

Temperatures and the growth and development of maize and rice: a review

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Abstract

Because of global land surface warming, extreme temperature events are expected to occur more often and more intensely, affecting the growth and development of the major cereal crops in several ways, thus affecting the production component of food security. In this study, we have identified rice and maize crop responses to temperature in different, but consistent, phenological phases and development stages. A literature review and data compilation of around 140 scientific articles have determined the key temperature thresholds and response to extreme temperature effects for rice and maize, complementing an earlier study on wheat. Lethal temperatures and cardinal temperatures, together with error estimates, have been identified for phenological phases and development stages. Following the methodology of previous work, we have collected and statistically analysed temperature thresholds of the three crops for the key physiological processes such as leaf initiation, shoot growth and root growth and for the most susceptible phenological phases such as sowing to emergence, anthesis and grain filling. Our summary shows that cardinal temperatures are conservative between studies and are seemingly well defined in all three crops. Anthesis and ripening are the most sensitive temperature stages in rice as well as in wheat and maize. We call for further experimental studies of the effects of transgressing threshold temperatures so such responses can be included into crop impact and adaptation models.

Keywords: cardinal temperatures, climatic change impacts, development, growth, lethal temperatures, maize, rice

Received 27 January 2013; revised version received 24 July 2013 and accepted 19 August 2013

Introduction

The Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment has forecast that the increase in global average temperature will be between 1.8 and 4.0 °C in 2100, depending on the level of greenhouse gas emissions. The increase can even be larger (perhaps up to 6.4 °C) if the human population and the global economy continue growing at their current rates. An increase of 2–3 °C in global average temperature is predicted if CO₂ levels stabilize around 450 ppm (Meehl *et al.*, 2007).

Changes to the global climate, notably to regional spatial and temporal temperature patterns from increased atmospheric concentrations of greenhouse gases are predicted to have important consequences for crop production (Parry *et al.*, 2004; Lobell & Field, 2007). Both plant growth and development are affected by temperature (Stone, 2001; Barnabás *et al.*, 2008). Investigations of the effects of changes in mean annual temperature on agricultural crops (Wheeler *et al.*, 2000; Challinor *et al.*, 2007) have used crop–climate simulation models

(Hawkins *et al.*, 2012; Lobell *et al.*, 2012) and experiments (Wheeler *et al.*, 1996b; Lobell *et al.*, 2011). Impacts of mean temperature changes on crops preceded consideration of the effects that changes in climatic variability and extreme conditions might have. A changing or changed climate may exhibit increased climatic variability and small changes in climatic variability can produce relatively large changes in the frequency of extreme climatic events (Porter & Semenov, 2005).

This article reviews the threshold temperature literature for maize and rice, complementing an earlier study for wheat (Porter & Gawith, 1999). Our primary purpose is to synthesize available results and make this information more accessible to the climatic change community, allowing identification of whether the frequency of extreme temperature events that affect crop production is either changing or will change under climate change. This may include increases in the frequency of discrete events such as plant mortality caused by low or high temperatures. Less extreme but still important temperature changes may increase plant sterility and reduce grain set. We hope that modellers can use the data presented to assess quantitatively the effects of temperature change on crop processes.

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In our literature review we describe the responses of maize and rice plants to extreme temperatures under experimental conditions. Cardinal temperature thresholds for different phenological processes are identified and we outline the effects of temperature on rates of growth and development. Finally, we assess the implications of the above for future climatic impact studies.

Materials and methods

For both crops we estimated the minimum, optimum and maximum temperatures (termed the cardinal temperatures) plus their standard errors (SE) for the following processes: mortality, leaf initiation, shoot growth, root growth and crop development for the following phenological phases and stages: germination and emergence, tillering (rice), panicle (rice) or ear (maize) initiation, anthesis, grain filling and the whole plant life cycle.

We collected literature reporting temperatures for these processes, phenological phases and stages from field, laboratory and experimental greenhouse studies. About 70 articles were selected from the reviewed literature for each of the two crops species: rice (*Oryza sativa* L.) and maize (*Zea mays* L.). Temperature data were extracted from the articles and classified into three thresholds according to the following criteria: (i) Optimal temperature (Topt), defined as the temperature giving the highest rate of a crop process; (ii) Minimum or base temperature (Tmin) defined as the lower limits; and (iii) maximum temperature (Tmax) defined as the upper limits at which plants suffered tissue injuries or where a physiological process may cease. In the case of cardinal temperatures, the plant did not suffer irreversible damage but has a possible recovery of function; lethal temperatures caused irreversible damage. Relevant literature from databases was downloaded, data extracted, sorted and presented in Tables S1-S7 (Supporting Information Tables) and Data S1 (Supporting Information References). Data are organized such that the three temperature thresholds (Tmin, Tmax, Topt) are evident, as are the cultivar used and the source of temperature data in the reviewed study. In the case of rice, we also specified subspecies (ssp. *japonica* or ssp. *indica*), when it was specified in the reviewed study.

We used the compiled data (*n* samples) to calculate the mean minimum, optimum and maximum temperatures by processes and phenological phases and stages for both crops. The SE of the mean were calculated from the standard deviation of the compiled data used to estimate the mean. When temperature data were presented as interval and not as a specific temperature value, we calculated the arithmetic mean value of the interval. When values were defined as less (<) or greater than (>) a particular value, we calculated the mean and standard error of a cardinal value accordingly.

Limitations of our analysis are that differences exist between experimental designs leading to a confounding of the effects of different growing conditions, such as the relation between temperature and vapour pressure. Also, reported temperatures are normally ambient air and not actual plant

temperatures. However, these limitations have also been the case in other recent papers examining plant temperature responses (Parent *et al.*, 2010; Parent & Tardieu, 2012).

Rice

Meta-data analysis of published material was assisted by the Faculty of Life Science library at the University of Copenhagen (<http://www.bvfb.life.ku.dk>). Most articles were found in the major scientific databases, such as Google Scholar, CAB Abstract, Web of Science, Agris and Agricola. A physical search was also made where necessary, especially as some of the literature dates from 1933 and much of the older literature is written in Chinese or Japanese without English text translation but with English summaries of figures and tables.

Maize

As with rice, a physical search was performed in specialist library at University of Copenhagen, Faculty of Life Sciences and a keyword search was performed in the major scientific databases/search engines including Web of Science, Agris, Agricola, Google Scholar, CAB Abstract and CAB reviews. The first identified reference came from Lehenbauer (1914), one of the first to make a scientific study of temperature and development in maize.

Results

Readers are asked to note that the original data used to provide the following summary results for rice and maize are available as online supplementary information (Data S1, Tables S1–S7) to this article.

Wheat

Original data used to define cardinal temperatures for wheat (minimum temperature, Tmin; optimum temperature, Topt; maximum temperature, Tmax) are from Porter & Gawith (1999) and are in Table S7 of this article.

Lethal limits for wheat were identified by Porter & Gawith (1999) as mean temperatures of -17.2 °C (SE 1.2 °C) for Tmin and 47.5 °C (SE 0.5 °C) for Tmax. They also reported temperature tolerances for different plants parts and phenological phases. Cardinal temperatures below 2 °C and higher than 25 °C (SE 5.0 °C) may accelerate root senescence. Shoot elongation is slower at temperatures below ca. 20 °C and at temperatures higher than ca. 21 °C, being the mean minimum temperature 3.0 °C (SE 0.4 °C). Leaf initiation is inhibited at a temperature of -1.0 (SE 1.1 °C) (Fig. 1a, b and c.).

Porter & Gawith (1999) also reviewed temperature sensitivity variations during the course of development.

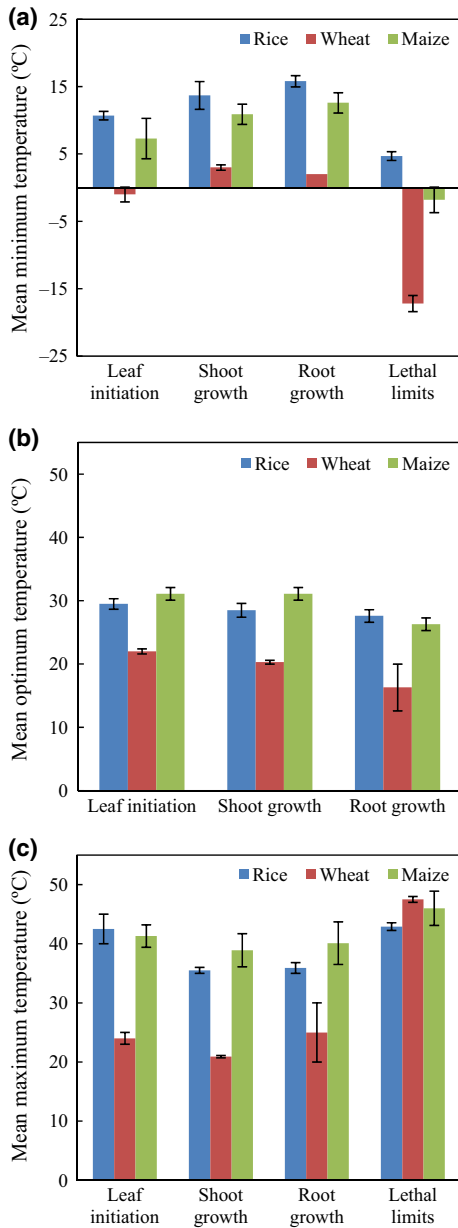


Fig. 1 Rice, wheat and maize (in separate columns with SE). (a) Mean minimum temperature for leaf initiation, shoot growth, root growth and lethality, (b) Mean optimum temperature for leaf initiation, shoot growth and root growth, (c) Mean maximum temperature for leaf initiation, shoot growth, root growth and lethality.

Despite temperature sensitivity for anthesis varies during its course, T_{max} seems to be ca. 31 °C and T_{min} 9.5 °C (SE 0.1 °C). Exposure to suboptimal or superoptimal temperatures may reduce grain yields by inducing pollen sterility. Cardinal temperatures are generally highest during grain filling, showing a wider range of cardinal temperatures than for anthesis. T_{max} and T_{opt}

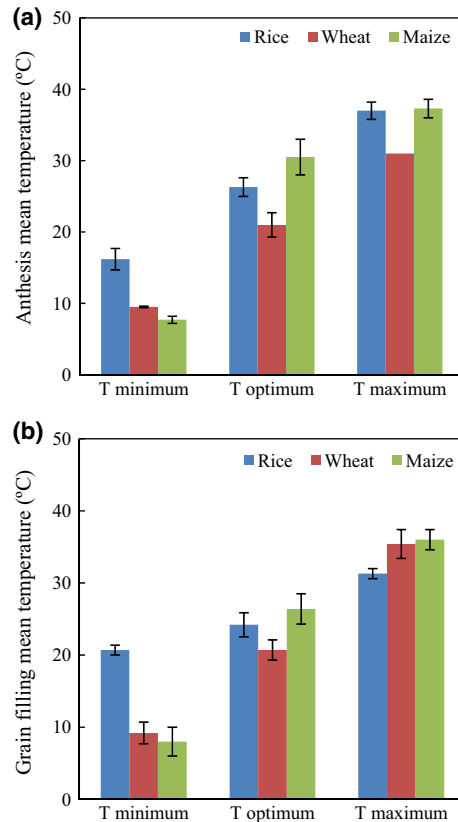


Fig. 2 Rice, wheat and maize (in separate columns with SE). (a) Mean minimum, optimum and maximum temperatures for anthesis, (b) Mean minimum, optimum and maximum temperatures for grain filling.

for grain filling are 35.4 °C (SE 2.0 °C) and 20.7 °C (SE 1.4 °C) respectively (Fig. 2a and b).

Rice

Table 1 summarizes the mean lethal and cardinal temperatures for rice (*Oriza sativa* L.) and for their two subspecies (ssp. *japonica* and ssp. *indica*). Mean lethal temperatures are 42.9 °C (SE 0.7 °C) for T_{max} and 4.7 °C (SE 1.3 °C) for T_{min} in rice. Above the defined upper and below the lower limit, physiological processes are affected to the extent of causing irreversible tissue damage. The SE of maximum lethal temperature is small, suggesting that the majority of the development stages during vegetative growth of rice plants are susceptible to heat damage from 40 °C to 45 °C. For instance, at a constant day–night air temperature treatment of 40 °C and under CO₂ enrichment conditions (700 ppm), rice plants died during the early vegetative phase (Baker, 2004). Puteh *et al.* (2010) estimated a zero seed germination rate for the rice variety MR73 at 43 °C, based on a linear model. Chaudhary & Ghildyal

Table 1 Summary of mean (\pm SE) of: lethal minimum (TLmin) and lethal maximum (TLmax) temperatures; base (Tmin), optimum (Topt) and maximum (Tmax) temperatures for relevant processes and development phases in rice; n, number of literature sources

Processes	Mean temperature (\pm SE)(°C)					
	<i>Specie Oryza Sativa</i>	<i>N</i>	<i>Sub-specie Indica</i>	<i>n</i>	<i>Sub-specie Japonica</i>	<i>n</i>
Lethal Limits						
TLmin	4.7 (1.2)	8			2.2 (1.8)	2
TLmax	42.9 (0.7)	9			42.7 (1.5)	3
Leaf initiation						
Tmin	10.7 (0.6)	7	11.8 (0.2)	2	10.5 (0.5)	2
Topt	29.5 (0.8)	9	29.6 (1.2)	6	29.7 (1.2)	3
Tmax	42.5 (2.5)	2	40	1		
Shoot growth						
Tmin	13.7 (2.1)	4	14.5 (3.0)	2	11.5	1
Topt	28.5 (1.1)	5	27.5 (0.9)	4	27	1
Tmax	35.5 (0.5)	2	35.5 (0.5)	2		
Root growth						
Tmin	15.8 (0.8)	7	17.5	1	15.5 (3.5)	2
Topt	27.6 (0.0)	11	26.8 (0.8)	2	26	1
Tmax	35.9 (0.6)	7	35.5 (0.5)	2	32	1
Phenological phases						
Germination/Emergence						
Tmin	11.3 (1.1)	8	7	1	10 (1.7)	4
Topt	27.9 (2.8)	6	29.9 (4.9)	2	21.7 (2.7)	2
Tmax	40.1 (1.3)	5	41	1	35	1
Tillering						
Tmin	16.4 (0.8)	9	15	1	18.3 (2.1)	3
Topt	28.4 (1.2)	10	29.7 (2.4)	3	29 (3.1)	3
Tmax	35.3 (1.1)	6	37.5 (2.5)	2	32	1
Panicle initiation						
Tmin	15.8 (0.3)	6	11.4	1	14.9 (1.2)	4
Topt	26.7 (4.3)	2			26.7 (4.3)	2
Tmax	33.1 (1.7)	3	33.3	1	33.1 (1.7)	3
Anthesis						
Tmin	16.2 (1.5)	8	16.3 (5.8)	2	14 (2)	2
Topt	26.3 (1.3)	8	28.3 (1.2)	3	24.3 (1.4)	4
Tmax	37 (1.2)	9	37.7 (1.7)	5	36.9 (2.2)	3
Grain filling						
Tmin	20.7 (0.7)	17	21.2 (0.1)	4	17.9 (2.3)	4
Topt	24.2 (1.7)	7	30	1	21.2 (0.8)	3
Tmax	31.3 (0.7)	12			29.8	1
Whole plant						
Tmin	<13.5 (2.1)	7				
Topt	27.6 (2.0)	6			28	1
Tmax	>35.4 (2.0)	7			36	1

(1969) found that rice seeds did not germinate under a constant temperature of 43 °C. Livingston & Haasis (1933) and Yoshida (1981) estimated a maximum lethal temperature of 45 °C. At the second-leaf stage and at 45 °C, heat damage appeared in rice seedlings (Han *et al.*, 2009). Cells of rice seminal roots stopped division and elongation ceased at 43 °C (Yamakawa & Kishikawa, 1957) and Ehrler & Bernstein (1958) found that at 42 °C root temperature, plants did not survive.

The standard error of Tmin lethal temperature is larger than that for Tmax in rice (Fig. 1a and c.), perhaps because, within the same variety, cold tolerance depends on development stage. Between varieties, the *ssp. japonica* showed a higher cold tolerance with a mean lethal temperature of 2.2 °C (SE 1.8 °C) for Tmin (Table 1). Despite this, rice plants are not able to live below 0 °C. Nishiyama (1976) reported a temperature of 0 °C, at which rice seeds did not germinate and an

interval from 2 °C to 5 °C at which seedlings did not grow. Puteh *et al.* (2010) estimated a zero germination rate for the MR73 variety at a minimum lethal temperature of 0.4 °C, based on a linear model. Chaudhary & Ghildyal (1969) and Fadzillah *et al.* (1996) observed minimum lethal temperatures around 4 °C for the processes of germination and shoot growth. Lee (1979) recorded the highest percentage of dead seedling of rice plants at the two-leaf stage at a daytime temperature of 10 °C in all his/her (*ssp. japonica* × *ssp. indica*) hybrid lines. Survival rate at this temperature was progressively increased at the four- and six-leaf stages. A higher minimum lethal temperature of around 8 °C has also been found (Hamdani, 1979; Yoshida, 1981) for germination and seedling growth.

The mean cardinal temperatures in Table 1 show the temperature tolerances for root and shoot growth, leaf initiation and leaf emergence, and for the most relevant phenological phases and development stages (germination to emergence, tillering, panicle initiation, anthesis and ripening). T_{opt} for root growth is calculated as 27.6 °C (SE 1.0 °C) in rice. Ueki (1960) observed damage in the development of grain spikelets as a result of applying water temperatures higher than 32 °C to rice roots of *ssp. japonica* varieties. Mean T_{max} for root growth is 35.9 °C (SE 0.9 °C) and T_{min} is 15.8 °C (SE 0.8 °C) in rice. There seems to be a close correspondence between roots and shoot response to cardinal temperatures (Ehrler & Bernstein, 1958; Herath & Ormrod, 1965; Chaudhary & Ghildyal, 1970a). T_{max} and T_{opt} for shoot growth are 35.5 °C and 28.5 °C, respectively, with low standard errors, similar to the results for root growth in rice (Fig. 1a and b). T_{min} for shoot growth is 13.1 °C lower than that for roots, but their standard errors overlap (Fig. 1a). The response of leaf appearance to temperature is one of the most relevant aspects of cereal development (Gao *et al.*, 1992; Ellis *et al.*, 1993; Yin & Kropff, 1996). The mean temperature range from a T_{min} of 10.7 °C (SE 0.6 °C) to a T_{max} of 42.5 °C (SE 2.5 °C) for leaf initiation, is the widest for all processes except the lethal limits (Fig. 1a and c). T_{opt} for leaf appearance is 29.5 °C (SE 0.8 °C) in rice. Mean cardinal temperatures for root and shoot growth, leaf initiation and leaf emergence showed insignificant differences between *ssp. indica* and *ssp. japonica* and the mean cardinal temperatures of the common species *Oryza sativa* L. (Table 1).

The phenological phases, defined as the period of time between the stages of rice development, show small differences in optimum temperatures between phases and stages, but wider ranges in minimum and maximum temperatures. Germination of rice seeds has a range in temperature from 11.3 °C (SE 1.1 °C) to 40.1 (SE 1.3 °C), making them the highest values we found

for T_{min} and T_{max} for development phases and stages in rice (*Oryza sativa* L.) (Table 1). Owen (1971) established that tillering ability (tiller number and leaf number of main stem) is dependent on the management of rice. Oda & Honda (1963) also found differences in tillering temperature response between photoperiod sensitive and insensitive varieties. All mean cardinal temperatures for tillering have standard errors close to 1.0 °C in rice and about 2.0 °C in the *ssp. japonica* and *ssp. indica* (Table 1). Both low and high temperatures at panicle initiation increase spikelet sterility, giving a reduction in yields. Spike sterility is higher when a low temperature is applied 5–10 days before heading (Lee, 1979) and may be recognizable by a delay in heading as the panicle continues to develop (Dingkuhn *et al.*, 1995). In rice, T_{min} is 15.8 °C (SE 0.3 °C). The highest standard error for T_{opt} (4.3 °C) is for the panicle initiation stage. T_{max} was found to be 33.1 °C (SE 1.7 °C).

Rice is most sensitive to temperature during the period immediately preceding anthesis, greatly affecting yields. Enomoto *et al.* (1956) found the germination of pollen in rice in medium fast varieties to be more tolerant to maximum and minimum temperature limits than early and late ones. In the same experiment when comparing Japanese varieties with foreign ones, the minimum cardinal temperature was lower in foreign than in Japanese varieties. The difference between tolerant and susceptible varieties in the temperatures that caused sterility was about 3 °C (Matsui *et al.*, 2001). Chilling and mainly heat stress below and above cardinal temperature limits may produce sterility around the anthesis stage. These limits have been established as T_{min} of 16.2 °C (SE 1.5 °C) and T_{max} of 37 °C (SE 1.2 °C) for anthesis in rice. Similar limits have been found for the *ssp. indica* and *ssp. japonica*. Sterility is usually associated with poor anther dehiscence, malformation of spikelets, low viability of pollen, decreased number of germinated pollen grains on stigmata or ineffective fertilization (Chaudhary & Ghildyal, 1970b; Satake & Yoshida, 1978; Prasad *et al.*, 2006). Ripening or grain filling seems to be during the more temperature-sensitive stages after anthesis and yields can be greatly affected during this period. Yoshida (1981) concluded that grain weight is affected by temperature during ripening, as well as that grain filling period is shorter under high temperature and the combination of high temperature and low light may seriously affect grain weight and percentage of filled spikelets. T_{min} for ripening appears to be the highest value (20.7 °C, SE 0.7 °C) compared with other mean minimum temperatures for development processes in rice. T_{max} appears to be the lowest value (31.3 °C, SE 0.7 °C) compared with other mean maximum temperatures, meaning that the cardinal temperature range for ripening is

narrow and standard errors for both temperatures are relatively low (Fig. 2b). Finally, whole plant cardinal temperatures for development range from Tmin of 13.5 °C (SE 2.1 °C) to a Tmax of 35.4 °C (SE 2.0 °C) with a Topt of 27.6 °C (SE 2.0 °C).

Maize

Table 2 summarizes the same mean cardinal temperatures for maize as Table 1 does for rice and the following results for maize are presented more concisely. The Tmin lethal limit is calculated to be -1.8 °C (SE 1.9 °C) and the Tmax lethal limit to be 46 °C (SE 2.9 °C). Maize is known to be very susceptible to frost damage, and frost damage is often recorded in temperate growth regions (Crowley, 1998). Carter & Hesterman (1990) found that lethal damage to stem, leaf and ear occurs when temperatures is below -2.2 °C for a few minutes and below 0 °C for more than 4 h. There seems to be larger variation in the literature on the upper lethal limit as reflected in the higher SE and thus variability (Lehenbauer, 1914; Brooking, 1990). Birch *et al.* (1998b) estimated a temperature of 44 °C and Sinsawat *et al.* (2004) found that temperatures over 45 °C caused irreversible damage to maize plant tissue. However, the same author found that plants grown at a mean temperature of 41 °C were not damaged after being exposed to temperatures of 50 °C. Although there seems to be variation in tolerance to extreme temperatures, maize thrives at temperatures between 28 °C and 32 °C for an entire growth season (Arnold, 1974; Yin *et al.*, 1995). Tmin on a whole season basis is 6.2 °C (SE 1.1 °C) (Olsen *et al.*, 1993; Shaykewich, 1994). Tmax is calculated as 42 °C (SE 3.3 °C) above which growth stops (Brooking, 1990; Yin *et al.*, 1995; Table 2).

Tmin for root growth was calculated as 12.6 °C (SE 1.5 °C). Hund *et al.* (2008) found a significant decline in root growth in four inbred maize cultivars with a 2 °C decrease in topsoil temperature from 17 °C to 15 °C. Tmax was 40.1 °C (SE 3.6 °C) with a Topt of 26.3 °C (SE 1.8 °C). As with other stages and phases, the maximum temperature shows a higher standard error, suggesting variability in heat tolerance between cultivars and in experimental design (Fig. 1c). Mean Tmin was higher for root than for shoot growth (Fig. 1a), agreeing well with the smaller range as between minimum and maximum temperature for roots than leaves and shoots (Birch *et al.*, 2002; Hund *et al.*, 2008). Table 2 shows Topt for shoot elongation to be 31.1 °C (SE 0.8 °C). Tmin is 10.9 °C (SE 1.5 °C), which is lower than that for root growth and similar to leaf initiation as the two processes to a great extent happen simultaneously (Fig. 1a). Tmax for shoot elongation is lower than that for root growth at 38.9 °C (SE

Table 2 Summary of mean (\pm SE) of: lethal minimum (TLmin) and lethal maximum (TLmax) temperatures; base (Tmin), optimum (Topt) and maximum (Tmax) temperatures for relevant processes and development phases in maize; *n*, number of literature sources

Processes	Mean Temperature (\pm SE)(°C)	<i>n</i>
Lethal limits		
TLmin	-1.8 (1.9)	8
TLmax	46.0 (2.9)	6
Leaf initiation		
Tmin	7.3 (3.0)	8
Topt	31.1 (1.7)	11
Tmax	41.3 (1.9)	3
Shoot growth		
Tmin	10.9 (1.5)	3
Topt	31.1 (0.8)	3
Tmax	38.9 (2.8)	4
Root growth		
Tmin	12.6 (1.5)	3
Topt	26.3 (1.8)	5
Tmax	40.1 (3.6)	3
Phenological phases		
Sowing to emergence		
Tmin	10.0 (2.2)	3
Topt	29.3 (2.5)	3
Tmax	40.2 (2.1)	1
Sowing to tassel initiation		
Tmin	9.3 (2.7)	12
Topt	28.3 (3.8)	11
Tmax	39.2 (0.6)	4
Anthesis		
Tmin	7.7 (0.5)	3
Topt	30.5 (2.5)	3
Tmax	37.3 (1.3)	4
Grain filling		
Tmin	8.0 (2.0)	2
Topt	26.4 (2.1)	5
Tmax	36.0 (1.4)	4
Whole plant		
Tmin	6.2 (1.1)	9
Topt	30.8 (1.6)	8
Tmax	42.0 (3.3)	12

2.8 °C) (Fig. 1c). Tollenaar *et al.* (1979) found Tmin for both leaf appearance and initiation to be 6 °C. However, as this experimental design did not include average daily mean temperatures below 10 °C, Tmin is derived from extrapolation of a polynomial fit to the temperature data. A slightly lower Tmin for leaf appearance and initiation was found by Warrington & Kanemasu (1983) as 2 °C and 4 °C where the minima were night temperatures. Mean Tmin for leaf initiation is 7.3 °C (SE 3.0 °C). Topt for leaf emergence was found to be from 31 °C to 34 °C (Fournier & Andrieu, 1998;

Kim *et al.*, 2007), with a mean of 31.1 °C (SE 1.7 °C) and a Tmax of 41.3 °C (SE 1.9 °C).

Cardinal temperatures from sowing to emergence show that Topt is from 26 °C to 33 °C. Tmin ranges from 6 °C to 13 °C and Tmax is approximately 40 °C. Calculated means for Tmin, Topt and Tmax are 10 °C, 29.3 °C and 40.2 °C, respectively, with SE from 2.1 °C to 2.5 °C. An important period in maize development is from emergence to the end of tassel initiation as, in this phase, maize goes through its juvenile stage after which some cultivars become long photoperiod sensitive, delaying tassel initiation and anthesis (Birch *et al.*, 1998a). Temperature in this phase is important for potential crop yields, because during tassel initiation the potential number of kernels is defined (Tollenaar & Bruulsema, 1988). Heat- or chilling stress during this period can be severe for crop yields. Tmin and Tmax in Table 2 for this phase are 9.3 °C (SE 2.7 °C) and 39.2 °C (SE 0.6 °C), respectively, with Topt as 28.3 °C (SE 3.8 °C). This indicates that maize is not particularly temperature sensitive during this period compared to other phases. A Topt of ca. 28 °C is close to that for other phenological phases and processes during vegetative growth, however, the SE of Topt (3.8 °C) is the largest standard error for Topt in Table 2. This indicates that variation between experiments or more probably cultivars is high. Experimental variation was reported by Ellis *et al.* (1992), who in three experiments with 12 cultivars adapted to tropical, subtropical and temperate climates, found Topt to be between 19 °C and 31 °C.

Maize is particularly sensitive to high and extreme temperatures in the phase before and during anthesis. Especially pollination can be seriously affected by high temperatures. Temperatures over 32 °C reduced the percentage of non-germinated pollen by up to 51% (Schoper *et al.*, 1987). Herrero & Johnson (1980) found that maize pollen continuously exposed to 38 °C failed to germinate (Carberry *et al.*, 1989) in semiarid tropical conditions. Tmin was found to be 7.7 °C (SE 0.5 °C), Topt 30.5 °C (SE 2.5 °C) and Tmax 37.3 °C (SE 1.3 °C).

Maize kernel yield is affected by high temperatures, which decrease yield and shorten kernel filling, as do low temperatures. Brooking (1993) reported a decrease in kernel filling rate below 13.5 °C and a linear response between 13 °C and 32 °C. Muchow (1990) and Tollenaar & Bruulsema (1988) both studies found a growth rate of 0.3 mg kernel⁻¹ day⁻¹°C⁻¹ from 10 °C to 32 °C. Table 2 shows Tmin to be 8.0 °C (SE 2.0 °C). Mean Topt is 26.4 °C (SE 2.1 °C) with a mean Tmax of 36.0 °C (SE 1.4 °C). Both Topt and Tmax are slightly lower compared to all other stages and phases (Fig. 2b). As the duration of kernel filling is a major part of the entire growth season of maize, it is thus sensitive to

high temperatures for a large part of its developmental cycle.

Discussion

The above literature review has identified cardinal temperatures for rice and maize in the same manner as Porter & Gawith (1999) did for wheat, thus now affording the chance to contrast and compare the cardinal temperatures for the three main global cereals (Fig. 1a, b and c, Fig. 2a and b). The main conclusions with relevance to climate change are that maximum lethal temperatures are similar for the three crops and range from 43 °C to 48 °C (Fig. 1c). The highest standard error of a lethal temperature (2.9 °C) is found in maize; this may be because, of the three crops, maize is planted over the widest range of latitude, ranging from ca. 60°N in Finland and northern Eurasia to 40°S in Australia, Africa and South America. Standard lethal temperature errors for wheat and rice are smaller and close to each other. Minimum lethal temperatures differ in a broad range, showing that wheat has the lowest average minimum (-17.2 °C); maize dies at temperatures just below freezing and rice at temperatures under 5 °C (Fig. 1a). Again, the largest SE (1.9 °C) is in maize, but the maize standard error for minimum lethal temperature is lower than that for the maximum lethal temperature.

All threshold temperatures are important for crop development and growth but we wish to highlight a couple of them that are especially important for yields of the three main global cereals. Maize and rice are very sensitive to the same maximum temperature (ca. 37 °C) with similar small standard errors around anthesis (Fig. 2a); wheat has a lower maximum (ca. 32 °C). The reduction in grain set caused by overstepping these thresholds can be dramatic (Wheeler *et al.*, 1996a) and all three crops can suffer large yield losses due to sterility at high extreme temperatures. An under-researched topic is the mechanisms by which high temperatures affect pollen meiosis in cereals and plants in general. Reproduction in both animals and plants seems to have rather narrow temperature ranges (Cossins & Bowler, 1987) suggesting a generic research theme relevant to global warming impacts.

Grain-filling temperature optima are similar for the three crops and closer than the optimal anthesis temperatures (Fig. 2b). Maximum grain-filling temperatures are lower for rice than for maize and wheat and are all well defined. The minimum rice temperature for grain filling is markedly higher than for maize and wheat. The largest temperature response variation appears on the optimum temperature with the higher standard errors for all the crops, although maize also shows a high standard error of minimum temperature.

Caveats for such comparisons are the differences in conditions between experiments identified in the study. It would clearly be desirable to have had all three crops simultaneously monitored under the same controlled environmental conditions, but this was not the case. Differences exist in experimental design, temperature regimes and growth conditions and origins of the varieties studied that may make direct comparison difficult. Details of experiments are provided in the supplementary material (S1–S6). Standard errors of all cardinal temperatures were ca. 8% of mean values for both rice and maize, thus adding confidence to the robustness of the estimates. Another possible source of uncertainty is the degree to which measured temperatures were, in fact, plant and not air temperatures, thus confounding air dryness effects with temperature. Plant canopies can be both warmer and cooler than surrounding conditions. Fischer (2011) shows that air temperatures can be up to several degrees higher than plant (wheat) temperatures following heat shocks but mostly differences are 1–3 °C. The mean SE of all temperatures found in our reviews are about 2 °C; thus within the potential error caused by air-plant differences. In addition, plant temperature thresholds are absolute rather than relative phenomena and if evaporative cooling does not bring plant (or crop) temperature below the threshold then the effects will be the same for air as for plant temperature.

An important point in this and other studies on crop temperature responses is that we are dealing with absolute and not relative thresholds; that is to say moving temperature above a given level induces nonlinear responses from plants that are not evident if temperatures remain in the range below or above the threshold. Thresholds do not seem to be defined in terms of a relative change in temperature (i.e. a 'delta') but as step changes in plant development and thereby growth. Such threshold responses are not often included in the current suite of statistical and process-based crop models used to analyse and predict the effects of global warming on crop production in different parts of the world. As a result, ensembles of crop models are able to predict mean yields (Rötter *et al.*, 2011) but do less well when predicting yield variability. This infers that the vast majority of currently used yield impact models are likely too optimistic when predicting the effects of warming on food production. This is especially the case for high radiative forcing scenarios leading to land surface warming in excess of 2 °C, relative to pre-industrial scenario. Such experiments would be central to defining response functions for extreme temperatures and we suggest a priority would be for events around anthesis and grain filling in the major annual cereals. The standard error data presented in this and a previous article (Porter & Gawith, 1999)

would allow probabilistic modelling of impacts in combination with new scenarios (RCPs) and CMIP5 climate data series. In addition, integrated experimental studies that include CO₂, drought, nutrients and high levels of warming are needed urgently given the current levels of greenhouse gas emissions (Schellnhuber *et al.*, 2012).

Acknowledgements

We acknowledge Dr. Ana Iglesias of Technical University of Madrid for helpful comments on the manuscript. We thank both the CRES project (544200-50-29838) funded by the Danish Strategic Research Council and the SmartSOIL project (289694) funded by the European Commission for support.

The authors declare no competing financial interests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. References of supporting information. [S1_references_supporting_information.pdf](#).

Table S1. Lethal temperature limits for rice. [S1_rice_lethal_temperature.pdf](#).

Table S2. Base (Tmin), optimum (Topt) and maximum (Tmax) cardinal temperatures for different key growth processes in rice. [S2_rice_processes_temperature.pdf](#).

Table S3. Base (Tmin), optimum (Topt) and maximum (Tmax) cardinal temperatures for key phenological phases and development stages in rice. [S3_rice_development_temperature.pdf](#).

Table S4. Lethal temperature limits for maize. [S4_maize_lethal_temperature.pdf](#).

Table S5. Base (Tmin), optimum (Topt) and maximum (Tmax) cardinal temperatures for different key growth processes in maize. [S5_maize_processes_temperature.pdf](#).

Table S6. Base (Tmin), optimum (Topt) and maximum (Tmax) cardinal temperatures for key phenological phases and development stages in maize. [S6_maize_development_temperature.pdf](#).

Table S7. Summary of mean (\pm SE) of: lethal minimum (TLmin) and lethal maximum (TLmax) temperatures; base (Tmin), optimum (Topt) and maximum (Tmax) temperatures for relevant processes and development phases in wheat from Porter & Gawith (1999).

[S7_wheat_temperature_Porter_Gawith.pdf](#).