield and HI)	Williams et al. (1975)
			23 ∼ 24 (pod yield, seed yield, pod HI, seed size)		Prasad et al. (2003) and Hatfield et al. (2008)
Soybean		6 (time to AT)	26 (Time to AT)		Boote et al. (1998)
			23 (PA, SSGR, SS, yield)	39 (lethal, SGR, SS, Seed HI)	Egli and Wardlaw (1980), Baker et al. (1989), Pan (1996), Thomas (2001), Boote et al. (2005)
		13.2 (PG)	30.2 (PG)	47.2 (PG)	Hatfield et al. (2008)
		12.1 (PTG)	36.1 (PTG)	47.0 (PTG)	As above
Cotton		14 (leaf and RP)	37 (leaf)		Reddy et al. (1999) and (2005)
			28 ∼ 30 (RP)		Reddy et al. (1997) and (1999)
			25 ∼ 26 (boll growth rate)		Reddy et al. (2005)
			28 (boll harvest index)	33 ∼ 34 (boll harvest index)	As above
			<20 (boll size)		As above
			30(boll number set)		As above
			25 (yield)	35 (yield)	As above

[a]These cardinal temperatures apply to other phenophases

[b]Lethal if crop exposed to this temperature for longer time

LPR leaf photosynthesis rate, *PV* pollen viability, *PP* pollen production, *VD* vegetative development, *VG* vegetative growth, *RD* reproductive development, *RG* reproductive growth, *DMP* dry matter production, *HI* harvest index, *SS%* percent seed set, *IF* inflorescence, *FI* floral initiation, *AT* anthesis, *FS* fruit set, *FG* fruit growth, *LAR* leaf appearance rate, *TAR* Truss appearance rate, *PAR* rate of progress to anthesis, *LP* leaf photosynthesis, *FDMR* fruit development and maturation rate, *IFGR* individual fruit growth rate, *FSR* fruit set rate, *SPGR* single pod growth rate, *PA* post-anthesis, *SSGR* single seed growth rate, *SS* seed size, *PG* pollen germination, *PTG* pollen tube growth, *RP* reproductive progression of 25 ∼ 26°C while boll harvest index has a Topt of 28°C and a Tfp of 33 ∼ 34°C. This study also found that boll size has a Topt of less than 20°C and boll number set has a Topt of 35/27°C.

Temperature thresholds for non-wheat crops across phenophases were summarised in Table 2.

3 Temperature impacts

Temperature impact can be imposed on any growth and development processes, on grain yield components and final grain yield, on grain quality and other aspects. For example, T in the mid 30s°C can lead to a reverse of the vernalisation effects of cold Ts in wheat (Porter and Semenov 2005). Temperature impacts reviewed here mainly refer to yield components and yield.

3.1 Cereal crops

Wheat Extreme temperature effects on yield components and yield have been experimentally studied at reproductive stages. Heat stress at grain filling (GF) stage is one of the key factors which negatively affect wheat yield in Australia. Several experimental studies examined effects of high temperature on wheat yield components and yield. Experimental design ranges from the timing of heat stress, the way heat stress is imposed and the interaction of very high and moderate high temperatures. Stone and Nicolas (1995a) examined the effects of timing of heat stress (40/19°C vs. 21/16°C) during grain filling on wheat grain growth based on cultivars of Oxley and Egret and found that mature individual kernel mass (MIKM) was most sensitive to heat stress applied early in grain filling and became progressively less sensitive throughout grain filling, for both varieties. Stone and Nicolas (1995b) investigated the effects of sudden (ca 20–40°C) and gradual (6°C h^{-1}) increase in T on wheat grain growth during grain filling by using the same cultivars as used in Stone and Nicolas (1995a). This study revealed that the reduction of IKM following sudden heat stress was greater than that resulting from a gradual heat stress of equivalent thermal time and/or equal days of treatment. It was concluded that heat acclimation may help to mitigate wheat yield losses due to high T and that the ability to acclimation to high T varies between wheat genotypes. Another study by Stone et al. (1995) examined the interaction of moderately high T (21/16, 27/22, 30/25) and very high T (40/16°C) during GF and their effects on wheat grain yield. For all moderately high T treatments, a brief "heat shock"/sudden rise in T significantly reduced MIKM by 17%, on average. In the absence of "heat shock", increasing moderately high T progressively reduced MIKM by ca. 2.5% for each 1°C increase in average daily T. After a "heat shock" event, however, there was not a progressive reduction in MIKM with increasing moderately high T. A short period of very high T applied early in GF therefore reduced the response of wheat to subsequent moderately high Ts. It is concluded that reduction in yield caused by "heat shock" is not alleviated by cool post-shock conditions.

Recent experimental studies on the effects of high temperature on grain yield and yield components have been focused on pre/post-anthesis phases (rather than grain filling period). A number of recent studies have found that the effects of high temperature imposed at pre-anthesis phase on grain yield and/or yield components are greater than that of imposed at post-anthesis phase.

Temperatures of 36/31°C for 2 to 3 days prior to anthesis of wheat causes small unfertilized kernels with symptoms of parthenocarpy (Tashiro and Wardlaw 1990). Ferris et al. (1998) reported that grain yield of wheat varied from 3.7 to 9.5 Mg/ha as a result of differences in maxT imposed during a 12-day period starting 7–9 days before 50% anthesis. Some 97% of the variation in grain yield was explained by differences in grain number per square meter which was closely related to a maxT during the 4 day period encompassing 50% anthesis. Calderini et al. (2001) examined the effect of temperature during the pre- and post-anthesis periods on mass per grain in Argentina and Mexico. It was concluded that average temperature between booting and anthesis was closely related to the observed difference of mass per grain, probably as a consequence of the effects of this factor on carpel growth. Study by Wollenweber et al. (2003) found that there was no significant difference in the grain yield of wheat between those warmed at anthesis and those warmed at double ridge and anthesis. This means that the plants experienced warming periods independently and that a critical temperature of 35°C for a short period around anthesis had severe yield reducing effects (Porter and Semenov 2005). A recent study by Ugarte et al. (2007) investigated the effects of increasing pre-anthesis temperature (5.5°C higher than control) on the yield of barley, wheat and triticale in Argentina under irrigated condition. It was found that thermal treatments consistently reduced grain yield, the magnitude of the effect ranged from 5% to 52% across seasons, phases and crops. The highest effect was found when T increased during stem elongation (46%), lowest when treatments were imposed during heading-anthesis (15%) and intermediate for thermal treatments imposed during booting-anthesis (27%). This study also found that most effects of thermal treatments on yield were due to parallel effects on grain number. However, thermal treatments significantly decreased mass per grain during the three seasons. The most adverse treatment on mass per grain was when the crops were heated during the Booting-anthesis period (−23%).

Maize Jones et al. (1984) reported that thermal environment during endosperm cell division phase (8–10 days post-anthesis) of maize is critical. A temperature of 35°C, compared to 30°C during this period dramatically reduced subsequent kernel growth rate (potential) and final kernel size. Study by Commuri and Jones (2001) found that temperatures above 30°C increasingly impaired cell division and amyloplast replication in maize kernels, and thus reduced grain sink strength and yield.

Rice As mentioned earlier rice is most sensitive to high Ts at heading, and next most sensitive at about 9 days before heading (Yoshida 1981). At heading, spikelet fertility is reduced from 90 to 20% by only 2 h exposure to 38°C and to 0% by 1 h exposure to 41°C. Study by Kim et al. (1996) found that pollen viability and production of rice begins to decline as daytime maximum temperature exceeds 33°C, and reaches zero at Tmax of 40°C. Studies of Baker and Allen (1993) and Peng et al. (2004) found that rice grain yield is reduced about 10% per 1°C temperature increase above 25°C, until reaching zero yield at 35–36°C mean temperature, using a 7°C day/night temperature differential.

Sorghum Prasad et al. (2006) examined the effects of high Ts on sorghum growth and development and found that panicle emergence was delayed 20 days as T above 36/26°C to 40/30°C, and no panicles were formed at 44/34°C.

3.2 Legume crops

Common beans/dry bean High T (32/27°C, day/night) during the period shortly before and at anthesis reduced pod set, pod abscission and seed set substantially (Gross and Kigel 1994). No pods were set when high T occurred at sporogenesis, or 10 days before anthesis. A study by Prasad et al. (2002) reported that pollen production per flower was reduced above 31/21°C, pollen viability was dramatically reduced above 34/24°C and seed size was reduced above 31/21°C.

Cowpea High temperatures for 6 days before anthesis substantially reduced pod set (Hall 1992). Cowpea is sensitive to the effects of high night Ts (30°C) during early bud development and at floral bud development. The most sensitive phase was 7–9 days prior to anthesis (Ahmed et al. 1992).

Peanut/groundnut Prasad et al. (1999) found that 3–6 days before anthesis when microsporogenesis occurs, and at anthesis were two critical stages when peanut is sensitive to high T (38°C). Two processes determine successful fruit production in peanut: flowering rate and fruit set (Vara Prasad et al. 2000). This study found that the number of flowers produced by groundnut cv.ICGV 86015 was a simple negative function of air temperature (maximum temperature) between 28°C and 48°C. The proportion of flowers which set fruit was not affected by air temperature less than 37°C. However, fruit set declined rapidly at greater than 37°C until no fruit at all were set at 44°C. Studies of Prasad et al. (2001) found that for peanut individual flower, the sensitive period to increased temperature starts 6 days prior to opening of a given flower and ends 1 day after, with the greatest sensitivity on the days of flower opening.

Soybean Ferris et al. (1999) studied the effects of an increase in T by 10°C for 8 days during the late flowering stage/early pod filling stage of soybean. Seed yields at harvest maturity were 29% less due to the high temperature treatment. Salem et al. (2007) examined the growth of soybeans under two temperature regimes (38/30°C vs. 30/22°C) and found that the elevated temperature reduced pollen production by 34%, pollen germination by 56% and pollen tube elongation by 33%. Baker et al. (1989) and Boote et al. (2005) reported that seed harvest index reduced at T above $23 \sim 27$°C.

3.3 Horticulture crops

Broccoli Bjorkman and Pearson (1998) identified sensitive developmental stage of broccoli. 'Galaxy' broccoli was exposed to 35°C for 1 week varying at developmental stages. This study found that meristems were affected only if heat was applied during inflorescence production or the floral initiation process. Shorter heat exposures produced little injury, and longer exposures were lethal. This study also found that broccoli plants are more sensitive to freezing injury during floral initiation.

Citrus Rosenzweig et al. (1996) reported that Tmax of greater than 38°C may cause losses in citrus fruit set near the end of bloom. There is a 50% loss if Tmax is greater than 48°C. Another study found that Tmax of greater than 40°C can cause sunburn and increase in fruit drop (Tahir Khurshid, pers. comm.).

Tomato Peat et al. (1998) observed that the number of fruits per plant (percent fruit-set) at 32/26°C was only 10% of that at 28/22°C.

3.4 Other crops

Canola Aksouh-Harradj et al. (2006) investigated the effects of two temperature regimes following a 24-h acclimation period on three canola cultivars (*B. napus*, Insignia, Emblem, Surpass400) through controlled growth cabinets in Australia. These three cultivars have different thermotolerance. A long, moderately high T treatment of 28°C/23°C (day/night) was applied for 10 days (from 20 to 30 days after flowering (DAF)). A short, very high T regime of 28/23°C including a peak of 38°C reached for 5 h around midday for 5 days (from 25 to 29 DAF). It was found that the short and very high T treatment reduced yield on the main stem by up to 52% for a sensitive cultivar (Surpass400) by reducing seed weight. Qaderi et al. (2006) examined the growth and physiological response of canola to enhanced temperature. It was found that higher T inhibits many processes of canola growth and development.

Cotton Kakani et al. (2005) reported that instantaneous air temperature above 32°C reduces cotton pollen viability, and temperature above 29°C reduces pollen tube elongation. T of 40/32°C led to zero boll yield (Reddy et al. 1992a, b). Pettigrew (2008) evaluated two cotton genotypes under a temperature regime 1°C warmer than ambient temperatures (26.4°C) and found lint yield was 10% lower in the warm regime.

4 Summary

This paper identified temperature thresholds and the effects of extreme temperature on crop yield and yield components across different phenophases and various crops. It is concluded that different crop components and different phenological stages as well as different crop growth and development processes have different temperature thresholds (Table 2) for most of the crops concerned if not for all crops. Temperature thresholds increase as the progression of crop growth and development (wheat and citrus, Fig. 2). However, this finding does not hold for other crops such as broccoli (Tan et al. 2000), peanut and pearl millet (Ong 1983a, b; Leong and Ong 1983).

Most of the studies reviewed here on the effects of extreme temperature on crop yield components and yield show that reproductive phases are more sensitive to extreme high temperatures such as anthesis (including pre and post anthesis) and grain filling. Wheeler et al. (2000) concluded that the time of flowering of many crop plants is sensitive to extremes of temperature. Wollenweber et al. (2003) pointed out that an extreme heat episode during vegetative development such as double ridge does not seem subsequently to affect the growth and developmental response of wheat to a second heat event at anthesis and that high-T episodes seem to operate independently of each other. The conclusion from such results for climate change are that yield damaging weather signals for cereals such as wheat are in the form of absolute T thresholds, are linked to particular development stages and can be effective over short time periods (Porter and Semenov 2005). This highlighted the necessity of identifying temperature thresholds at critical phenophases which was justified in the Introduction of this paper and the necessity of quantifying the probability of exceeding these thresholds as well as the impacts on crop yields due to the crossing of temperature thresholds.

There is a growing recognition that extreme climate events including extreme temperature events will be more frequent under future climate change scenarios (Cubasch et al. 2001). Quantifying the probability of exceeding the temperature thresholds and the possible impact of extreme climate events on crop production at regional level will be common climate change risk assessment exercises. However difficulties exist to quantify the effects of extreme temperature on crop production. Crop models are a common tool for estimating the potential impacts of climate change on crop production. However, they are not all sufficiently robust to simulate the effects of extreme temperature on crop yield/yield components. Extreme temperature effects are not adequately represented in all of the state-of-the-art crop models as pointed out in the Introduction.

Future crop model development should focus on capturing the impacts of extreme temperatures in addition to the effects of mean temperature. Section 3 provides useful information to improve and calibrate crop models so that effects of temperature on crop production can be quantified more accurately at regional level. To better understand temperature related risks and the mechanism of the effects of extreme temperature on crop production, more experimental studies are needed for both the identification of temperature thresholds and the effects of extreme temperature on crop production particularly under enhanced atmospheric pCO_2 and changed rainfall regime. There may be interactions between pCO_2 and temperature thresholds and between temperature thresholds and wet/dry conditions.

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References

Adams SR, Cockshull KE, Cave CRJ (2001) Effect of temperature on the growth and development of tomato fruits. Ann Bot 88:869–877

Ahmed FE, Hall AE, Demason DA (1992) Heat injury during floral development in cowpea (vigna unguiculata, Fabaceae). Am J Bot 79:784–791

Aksouh-Harradj NM, Campbell LC, Mailer RJ (2006) Canola response to high and moderately high temperature stresses during seed maturation. Can J Plant Sci 86:967–980

Alagarswamy G, Ritchie JT (1991) Phasic development in CERES-sorghum model, chapter 13. In: Hodges T (ed) Predicting crop phenology. CRC, Boca Raton, pp 143–152

Alocilja EC, Ritchie JT (1991) A model for the phenology of rice. Chapter 16. In: Hodges T (ed) Predicting crop phenology. CRC, Boca Raton, pp 181–189

Baker JT, Allen LH Jr (1993) Contrasting crop species responses to CO_2 and temperature: rice, soybean, and citrus. Vegetatio 104/105:239–260

Baker JT, Allen LH Jr, Boote KJ (1989) Response of soybean to air temperature and carbon dioxide concentration. Crop Sci 29:98–105

Baker JT, Boote KJ, Allen LH Jr (1995) Potential climate change effects on rice: carbon dioxide and temperature. In: Rosenzweig C, Jones JW, Allen LH Jr (eds) Climate change and agriculture: analysis of potential international impacts. ASA Spec. Pub. No. 59, ASA-CSSA-SSSA, Madison, Wisconsin, USA, pp 31–47

Bjorkman T, Pearson K (1998) High temperature arrest of inflorescence development in broccoli (Brassica oleracea var. italica L.). J Exp Bot 49(318):101–106

Bolhuis CG, deGroot W (1959) Observations on the effect of varying temperature on the flowering and fruit set in three varieties of groundnut. Neth J Agric Sci 7:317–326

Boote KJ, Jones JW, Hoogenboom G (1998) Simulation of crop growth: CROPGRO Model. Chapter 18. In: Peart RM, Curry RB (eds) Agricultural systems modeling and simulation. Marcel Dekker, New York, pp 651–692

Boote KJ, Allen LH, Prasad PVV, Baker JT, Gesch RW, Snyder AM, Pan D, Thomas JMG (2005) Elevated temperature and CO_2 impacts on pollination, reproductive growth, and yield of several globally important crops. J Agric Meteorol 60:469–474

Bunce JA (2000) Acclimation of photosynthesis to temperature in eight cool and warm climate herbaceous C3 species: temperature dependence of parameters of a biochemical photosynthesis model. Photosynth Res 63:59–67

Calderini DF, Savin R, Abeledo LG, Reynolds MP, Slafer GA (2001) The importance of the period immediately preceding anthesis for grain weight determination in wheat. Euphytica 119:199–204

Commuri PD, Jones RD (2001) High temperatures during endosperm cell division in maize: a genotypic comparison under in vitro and field conditions. Crop Sci 41:1122–1130

Cox FR (1979) Effect of temperature treatment on peanut vegetative and fruit growth. Peanut Sci 6:14–17

Crafts-Brandner SJ, Salvucci ME (2002) Sensitivity of photosynthesis in a C-4 plant, maize, to heat stress. Plant Physiol 129:1773–1780

Cubasch U, Meehl GA, Boer GJ, Stouffer RJ et al (2001) Projections of future climate change. In: Houghton JT, Ding Y, Griggs DJ, Noguer M, van der Linden PJ, Dai X, Maskell K, Johnson CA (eds) Climate change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, p 525–582

De Koning ANM (1996) Quantifying the responses to temperature of different plant processes involved in growth and development of glasshouse tomato. Acta Hortic 406:99–104

Downs RW (1972) Effect of temperature on the phenology and grain yield of Sorghum bicolor. Aust J Agric Res 23:585–594

Duchowski P, Brazaityte A (2001) Tomato photosynthesis monitoring in investigations on tolerance to low temperatures. Acta Hort 562:335–339

Dupuis L, Dumas C (1990) Influence of temperature stress on in vitro fertilization and heat shock protein synthesis in maize (Zea mays L.) reproductive systems. Plant Physiol 94:665–670

Egli DB, Wardlaw IF (1980) Temperature response of seed growth characteristics of soybean. Agron J 72:560–564

Ferris R, Ellis RH, Wheeler TR, Hadley P (1998) Effect of high tempearture stress at anthesis on grain yield and biomass of field-grown crops of wheat. Ann Bot 82:631–639

Ferris R, Wheeler TR, Ellis RH, Hadley P (1999) Seed yield after environmental stress in soybean grown under elevated CO_2. Crop Sci 39:710–718

Gross Y, Kigel J (1994) Differential sensitivity to high temperature of stages in the reproductive development of common bean (Phaseolus vulgaris L.). Field Crops Res 36:201–212

Hall AE (1992) Breeding for heat tolerance. Plant Breed Rev 10:129–167

Hatfield J, Boote K, Fay P, Hahn L, Izaurralde C, Kimball BA, Mader T, Morgan J, Ort D, Polley W, Thomson A, Wolf D (2008) Agriculture. In: The effects of climate change on agriculture, land resources, water resources, and biodiversity in the United States. A Report by the U.S. Climate

Change Science Program and the Subcommitee on Global Change Research. Washington, D.C., USA, 362 pp
Herrero MP, Johnson RR (1980) High temperature stress and pollen viability in maize. Crop Sci 20:796–800
Jones RJ, Ouattar S, Crookston RK (1984) Thermal environment during endosperm cell division and grain filling in maize: effects on kernel growth and development in vitro. Crop Sci 24:133–137
Kakani VG, Reddy KR, Koti S, Wallace TP, Prasad PVV, Reddy VR, Zhao D (2005) Differences in in vitro pollen germination and pollen tube growth of cotton cultivars in response to high temperature. Ann Bot 96:59–67
Kim HY, Horie T, Nakagawa H, Wada K (1996) Effects of elevated CO_2 concentration and high temperature on growth and yield of rice. II. The effect of yield and its component of Akihikari rice. Japan J Crop Sci 65:644–651
Laing DR, Jones PG, Davis JH (1984) Common bean (Phaseolus vulgaris L.). In: Goldsworthy PR, Fisher NM (eds) The physiology of tropical field crops. Wiley, New York, pp 305–351
Leong SK, Ong CK (1983) The influence of temperature and soil water deficit on the development and morphology of grounnut (Arachis Hypogaea L.). J Exp Bot 34:1551–1561
Maiti RK (1996) Sorghum science. Science, Lebanon
Matsushima S, Tanaka T, Hoshino T (1964) Analysis of yield determining process and its application to yield-prediction and culture improvement of lowland rice. LXX. Combined effect of air temperature and water temperature at different stages of growth on the grain yield and its components of lowland rice. Proc Crop Sci Soc Japan 33:53–58
Ong CK (1983a) Response to temperature of a stand of pearl millet (*Pennisetum typhoides S. & H.*). 1. Vegetative developemt. J Exp Bot 34:322–336
Ong CK (1983b) Response to temperature of a stand of pearl millet (*Pennisetum typhoides S. & H.*). 2. Reproductive developemt. J Exp Bot 34:337–348
Ong CK (1986) Agroclimatological factors affecting phenology of groundnut. In: Sivakumar MVK, Virmani SM (eds) Agroclimatology of groundnut. ICRISAT, Patancheru, India, pp 115–125
Pan D (1996) Soybean responses to elevated temperature and doubled CO_2. PhD dissertation. University of Florida, Gainesville, p 227
Peat MM, Sato S, Gardner RG (1998) Comparing heat stress effects on male-fertile and male-sterile tomatoes. Plant Cell Environ 21:225–231
Peng S, Huang J, Sheehy JE, Lanza RC, Visperas RM, Zhong X, Centeno GS, Khush GS, Cassman KG (2004) Rice yields decline with higher night temperatures from global warming. Proc Natl Acad Sci USA. http://www.pnas.org/cgi/content/full/101/27/9971, 10 pp
Pettigrew WT (2008) The effect of higher temperature on cotton lint yield production and fiber quality. Crop Sci 48:278–285
Porter JR, Gawith M (1999) Temperatures and the growth and development of wheat: a review. Eur J Agron 10:23–36
Porter JR, Semenov MA (2005) Crop responses to climatic variation. Philos Trans R Soc B: Biol Sci 360:2021–2035
Prasad PVV, Craufurd PQ, Summerfield RJ (1999) Sensitivity of peanut to timing of heat stress during reproductive development. Crop Sci 39:1352–1357
Prasad PVV, Craufurd PQ, Kakani VG, Wheeler TR, Boote KJ (2001) Influence of high temperature during pre- and post-anthesis stages of floral development on fruit-set and pollen germination in peanut. Aust J Plant Physiol 28:233–240
Prasad PVV, Boote KJ, Allen LH Jr, Thomas JMG (2002) Effects of elevated temperature and carbon dioxide on seed-set and yield of kidney bean (*Phaseolus vulgaris* L.). Glob Change Biol 8:710–721
Prasad PVV, Boote KJ, Allen LH Jr, Thomas JMG (2003) Supra-optimal temperatures are detrimental to peanut (*Arachis hypogaea* L) reproductive processes and yield at ambient and elevated carbon dioxide. Glob Change Biol 9:1775–1787
Prasad PVV, Boote KJ, Allen LH Jr (2006) Adverse high temperature effects on pollen viability, seed-set, seed yield and harvest index of grain-sorghum [*Sorghum bicolor* (L.) Moench] are more severe at elevated carbon dioxide due to high tissue temperature. Agric For Meteorol 139:237–251
Prasil IT, Prasilova P, Marik P (2007) Comparative study of direct and indirect evaluations of frost tolerance in barley. Field Crops Res 102:1–8
Qaderi MM, Kurepin LV, Reid DM (2006) Growth and physiological responses of canola (*Brassica napus*) to three components of global climate change: temperature, carbon dioxie and drought. Physiol Plant 128:710–721

Reddy KR, Hodges HF, McKinion JM, Wall GW (1992a) Temperature effects on Pima cotton growth and development. Agron J 84:237–243
Reddy KR, Hodges HF, Reddy VR (1992b) Temperature effects on cotton fruit retention. Agron J 84:26–30
Reddy KR, Hodges HF, McKinion JM (1997) A comparison of scenarios for the effect of global climate change on cotton growth and yield. Aust J Plant Physiol 24:707–713
Reddy KR, Davidonis GH, Johnson AS, Vinyard BT (1999) Temperature regime and carbon dioxide enrichment alter cotton boll development and fiber properties. Agron J 91:851–858
Reddy KR, Prasad PVV, Kakani VG (2005) Crop responses to elevated carbon dioxide and interactions with temperature: cotton. J Crop Improv 13:157–191
Roberts EH, Summerfield RJ (1987) Measurement and prediction of flowering in annual crops. In: Atherton JG (ed) Manipulation of flowering. Butterworths, London, pp 17–50
Rosenzweig C, Phillips J, Goldberg R, Carroll J, Hodges T (1996) Potential impacts of climate change on citrus and potato production in the US. Agric Syst 52:455–479
Salem MA, Kakani VG, Koti S, Reddy KR (2007) Pollen-based screening of soybean genotypes for high temperature. Crop Sci 47:219–231
Schoper JB, Lambert RJ, Vasilas BL, Westgate ME (1987) Plant factors controlling seed set in maize. Plant Physiol 83:121–125
Slafer GA, Rawson HM (1995) Base and optimum temperatures vary with genotype and stage of development in wheat. Plant Cell Environ 18:671–679
Stone PJ, Nicolas ME (1995a) Effect of timing of heat stress during grain filling on two wheat varieties differing in heat tolerance. I. Grain Growth. Aust J Plant Physiol 22:927–934
Stone PJ, Nicolas ME (1995b) Comparison of sudden heat stress with gradual exposure to high temperature during grain filling in two wheat varieties differing in heat tolerance. I. Grain Growth. Aust J Plant Physiol 22:935–944
Stone PJ, Savin R, Wardlaw IF, Nicolas ME (1995) The influence of recovery temperature on the effects of a brief heat shock on wheat. I. Grain Growth. Aust J Plant Physiol 22:945–954
Tan DKY, Wearing AH, Joyce DC, Rickert KG, Birch CJ (1999) Freeze-induced reduction of broccoli yield and quality. Aust J Exp Agric 39:771–780
Tan DKY, Birch CJ, Wearing AH, Rickert KG (2000) Predicting broccoli development: I. Development is predominantly determined by temperature rather than photoperiod. Sci Hortic 84:227–243
Tashiro T, Wardlaw IF (1990) The response to high temperature shock and humidity changes prior to and during the early stages of grain development in wheat. Aust J Plant Physiol 17:551–561
Thomas JMG (2001) Impact of elevated temperature and carbon dioxide on development and composition of soybean seed. PhD Dissertation. University of Florida. Gainesville, Florida, USA, p 185
Ugarte C, Calderini DF, Slafer GA (2007) Grain weight and grain number responsiveness to pre-anthesis temperature in wheat, barley and triticale. Field Crops Res 100:240–248
Vara Prasad PV, Craufurd PQ, Summerfield RJ, Wheeler TR (2000) Effects of short episodes of heat stress on flower production and fruit-set of groundnut (Arachis hypogaea L.). J Exp Bot 51:777–784
Wheeler TR, Craufurd PQ, Ellis RH, Porter JR, Vara Prasad PV (2000) Temperature variability and the yield of annual crops. Agric Ecosyst Environ 82:159–167
Williams JH, Wilson JHH, Bate GC (1975) The growth of groundnuts (Arachis hypogaea L. cv. Makulu Red) at three altitudes in Rhodesia. Rhod J Agric Resour 13:33–43
Wollenweber B, Porter JR, Schllberg J (2003) Lack of interaction between extreme high-temperature events at vegetative and reproductive growth stages in wheat. J Agron Crop Sci 189:142–150
Yoshida S (1981) Fundamentals of rice crop science. IRRI, Los Baños, p 269