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Temperatures and the growth and development of wheat: a review

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Abstract

We start by outlining the general effects of climatic variability and temperature extremes on wheat yields in the context of extreme event effects on crop processes for climatic impacts studies. We then review literature describing the responses of wheat plants to extreme temperatures. Cardinal temperature thresholds for different phenological processes in wheat 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.

Our summary shows how relatively small and consistent are the standard errors of the cardinal mean temperatures for many of the processes examined. Cardinal temperatures are conservative between studies and are seemingly well-defined in wheat. Into this category we put the lethal limits for wheat, the sterility response at anthesis, the cardinal temperatures for vernalization and some of the base and optimal temperatures. Important questions for the future involve the effects of combinations of extreme events and the modelling of specific effects such as the influence of high temperatures on grain set. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Changes to the global climate, notably to regional spatial and temporal temperature patterns (Houghton et al., 1996), from increased atmospheric concentrations of greenhouse gases are predicted to have important consequences for crop production (Parry, 1990). Both plant growth and development are affected by temperature (Porter and Moot, 1998). Investigations of the effects of changes in mean annual temperature on agricultural crops (Kenny et al., 1993) have used crop-climate simulation models (e.g. Rosenzweig and Iglesias, 1994) and experiments (e.g. Wheeler et al., 1996a,b). Such efforts have advanced understanding of the effects of annual mean climatic changes on crop production to the extent that we can now predict the implications of mean climatic change for wheat production with some confidence (Houghton et al., 1996).

Improved understanding of the impacts of mean temperature changes on wheat precedes consideration of the effects that changes in climatic variability and extreme conditions might have on wheat. This is a more complex question. A changing or

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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 (Kattenberg et al., 1996).

Temperatures that lie outside the range of those typically experienced can have severe consequences for crops, significantly reducing yields. Both high and low temperatures decrease the rate of dry matter production and, at extremes, can cause production to cease (Grace, 1988). It seems to be the case that plants respond to absolute rather than relative changes in temperature, i.e. there are discontinuous threshold responses to temperature. This is different from their response to water deficit, for example. Here there is an ongoing and resilient relationship between water uptake and dry matter production over a large range of water availability (Tanner and Sinclair, 1983), because water loss and CO_2 uptake share much of the same physical pathway into and out of leaves.

The special significance of increased climatic variability and extremes on crop yields is an emerging perception amongst the climatic impacts community (Semenov and Porter, 1995; Wilks and Riha, 1996). This implies that studies of the impacts of climatic change need to specifically examine, as a separate issue, the influence of climatic extremes on crop growth (Porter and Moot, 1998). Knowledge of crop responses to weather extremes is incomplete and is not explicitly included in crop-climate models (van Haren, 1996). As a result, simulation models can perform poorly outside of a range of mean conditions, and the prediction of yields in response to extreme events is unreliable (Goudriaan, 1996).

Considerable experimental work has been undertaken in order to understand how wheat responds to extreme conditions. A wealth of information exists in the literature on the relationship between wheat growth and development and extreme temperatures (both high and low), which is of value to modellers and experimentalists alike. This paper presents a review of this literature. Our primary purpose is to synthesise available results and make this information more accessible to the climatic change impacts community and general circulation modellers. They should thereby be able to identify whether the frequency of extreme temperature events that can affect wheat is either changing or will change under climate change. Qualitatively, these would be increases in the frequency of discrete events such as plant lethality caused by high or low temperatures. Less extreme but still important temperature changes may increase plant sterility and poor grain set. Additionally, using the presented data on the rate responses of processes to temperature, impact modellers can quantitatively assess the effects of temperature change on crop processes.

In our literature review, we describe the responses of wheat plants to extreme temperatures under experimental conditions. Cardinal temperature thresholds for different phenological processes in wheat 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.

2. Literature review

We have reviewed the literature on extreme temperatures effects in wheat with the object of identifying cardinal temperatures for development stages and the responses of key growth and developmental rates to temperature. Key word searches were conducted in electronic databases to identify candidate literature. Physical searches were then made in specialist libraries in Denmark (The Danish Agricultural and Veterinary Library, Copenhagen) and the UK (The Department of Plant Sciences Library and the Radcliffe Science Library, University of Oxford) and references to further literature pursued. About 65 papers were consulted, from which mean minimum and maximum lethal temperatures and base and optimal temperatures for leaf initiation, shoot growth and phenological phases were derived (Table 1). More detailed information is presented on lethal limits for wheat plants (Table 2), minimum, optimum and maximum temperatures and growth rates for root growth, leaf initiation and emergence, spikelet initiation and culm elongation (Table 3) and minimum, optimum and maximum temperatures for

Table 1
Summary of mean (±se) of lethal minimum (*T*Lmin), lethal maximum (*T*Lmax), base (*T*min), optimum (*T*opt) and maximum (*T*max) temperatures for various processes and phenological phases in wheat

Processes		Mean temperature (±se) (°C)	*n*
Lethal limits	*T*Lmin	−17.2 (1.2)	17
	*T*Lmax	47.5 (0.5)	2
Leaf initiation	*T*min	−1.0 (1.1)	12
	*T*opt	22.0 (0.4)	9
	*T*max	24.0 (1.0)	5
Shoot growth	*T*min	3.0 (0.4)	5
	*T*opt	20.3 (0.3)	6
	*T*max	>20.9 (0.2)	6
Root growth	*T*min	2.0	1
	*T*opt	<16.3 (3.7)	3
	*T*max	>25.0 (5.0)	3
Phenological phases			
Sowing to emergence	*T*min	3.5 (1.1)	8
	*T*opt	22.0 (1.6)	11
	*T*max	32.7 (0.9)	10
Vernalization	*T*min	−1.3 (1.5)	6
	*T*opt	4.9 (1.1)	11
	*T*max	15.7 (2.6)	7
Terminal spikelet	*T*min	1.5 (1.5)	2
	*T*opt	10.6 (1.3)	5
	*T*max	>20.0	1
Anthesis	*T*min	9.5 (0.1)	3
	*T*opt	21.0 (1.7)	2
	*T*max	31.0	1
Grain-filling	*T*min	9.2 (1.5)	6
	*T*opt	20.7 (1.4)	7
	*T*max	35.4 (2.0)	5

n is the number of literature sources used to calculate means and se.

different phenological stages (Table 4) and phases (Table 5) in wheat.

Direct comparison between published reports was not always possible for all developmental phases, because of differences in experimental approach and design. Some studies, for example, examined the period from sowing to terminal spikelet initiation, whilst others looked at emergence to anthesis. Different cultivars and temperature regimes were also often used. Where possible, we note such inconsistencies in the Tables. We have defined the lethal minimum (*T*Lmin) and lethal maximum temperatures (*T*Lmax). Base temperatures (*T*min) are those below which a physiological process stops, or nearly does so. The optimum temperature (*T*opt) is that for which the rate of a process is the maximum observed and the corresponding upper base temperature is designated as *T*max. *T*min, *T*opt and *T*max are referred to collectively as the cardinal temperatures. In cases where a cardinal temperature has been reported as being greater than (>) or less than (<) a particular value, we calculated the mean and standard error of a cardinal value accordingly. Cardinal and lethal temperatures are distinguished by the fact that recovery of function is possible within the range of cardinal temperatures but is irrecoverably lost beyond the lethal limits. In our terminology, a more sensitive process has a larger rate of change with respect to temperature than a less sensitive one.

3. Temperature thresholds

3.1. Lethal temperatures

The first set of extreme temperatures identified in our literature review were lethal limits for wheat (Table 2). From the surveyed literature (Table 1), wheat seems to have a lethal low temperature of −17.2±1.2°C, and a lethal high temperature of 47.5°C. However, Single (1985) gave a *T*Lmin value of −2 to −5°C for an Australian winter wheat cultivar, perhaps reflecting its localised selection and breeding. Drozdov et al. (1984) reported that temperatures of −2°C injured the leaves of unhardened winter wheat plants and −4°C was lethal, but this threshold could be increased to −13°C if plants were cold-hardened.

Thus, whilst cultivars seem to differ in their tolerance to extreme temperature (Pomeroy and Fowler, 1973; Blum and Sinmena, 1994; Páldi et al., 1996), wheat is generally considered to enjoy an optimum temperature range of 17–23°C over the course of an entire growing season, with a *T*min of 0°C and a *T*max of 37°C, beyond which growth stops (Table 3). Our summary (Table 1) shows how relatively small and consistent are the standard errors of the mean temperatures for many of the processes. The largest standard error found

Table 2
Lethal temperature limits for wheat plants

Literature source	*T*Lmin (°C)	Conditions	*T*Lmax (°C)	Conditions
Drozdov et al. (1984)	−4	Gradual cooling; winter wheat	47	Unhardened plants
	−13	Gradual cooling of air; root zone +2°C; winter wheat	48	Hardened plants
Bauer and Black (1990)	−16 to −20	Crown depth of 4 cm		
	−15 to −20	Gradual freezing		
	−15	Rapid freezing		
Single (1985)	−2 to −5	Australian cultivar		
Okuda et al. (1994)	−20 at.			
Pomeroy et al. (1975)	−20 at.			
Korovin and Mamaev (1975)	−15 at.	FC 20–30 and 50–60%		
	−17 at.	FC 20–30 and 50–60%		
	−20 at.	FC 80–90%		
	−23 at.			
Dyubin and Kukekov (1983)	−10.7	after a long cold autumn		
	−11.3	after a long cold autumn		
	−14.5	after a long cold autumn		
Musich et al. (1981)	−18.5 to −24	cv. Odessa 16		
	−18 to −22.5	cv. Odessa 51		
	−15.5 to −21	cv. Bezostaya 1		
Narciso et al. (1992)	−15	During winter but without snow coverage		

FC: field capacity; temp.: temperature; *T*Lmin: lethal minimum temperature; *T*Lmax: lethal maximum temperature; at: air temperature.

was 5.0°C for the maximum temperature for root growth, followed by 3.7°C for the optimum temperature of root growth. Others, such as the base and optimum temperatures for shoot growth, the optimum temperature for leaf initiation and the base temperature for anthesis have standard errors of less than 0.5°C. Thus, the consensus is that functionally important temperatures for wheat are conservative when compared between different studies.

Temperature responses may also be determined for plant processes, such as enzyme activities and photosynthesis, the rates and efficiencies of which are temperature-dependent. An example is the thermal kinetic window which describes the temperature range for optimal enzyme functioning (Makan et al., 1987). The thermal kinetic window for wheat has been identified by Burke et al. (1988) as lying between 17.5 and 23°C. Optimal rates of photosynthesis in wheat (cv. Crako) are, however, broader than these, being optimised at 25°C and declining at temperatures lower than 15°C and higher than 30°C (Wardlaw, 1974).

Temperature tolerance somewhat depends on experimental conditions, notably the rate and intensity of exposure to extreme temperature and soil water levels. Plants can gradually alter their metabolism to adjust to extreme temperatures, so-called 'hardening', and thereby acquire an increased range of temperature tolerance (Drozdov et al., 1984). The study by Bauer and Black (1990) showed a *T*Lmin of 0 to −15°C for rapid freezing but temperatures down to −20°C were tolerated with gradual cooling. However, wheat seemingly differs in this respect in its response to extreme heat and cold. Thus, plants develop cold hardiness, but not a tolerance to extreme heat (Drozdov et al., 1984) with heat tolerance increasing by only 1°C following gradual rather than abrupt warming.

3.2. Temperature thresholds and growth rates for different plant components

As optimum temperatures may be identified for the whole plant (Table 3), so temperature tolerances may be recognised for different plant parts;

Table 3
Base (*T*min), optimum (*T*opt) and maximum (*T*max) temperatures and, if available, absolute growth rates per unit temperature for root growth, leaf initiation and emergence, spikelet initiation and culm elongation. Figures in brackets are the standard errors of the mean

Literature source	*T*min (°C)	*T*opt (°C)	*T*max (°C)	Absolute production or growth rates (°C d^{-1} or as otherwise indicated)	Cultivar/conditions
Root growth					
Nielsen and Humphries (1966)		20			General case
MacDowell (1973)		±20	>20		cv. Marquis
Wardlaw and Moncur (1995)			35		
Petr (1991)	2	9–16	20–26		During the vegetative stage
Leaf initiation/emergence					
MacDowell (1973)		±20	>20		cv. Marquis
Slafer and Rawson (1995a) (rate of leaf appearance between 10 and 22°C)	−3.9 (2.7)	22	>25	0.0076 (0.0011) leaves	Sunset
	−5.7 (1.9)	22	>25	0.0077 (0.0008) leaves	Condor
	−4.6 (1.1)	22	>25	0.0082 (0.0005) leaves	Rosella
	−1.9 (1.5)	22	>25	0.0092 (0.0008) leaves	Cappelle Desprez
Cao and Moss (1989) (rate of leaf emergence at optimum temperatures)		21.6		0.207 leaves d^{-1}	Stephens
		21.3		0.208 leaves d^{-1}	Yamhill
		24.3		0.208 leaves d^{-1}	Tres
		22.9		0.221 leaves d^{-1}	Nugaines
				0.132 (0.012) leaves d^{-1} at 7.5°C	Mean of above four genotypes
				0.216 (0.014) leaves d^{-1} at 25°C	As above
Klepper et al. (1982)	3.0				
Nuttonson (1953)	4.4				
Kirby (1985)	±0			0.03 leaves	Winter wheat
Baker (1979)	0–2				
Baker et al. (1986)	−1.5–0.8				
Kemp and Blacklow (1982)	0.0				
Miglietta (1989)	2.5				
Spikelet initiation					
Kirby (1985)	0.0	20–25	>25	0.07 primordia	
Stem / shoot growth					
MacDowell (1973)		±20	>20		cv. Marquis
Slafer and Rawson (1995a) (culm elongation)	2.1	21	>21	1.5 (0.03) mm	Sunset
	2.8	20.5	>21	1.3 (0.09) mm	Condor
	2.6	21	>21	1.3 (0.11) mm	Rosella
	4.7	19	>21	1.7 (0.18) mm	Cappelle Desprez
	3.0	20.4	>21	1.5 mm	
Whole plant					
Reilly (1996)	0	20–25	30–35		
Burke et al. (1988)		17.5–23			
Maximov (1938)	0–5	15–30	31–37		

Table 4
Base (*T*min), optimum (*T*opt) and maximum (*T*max) temperatures for different phenological phases and stages in wheat

Phenological stage/phase	Literature source	*T*min (°C)	*T*opt (°C)	*T*max (°C)	Cultivar
Sowing	Russell and Wilson (1994)	5–7	7.1–20	20.1–30	
Germination/emergence	Petr (1991)	3–4.5	25	35	
	Petr (1991)	1–2	24–28	36–38	
	Petr (1991)	3.9–4.4	25	30–32.2	
	Wilsie (1962)	3.9–4.4	25	30–32.2	
	Ali et al. (1994)	0–2	22.1–29.8	>32	
	Slafer and Rawson (1995b)	<0	<22		
	Gupta (1978)	1	20	>30	Bread wheat
	Narciso et al. (1992)	<2	15–25	>30	S. European
	Petr (1991)	10	12.5–13.5		
	Blum and Sinmena (1994)			>35	Bread wheat
Vernalization	Petr (1991)	<−3–0	2–6	>10	
	Narciso et al. (1992)	<−1	0–3	>12	S. European
	Halevy (1985)	0	7	11	
	Chujo (1975)	<5	4–12	>15	Winter wheat
	Hänsel (1955)	−5	1–6	15	
	Lumsden (1980)	−4	3–10	17	
	Evans et al. (1975)			>30	
Tillering	Narciso et al. (1992)	<3	6–9	>9	S. European
Double ridges	Slafer and Rawson (1995b)		20		
	Slafer and Savin (1991)	4			
Spikelet Initiation	Qu and Wang (1982)		<10.5[a]		
	Halevy (1985)		15		
	Kirby (1985)	0		20–25	
Terminal spikelet	Qu and Wang (1982)		<7.5[b]		Winter wheat
	Qu (1989)				
	Petr (1991)	3	8–12		
Shoot elongation	Narciso et al. (1992)	<12	15–22	>40	S. European
Heading	Slafer and Savin (1991)	3.9	24.3		
Anthesis	Slafer and Savin (1991)	9.5			
	MacDowell (1973)	<10		>30	
	Russell and Wilson (1994)	<10	18–24	>32	
Pollination	Petr (1991)	>10	18–24	32	
Grain-filling	Jenner (1991,b)		20		
	Hawker and Jenner (1993)			>40	
	Slafer and Rawson (1995b)	7	>25		
	Stone et al. (1995)			30–40	
	Hunt et al. (1991)	4.7±0.6			Mean of 10 cultivars
	Wardlaw (1974)		15–18		cv. Crako
	Angus et al. (1981)	8.9			Spring wheat
	Pararajasingham and Hunt (1991)	7.8–8.8			
	Russell and Wilson (1994)	12	20	35	
Maturity	Narciso et al. (1992)	<15	22–25	>32	S. European

[a]Between floret initiation and terminal spikelet.
[b]Between single ridge and glume differentiation.

notably shoots, leaves and roots. The range of temperature tolerances for the growth and development of different plant parts is listed in Table 3.

3.2.1. Roots

Root growth is generally more sensitive to temperature than that of above-ground plant parts

Table 5
Base (*T*min), optimum (*T*opt) and maximum (*T*max) temperatures and rates of development for different phenological stages in wheat

Phase	*T*min (°C)	*T*opt (°C)	*T*max (°C)	Development rate (se) (°C d^{-1})	Cultivar
Sowing to emergence					
Slafer and Savin (1991)	4			0.0098 (0.0019)	Las Rosas; Marcos Juarez
				Between 12.5 and 18°C: 0.0072	Las Rosas INTA
Porter et al. (1987)	0.1				Avalon
Angus et al. (1981)	2.6 ± 0.2				Two spring wheat varieties
Weir et al. (1984)	1				
Slafer and Rawson (1994)	1			Between 2.5 and 20°C: 0.0083	Rosella
Addae and Pearson (1992)					
Saarikko and Carter (1996)	−2.9				Ruso
Emergence to DR					
Weir et al. (1984)	1				
Emergence to TS					
Slafer and Savin (1991)	4.1			0.0023 (0.0007)	Las Rosas; Marcos Juarez
				Between 14 and 18°C: 0.004175	Las Rosas INTA
Porter et al. (1987)	2.0				Avalon
Angus et al. (1981)	3.3 ± 0.7				Two spring wheat varieties
Emergence to heading					
Angus et al. (1981)	−5.8				
Sowing to TS					
Slafer and Rawson (1995b)	2.22	19.5	> 22	0.00539 (0.00063)	Sunset
	0.58	19.5	> 22	0.00378 (0.00064)	Condor
	−2.4	21		0.00257 (0.00034)	Rosella
	−8.23	20		0.00143 (0.00018)	Cappelle Desprez
	−0.9	< 22		0.00329	Mean of above four cultivars
Slafer and Savin (1991)	4				Las Rosas; Marcos Juarez
Sowing to heading					
Saarikko and Carter (1996)	−2.4				Ruso
	−3.2				Pollka
	−4.2				Kad
TS to heading					
Slafer and Rawson (1995b)	1.08	23.5		0.00263 (0.00021)	Sunset
	0.81	> 25		0.00280 (0.00014)	Condor
	1.83	23.5		0.00299 (0.00026)	Rosella
	1.03	> 25		0.00195 (0.00195)	Cappelle Desprez
	1.2	25		0.00259	Mean of above four cultivars
Heading to maturity					
Slafer and Rawson (1995b)	7.67	22		0.01357 (0.00106)	Sunset
	8.56	> 25		0.01347 (0.00168)	Condor
	8.96	> 25		0.01466 (0.00144)	Rosella
	7.28	> 25		0.01440 (0.00267)	Cappelle Desprez
	8.1	> 25		0.014	Mean of above four cultivars
Narciso et al. (1992)	< 13	18–22	> 32		Southern European cultivar
TS to anthesis					
Slafer and Savin (1991)	10.6			0.0049 (0.0008)	Las Rosas; Marcos Juarez
				Between 15 and 27°C: 0.005	Las Rosas INTA
Porter et al. (1987)	3.5				Avalon
Angus et al. (1981)	5.1 ± 2.1				Two spring wheat cultivars
Sowing to anthesis					
Slafer and Rawson (1995a)	4				Mean of four cultivars
DR to anthesis					
Weir et al. (1984)	1				
Anthesis to maturity					
Slafer and Savin (1991)	8.2			0.0029 (0.0004)	Las Rosas; Marcos Juarez
				Between 20 and 25°C: 0.00267	Las Rosas INTA
Porter et al. (1987)	5.7				Avalon
Angus et al. (1981)	8.9 ± 2.6				Two spring wheat cultivars
Wheeler et al. (1996b)	3.5				
TS to maturity					
Slafer and Savin (1991)	9.5				Las Rosas; Marcos Juarez
Sowing to ripening					
Saarikko and Carter (1996)	3.1 ± 2.6				Ruso; Kadett

DR: double ridge stage of the apical meristem; TS: terminal spikelet stage of the apical meristem; AT: anthesis.

(Nielsen and Humphries, 1966), meaning that the range between *T*min and *T*max for roots is shorter than for shoots and leaves. Such sensitivity is reflected in an observation by Petr (1991), that root growth in upper soil layers is highly variable because of fluctuations in diurnal temperature. Generally, the optimal soil temperature for growth of the roots of wheat plants during the vegetative stage is below 20°C (Nielsen and Humphries, 1966; MacDowell, 1973) and lower than that for shoots (Table 3). Temperatures higher than 35°C have been shown to reduce terminal root growth and accelerate its senescence (Wardlaw and Moncur, 1995). Root growth may cease altogether if soil temperatures drop below 2°C (Petr, 1991). Studies have shown an air temperature of −20°C to be lethal for root survival (Drozdov et al., 1984), although this has to be translated into a soil surface temperature, which would, in most cases, be higher.

3.2.2. *Leaf initiation and emergence*

Important developmental processes in modelling crop growth and development are the rate of leaf initiation as primordia (Jamieson et al., 1995) and leaf emergence (Porter, 1984). Several studies have investigated the influence of temperature on leaf initiation and emergence (Table 3). In the most comprehensive study we found (Miglietta, 1989), 42 wheat varieties were studied under a variety of temperature regimes to identify *T*min for leaf initiation, a value found to be 2.5°C. Cooler *T*min values were found for four Australian cultivars (Slafer and Rawson, 1995a) for which an average temperature of about −4°C was identified (Table 3). Cao and Moss (1989) found *T*opt for leaf emergence to range from 21.3°C to 24.3°C; values which concur with the *T*opt value of 22°C from Slafer and Rawson (1995a). Temperatures higher than 25°C have been found to inhibit leaf appearance (Table 3).

Leaf initiation and development rates are almost linear at temperatures between *T*min and *T*opt (Kirby, 1985; Baker et al., 1986). Between 0 and 15°C, leaves are initiated at about 0.03 leaf primordia per degree rise in temperature (Kirby, 1985). Rates of leaf emergence are slower than those of leaf initiation (Kirby, 1985). However, Cao and Moss (1989) observed differences in the relationship between leaf emergence rates and temperature between four winter wheat genotypes. These authors established that mean leaf emergence rates ranged from 0.132 (se = 0.012) leaves d^{-1} at 7.5°C, to 0.216 (se = 0.014) leaves d^{-1} at 25°C for their genotypes.

3.2.3. *Shoot elongation*

The rate of stem elongation is lower in the vegetative phase than in the reproductive phase (MacDowell, 1973), with rapid stem growth beginning shortly after the terminal spikelet stage of the main shoot apex (Kirby, 1985). Stem elongation is slower at temperatures below 20°C during the vegetative phase (Table 3), but with a *T*max seemingly only slightly higher than *T*opt (Table 1). However, the reported *T*max values (Table 3) were the highest we found rather than the defined limits. However, evidence of close proximity between *T*opt and *T*max for shoot growth is confirmed by Slafer and Rawson (1995a), in a study of four cultivars. Here shoot growth between terminal spikelet and flowering was not modified by temperatures up to 16°C but was significantly reduced by temperatures above 19°C.

Slafer and Rawson (1995a), using cv. Cappelle Desprez, found stem elongation to have a *T*min value of 4.7°C, and a growth rate of 1.7 (se = 0.2) mm $°C^{-1}$ d^{-1} until an optimum temperature of 19°C. Rates of stem elongation declined at temperatures higher than 21°C. Results of experiments on four other varieties (Slafer and Rawson, 1995a) were averaged to give a *T*min of 3.0°C and a *T*opt of 20.4°C. The absolute rate of stem elongation between *T*min and *T*opt was 1.5 mm $°C^{-1}$ d^{-1}.

4. Temperature and phenological development

Temperature sensitivity varies not only between plant components (Musich et al., 1981), but also changes during the course of development. Thus, base and optimum temperature thresholds increase with development (Lumsden, 1980; Angus et al., 1981; Slafer and Savin, 1991; Slafer and Rawson, 1995b). Thus, wheat is less sensitive to temperature during its vegetative phase than during its reproductive phase (Entz and Fowler, 1988), but there is no phase during which temperature does not modify development (Slafer and Rawson, 1994). Cardinal temperature thresholds for specific development phases are presented in Tables 4 and 5.

4.1. Cardinal temperatures for developmental stages

4.1.1. Sowing

One mechanism for reducing potentially adverse effects of climatic change on wheat growth and development may be to shift the time of sowing in response to altered temperature and rainfall regimes. Thus, we have tried to estimate the range of conditions suitable for sowing, germination and emergence.

Cardinal temperatures for the period from sowing to emergence have been established in several studies (Table 4). *T*min air temperatures range from 2.4 to 4.6°C, *T*opt from 20.4 to 23.6°C and *T*max from 31.8 to 33.6°C. Russell and Wilson (1994) add that soil temperature should be above 5°C. A study of 71 meteorological stations worldwide revealed that winter wheat is most commonly planted in months when the mean daily temperature is between 8 and 16°C (Bunting et al., 1982). This suggests that in practise, winter wheat is generally sown in sub-optimal temperatures and that warmer conditions during sowing should not have a negative impact on wheat establishment.

The matter of identifying ideal sowing temperatures is complicated by wheat's vernalization requirement. Certain winter varieties, which have an obligate chilling requirement in order to flower, thus respond positively to cold temperatures. In such varieties, high temperatures soon after vernalization is completed can reduce the effect of vernalization. This effect was noted by Chujo (1975), who found that vernalization at temperatures below 5°C was delayed by temperatures higher than 15°C in the same diurnal cycle. A synthesis of 11 studies revealed that optimum vernalization temperatures lie between 3.8 and 6.0°C (Table 1). Base temperatures for vernalization were found to average -1.3°C (se$=1.5$) and maximum temperatures were 15.7°C (se$=2.6$).

4.1.2. Terminal spikelet initiation

A key stage in crop development following emergence is initiation of the terminal spikelet (TSI). TSI is significant because it marks the end of the initiation of spikelet primordia and thus potential grain sites and is known to be highly sensitive to temperature (Slafer and Savin, 1991). Halevy (1985) found the period from TSI to heading to be more sensitive to temperature than sowing to floret initiation or floret initiation to TSI. However, Entz and Fowler (1988) found that temperature had its largest effect on development immediately prior to TSI but after the start of reproductive apical development.

The temperature sensitivity of the reproductive phase has important implications for grain yield. The number of grains produced is a function of both the number of spikelets and the number of kernels per spikelet. Spikelets may be initiated at temperatures higher than 1.5°C (Slafer and Rawson, 1995b). Optimum temperatures for this phase lie between 9.3 and 11.9°C, with temperatures greater than 25°C being sub-optimal (Table 4). High temperatures during early spike development reduced the number of spikelets per head or the number of seeds per spikelet (Johnson and Kanemasu, 1983).

4.1.3. Around anthesis

Temperatures above 31°C immediately before anthesis reduces grain yield by inducing pollen sterility, thus reducing grain numbers (Wheeler et al., 1996a). This effect has been shown in several experiments. Temperatures above 31°C for the five days prior to anthesis resulted in a high number of sterile grains (Wheeler et al., 1996b). Similarly, Tashiro and Wardlaw (1990) found that temperatures of 36°C during the day and 31°C at night just before anthesis resulted in a many sterile grains. Together, these results suggest 31°C as the *T*max value during the period immediately before anthesis.

At the slightly later stage of 50% anthesis, when half of the ears in a population have flowered, a temperature of 27°C also resulted in a high proportion of sterile grains (Wheeler et al., 1996a). Exposure to sub- or super-optimal temperatures during anthesis may also reduce yields through the production of infertile florets (Russell and Wilson, 1994). *T*min for the period around anthesis seems to be about 9.5°C (MacDowell, 1973; Slafer and Savin, 1991; Russell and Wilson, 1994) with *T*opt between 18 and 24°C (Russell and Wilson, 1994). Temperatures higher than 31°C or lower than 9°C during anthesis may therefore be considered as the limits to successful anthesis (MacDowell, 1973; Russell and Wilson, 1994). Caution should be employed, however, in identifying a single temperature threshold for anthesis, since its temperature sensitivity appears to vary during its course. Results for Australian varieties, for instance, reveal that plants are most sensitive to high temperatures in the first three days after anthesis (Stone and Nicolas, 1995a) during which time grain set may be reduced. Exposure to high temperatures more than eight days after anthesis caused neither a reduction in grain number or grain mass nor the number of deformed grains (Stone and Nicolas, 1995b,c). Stone et al. (1995) also showed that a short-but-early extreme heat treatment reduced grain growth to a greater extent than much longer periods of moderately high temperatures. The mature seed mass of wheat seems less sensitive to short periods of very high temperature as grain-filling progresses, regardless of variety. Unsurprisingly, in view of the above, there also seems to be only a poor correlation between anthesis date and the variability of grain yield. A survey of the relation between anthesis dates and grain yields for sites in the UK, Italy, Syria, New Zealand and Romania found an overall r^2 of only 0.07 (Porter, unpublished results). This was mainly because of the much smaller variation in anthesis date compared with that between grain yields at a site.

4.1.4. Grain growth

Experimental results reveal that a wider range of cardinal temperatures exist for grain-filling than for anthesis. Consistent with the pattern that temperature tolerance increases as plants develop, cardinal temperatures are generally highest during grain-filling. Literature reveals that *T*min values for grain-filling range from 4.1°C, for an average of ten cultivars (Hunt et al., 1991), to 8.9°C for spring wheat (Angus et al., 1981) to 12°C for winter wheat (Russell and Wilson, 1994). *T*opt reportedly lies between 19.3 and 22.1°C, and *T*max between 33.4 and 37.4°C. Cultivar differences in temperature sensitivity during grain-filling can extend to one cultivar being 35% more temperature-sensitive than another (Marcellos and Single, 1972), when measured via the relative effect of high temperature on grain yield.

The timing of a heat event during grain-filling appears to be important, exerting a particular influence on grain quality via the accumulation of protein. Thus two wheat varieties, (Egret and Oxley) exposed to five days of 40°C at five-day intervals throughout grain-filling, showed significant reductions in grain quality (Stone and Nicolas, 1996).

4.2. Temperature responses within developmental phases

Amongst the summary findings from studies which specifically identified development rates between different stages (Table 5) Angus et al. (1981) established that the rate of development from sowing to emergence did not differ between 10 Australian cultivars. This was despite the fact that these cultivars were known to differ in their temperature responses during crop establishment. Differences in response emerge as development progresses. Addae and Pearson (1992), for instance, observed a linear relationship between sowing and emergence and during grain-filling but a non-linear relationship between emergence and anthesis. In contrast, Slafer and Rawson (1995b) observed a linear relationship between temperature and development from emergence to anthesis between *T*min and *T*opt temperatures (4.0°C and 5.5°C, respectively), in the varieties Sunset and Rosella. However, a curvilinear relationship was observed in Condor (*T*min = 5.5°C) and Capelle Desprez (*T*min = 2.5°C) with the rate of development increasing between 10 and 19°C. Temperatures greater than 19°C had little effect on development.

A similarly complex story may be told for grain-filling. The rate of increase in grain dry weight increases with temperature. But both temperature sensitivity and growth rates vary between cultivars during grain-filling. Ten genotypes studied by Hunt et al. (1991), for example, had development rates during grain-filling ranging from 0.0017 to 0.0027 °C d $^{-1}$. Additionally, some of the genotypes in the study by Hunt et al. (1991) displayed a curvilinear response to temperature during grain-filling. Wheeler et al. (1996b) similarly identified a positive linear relationship between temperature and mean grain growth rate, up to temperatures of 16°C, but a negative relationship at temperatures higher than 16°C. These findings concur with those of Ishag and Mohamed (1996) who, in a study on five wheat cultivars from the Sudan, found that grain weight was negatively correlated with mean air temperature during grain-filling ($r^2 = -0.64$) and that a 1°C increase in temperature lead to a 4 mg decrease in mean grain weight. The rate of progress from anthesis to mass maturity was found by Wheeler et al. (1996b) to be a linear function of temperature between base and optimal temperatures.

Overall, these findings suggest that it is not possible to define a general relationship between temperature and rate of development for all development phases and for all wheat varieties. The inconsistencies highlight the significance for modelling studies of distinguishing between linear and non-linear growth and development responses when investigating potential impacts of climatic variability on crop production (Semenov and Porter, 1995).

5. Implications for impact studies

The tools available to those investigating potential impacts of future climatic change are experimentation and modelling. This review of the literature has revealed that certain temperature limits are well defined in wheat. In this category, we would put the lethal limits for wheat, the sterility response at anthesis, the cardinal temperatures for vernalization and some of the base and optimal temperatures (Table 1). Quantitative rate responses of both growth and development processes are more varied, perhaps because they are the net result of a flux of carbon gains and losses both of which respond to temperature. If climatic change impacts are to be assessed accurately, it is important that the full response range of growth and development processes for wheat is better understood. This would include the effects of combinations of extreme temperature events at different stages of growth and development. Increased climatic variability and, thereby, more frequent extreme conditions may result in plants being exposed to more than one extreme event in a single growing season. This might occur should climatic variability increase through a shift in the temperature distribution [Fig. 1(a)]. Would the effects of more than one extreme temperature event during a life-cycle of wheat be additive or do wheat plants carry a 'memory' of past extreme events? The null hypothesis would be that if a

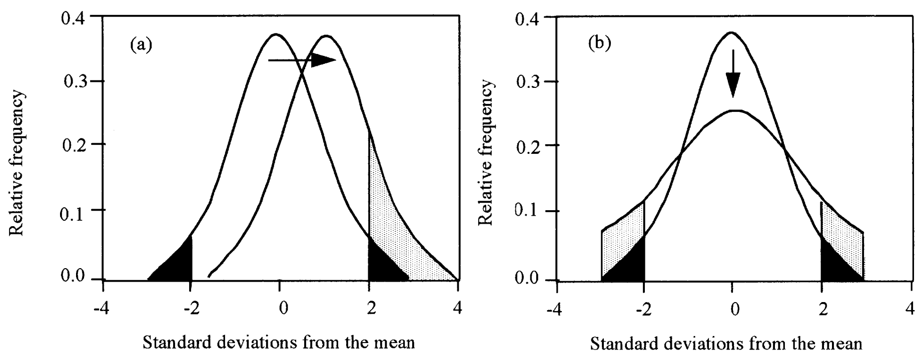

Fig. 1. Changes in frequency of extreme temperatures. For a distribution of temperatures an increase in the frequency of extreme temperatures can occur via: (a) a change in mean temperature; or (b) an increase in the variability of temperature but without change in the mean of the distribution (after Houghton et al., 1990). The solid area marks the 5% extremes of a normal distribution. The shaded area represents an increase in the number of extreme events outside the unperturbed 5% limits.

plant experiences extreme temperature conditions at, say, double ridges and again at anthesis, then the combined effects are additive. This needs to be tested. If temperature variability increases via a flattening of the frequency distribution [Fig. 1(b)], extreme hot and cold events may become equally more common. What would be the effect on wheat of an extreme cold event followed by an extreme hot event at a later stage in its development?

An important question for the modelling community concerns the modelling of grain sterility. Models need to take account of the independent effects of high temperatures on grain number. Crop-climate models, such as AFRCWHEAT2 or CERES-Wheat, accumulate dry matter for a period of time prior to anthesis and then convert this dry matter to grain number. Others, such as Sirius-wheat and SUCROS, employ an even simpler relation which empirically partitions dry matter to grains (Jamieson et al., 1998). The review presented here suggests that extreme high temperature events have autonomous effects on grain production processes which will require explicit modelling.

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