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Review

Simulating the impact of extreme heat and frost events on wheat crop production: A review

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ABSTRACT

Extreme weather events (frost and heat shock), already a significant challenge for grain producers, are predicted to increase under future climate scenarios. This paper reviews the current knowledge on the impacts of extreme heat (heat shock) and frost on crop production and how these impacts are incorporated into contemporary process-based crop models.

Heat shock and frost result in a range of physiological impacts on wheat. Based on the literature we conclude that the greatest impacts on production from frost are associated with sterility and the abortion of formed grains around anthesis. While the greatest yield impact from heat shock are reduced grain number (sterility and abortion of grains) during anthesis to early grain filling; as well as the reduced duration of grain filling. Crop models generally did not consider the non-linear response in grain yield from a heat shock or frost event due to these key physiological impacts. While frost damage was incorporated into a number of models through winterkill functions, seedling death or advanced senescence, only the STICS model incorporated a potential decrease in grain number around anthesis. In contrast, heat shock was rarely considered within crop models, with only two examples found in the literature; (1) APSIM-Nwheat which incorporated accelerated senescence in response to extreme heat and (2) MONICA which incorporated a reduction in grain number and yield.

We propose a conceptual model for the change in grain number and therefore yield in response to both a frost and heat shock event. We discuss the potential use of daily maximum/minimum temperatures, canopy temperature and heat/frost loads for determining crop response in the models. As well as identifying the need for a greater understanding on how the duration of temperature extremes impact on yield, as well as the cumulative effects of multiple heat/frost events and the interactions with other abiotic stresses including drought.

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1. Introduction

Wheat is the third largest crop in the world with over 600 million tonnes produced globally per year (Asseng et al., 2011). Extreme weather events, such as frost (<0 °C) and heat shock (short period of very high temperatures (>33 °C) (Wardlaw et al., 1989; Stone and Nicolas, 1994)) impact on crop production and represent a significant risk which needs to be managed to maintain profitable production.

Extreme weather events, are already a significant challenge for grain producers and are predicted to increase under future climate scenarios (Zheng et al., 2012). Since 1980 there has been a progressive increase in temperatures in all of the major cropping countries with the exception of the United States (Lobell et al., 2011). A worldwide analysis by Teixeira et al. (2013) to determine the potential 'hot-spots' predicted that continental lands in the high latitudes (between 40 and 60° N), particularly Central and Eastern Asia, Central North America and the Northern part of the Indian subcontinent were the key cropping areas facing heat stress risk. Gouache et al. (2012) showed that an increase in heat stress will be a significant contributor to reducing wheat yields in France, which is expected to increase under future climate projections.

In Australia, there has been an increased frequency of very hot (>40 °C) daytime temperatures since the 1990s (CSIRO and Bureau of Meteorology, 2012) and an increased incidence of frost across much of the Australian grain belt between 1960 and 2011 (Wahlquist, 2012). Future climate predictions suggest that the annual mean temperature in Australia is expected to increase up to 0.4–2.0 °C above 1990 levels by 2030 (Zheng et al., 2012), resulting in more very hot days (Zheng et al., 2012). The frequency of heat waves in southern Australia is also predicted to increase from once during a 20-year period under a current climate (1981–2000) to once every 3 years by the middle of the 21st century under the A2 scenario (IPCC, 2012). Climate change modelling also predicts higher average minimum temperatures, resulting in fewer frost days. However, the current trend of increased frost days in some regions (Wahlquist, 2012) is expected to remain around current levels until the mid-2030s (Crimp, 2014). When combined with warmer temperatures which are shortening the time to anthesis and maturity (Sadras and Monzon, 2006) there is still a significant frost risk despite the warming climate.

Grain growers, particularly in Mediterranean-type climates have historically managed the potential loss from frost by sowing late or selecting a cultivar that flowers after the significant frost risk window has passed. However, the choice of sowing time and cultivar is based on a small and variable window between reduced frost risk and limiting the risk of above average and extreme heat events later in the growing season. In Australia, delayed planting to reduce the risk of frost can result in a known opportunity costs up to 2–3 fold higher than direct losses from frost (Fuller et al., 2007). These opportunity costs are due to a range of factors including changes in temperature, radiation and vapour pressure deficit (VPD) which are primary drivers of growth (Rodriguez and Sadras, 2007) with the interaction of the factors altering the photo-thermal quotient (Fischer, 1985) and therefore potential yield. Delayed planting also increases the risk of crop exposure to heat shock and water stress. Following an extended dry period termed the millennium drought in southern Australia (ca. 1995–2009) the current trend is to plant rain-fed crops earlier, limiting the risk of heat and water stress during grain filling. However, this strategy has increased the potential for direct yielded losses due to the increased risk of anthesis occurring within the frost window (McDonald and Gardner, 1996). A landscape assessment of frost and heat wave risk across southern Australia showed that the relative risk of these constraints varied across different cropping regions, thus there is an opportunity to manage risk based on location (Barlow et al., 2013). In selecting management strategies (e.g. crop type, cultivar and planting time) growers need to balance the risks associated with frost, high temperatures over grain filling and terminal drought.

With temperature variability in the future identified as a major determining factor for crop production (Challinor et al., 2005), crop growth models provide an opportunity to balance the risks and maximise the growing season to optimise production. However, model comparison studies, especially for climate change scenarios, have noted the limited ability of crop models to account for climatic extremes. Sanchez et al. (2014) observed that a range of crop models adequately predict mean yields, but are less able to predict yield variability, due to their inability to handle climate extremes. Hochman et al. (2012) noted that APSIM does not account for extreme events such as severe frost and may be overly optimistic about water limited yield in some seasons and locations. Similarly, Eitzinger et al. (2013) compared seven widely used crop models and their response to heat and drought stress. This study found that while the models generally had a similar trend in simulated crop yields in response to increased temperatures, the models did not account for direct heat stress impacts which could result in further yield variations.

As a critical first step towards improved crop response functions which account for the impact of temperature extremes, we review the current knowledge on the impacts of extreme heat and frost on crop production and how these impacts are incorporated into contemporary process-based crop models. By combining our empirical knowledge of the impacts on wheat due to extreme heat and frost events, with the identified gaps in model applications we propose a conceptual model to develop heat and frost component modules for crop models.

2. Defining the impacts of climate extremes on crop production

Crop development is a key factor determining the impacts of climate extremes on wheat production. Throughout this review we discuss a range of developmental stages which are defined as: vegetative growth (Z00–Z29), reproductive growth (Z30–Z94), spike emergence (Z51), anthesis (Z61, Z65 and Z69 for 10%, 50% and 90%, respectively), and grain filling (Z70–Z94) (Zadoks et al., 1974).

2.1. Frost

One of the most common mechanisms for frost formation especially in Spring is when the ground and ambient air cools due to the loss of long-wave radiation (heat) to the atmosphere (termed radiation frost). These conditions most frequently occur after the passing of a cold front in Spring (Maqbool et al., 2010) where there are cold, still conditions and clear skies. During a radiant frost event, the ground and ambient temperature drops and wheat crop canopies experience temperatures 2–4 °C colder than that being measured within a nearby Stevenson Screen (Frederiks et al., 2008).

Damage to wheat from frost has been observed in all stages of growth from seedlings through to maturity (Shroyer et al., 1995; Porter and Gawith, 1999; Fuller et al., 2007). However, the size of the yield impact resulting from frost damage for both spring and winter wheat at the reproductive stage of growth is far greater than any other stage (Frederiks et al., 2012).

Frost during vegetative growth affects seedling survival (Fuller et al., 2007) as well as causing leaf damage resulting in the scorched appearance of leaves (Shroyer et al., 1995). While there is a distinct impact on crop yield with seedling death, other frost damage during the vegetative stages has a small potential impact on yield as the growing point of wheat is located in the soil typically protecting it from damage (Shroyer et al., 1995; Porter and Gawith, 1999). Many wheat cultivars have high levels of frost tolerance during the vegetative period (some winter types are tolerant to temperatures of −20 °C; Frederiks et al. (2008)), induced in winter wheat through a process of cold acclimation which produces 'hardened' wheat plants. Low temperature acclimation in winter wheat is a genetically regulated, cumulative process initiated below 10 °C (Fowler and Limin, 2004). Fuller et al. (2007) showed a gradient in seedling survival for winter wheat, with seedling survival starting to decline at −5 °C for non-acclimated plants and between −6 °C and −8 °C for acclimated winter wheat seedlings.

A single frost event during reproductive growth, can have a moderate to severe impact on crop yields (Shroyer et al., 1995). Both spring and winter wheat suffer significant frost damage in the reproductive stages, with frost sensitivity increasing with maturity (Frederiks et al., 2012) from the start of reproductive growth to anthesis, in particular they become more susceptible from spike emergence to anthesis. The transition from vegetative to reproductive stage is pivotal (Mahfoozi et al., 2001), as the frost tolerance observed by wheat in the vegetative stages is discontinued with the onset of reproductive growth (Fuller et al., 2007).

Around booting the most frequent damage to the stem occurs above the top node which can result in the loss of the head (Frederiks et al., 2008), although stem damage lower in the plant can also occur increasing the risk of lodging during grain filling. Crops with frost damage to stems during booting can continue to develop grain with little impact on yield assuming that other factors such as water supply are not limiting and that lodging does not occur (Rebbeck and Knell, 2007).

Once the head has developed but prior to emergence, frost can result in damage to the head through sterility of florets, reducing grain number (Frederiks et al., 2008). During ear emergence and early anthesis frost results in the death of anthers and embryos (Cromey et al., 1998), resulting in sterility of florets and whole spikelets (Marcellos and Single, 1984; Al-Issawi et al., 2012). Frost during grain filling may result in the death of partially filled grains and reduce grain weight culminating with grain that is small, shrivelled, shrunken or having a blistered appearance (Cromey et al., 1998).

Frost damage at ear emergence and anthesis, generally occurs within a narrow temperature range, where after reaching a threshold temperature a steep reduction in grain set occurs. The threshold canopy temperature identified by Marcellos and Single (1984) was between −4 °C and −5 °C for different cultivars studied (Fig. 1) which was consistent with other studies which noted good resistance down to around −5 °C (Fuller et al., 2007; Al-Issawi et al., 2012) near anthesis. Once this threshold temperature is reached, a 1 °C difference in night time minimum temperature could increase crop damage from 10% to 90% (Marcellos and Single, 1984; Rebbeck and Knell, 2007).

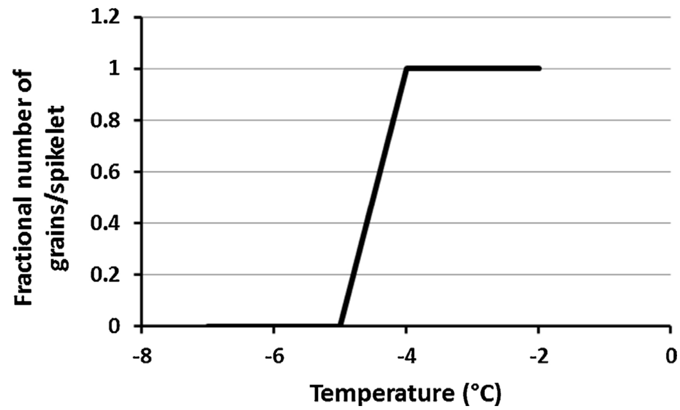

Fig. 1. Generalised relationship between canopy temperature and the fractional number of grains per spikelet that survived.
Adapted from Marcellos and Single (1984).

In addition to temperature the duration of freezing temperatures is important in determining the damage that occurs (Al-Issawi et al., 2012). The longer the duration the greater the chance of ice-nucleation occurring, and the greater spread of ice-nucleation through the ear and subsequent plant damage. The time for freezing to occur has not been consistent between studies (e.g. thermal imaging showed freezing of the ear at around 20 min (Fuller et al., 2007) to over 2 h (Marcellos and Single, 1984)) which may reflect different experimental methodologies. In the absence of consistent information on the duration at which a minimum temperature needs to be maintained, especially under field conditions, it would be difficult to take this into consideration in the development of frost models.

The study of frost at anthesis has focussed largely on single plants or individual heads of wheat which were at a consistent developmental stage in order to understand freezing mechanisms (e.g. Marcellos and Single, 1984; Al-Issawi et al., 2012), rather than at the crop canopy level. In the field there is variation in crop development due to micro-climates, variations in soil properties, as well as differences in development between the main stem and tillers. This variation is problematic for field studies of frost damage as differences in crop development cause substantial variation in the impact of a frost event at that scale (Frederiks et al., 2012).

2.1.1. Key physiological responses to frost

As frost results in a range of physiological impacts on wheat, crop models need to capture the physiological responses which have the greatest impact on yield. Based on the literature we conclude that the greatest impacts on production are associated with seedling death, sterility and the abortion of formed grains as shown in Table 1. The extent to which these processes are considered within crop models is considered in Section 3.

2.2. Heat shock

The sensitivity of wheat to heat is greatest during the reproductive period, particularly after heading (Marcellos and Single, 1972) which corresponds to the period in the growing season where high temperatures are most common (Balouchi, 2010; Pradhan et al., 2012). The response of wheat to high temperature events can be characterised by; (1) above optimum average temperatures for an extended period (weeks through to months), and (2) heat shock which is defined by short periods (1–3 days) of very high maximum temperatures (>33 °C (Wardlaw et al., 1989; Stone and Nicolas,

Table 1
The key physiological damage to wheat in response to a frost event.

Growth stage	Damage observed	Wheat susceptibility	Potential yield impact	Potential for compensatory growth	Critical plant temperatures for damage to be initiated
Vegetative	Seedling death	Low–moderate	0–100%	No	After 2 h exposure a threshold temperature of −4 °C was observed. In spring wheat 100% loss around −7 °C, in acclimated winter wheat 100% loss around −13 °C (Fuller et al., 2007)
Anthesis	Sterility	High	10–100%	Low	After 2 h exposure a threshold temperature of −4 °C to −6 °C was observed. A 1 °C drop below threshold can result in 100% yield loss (Marcellos and Single, 1984). −5 °C for 2 h, with ice nucleation beginning after 15 min (Al-Issawi et al., 2012).
Grain filling	Death of formed grains (small, shrivelled grains)	Moderate–high	0–80%	Low	Field frost (duration not defined) where a minimum temperature of −2 °C[a] (early milk) resulted in a 13–33% yield loss (Cromey et al., 1998)

[a] Temperature was freezer temperature rather than a direct measure of plant temperature.

1994): >35 °C (Blumenthal et al., 1994)). This review distinguishes between both impacts on wheat, specifically focusing on yield declines associated with heat shock during the reproductive period.

The optimum temperature for grain development ranges from 12 to 22 °C (Farooq et al., 2011), with Porter and Gawith (1999) listing optimum temperatures of 22, 10.6, 21 and 20.7 °C for sowing-emergence, terminal spikelet, anthesis and grain filling, periods, respectively. Above optimum temperatures especially during grain filling impact on yield through both grain number and weight (Pradhan et al., 2012) with grain weight the most sensitive yield component (Wardlaw et al., 1989; Stone and Nicolas, 1994). Accelerated crop development, due to increased temperature, limits the duration of the grain filling period (Wardlaw and Moncur, 1995; Shah and Paulsen, 2003; Lobell et al., 2012). While high temperatures can increase the supply of assimilate during grain filling, the wheat plant is unable to fully compensate for the shorter duration of the grain filling period (Lobell et al., 2012; Pradhan et al., 2012). This review does not consider these impacts in more detail as the focus is on heat shock events.

In identifying potential damage due to heat shock it is important to consider that canopy and plant temperature can differ significantly from standard measurements (e.g. 1.2 m Stevenson Screen). This difference is not constant and may be affected by a range of factors including, soil water content, soil type, crop density and stubble retention as well as minor variations in topography and aspect. During the day, canopy temperature can be cooler than air temperature (Stevenson Screen at 1.2 m height) due to evaporative cooling and higher relative humidity of the crop (Asseng et al., 2011; Fischer, 2011; Eitzinger et al., 2013). Conversely the canopy may be several degrees warmer in situations where there is reduced water available for transpiration (Asseng et al., 2011). In addition to this, the pivotal role of transpiration and other structural factors in canopy temperature depression can result in some organs experiencing warmer/cooler temperatures affecting the heat shock experienced. For example Ayeneh et al. (2002), found that canopy air temperature > spike temperature > leaf temperature.

Heat shock events are most common in the post-anthesis period of grain filling (Balouchi, 2010; Pradhan et al., 2012), however crops are most sensitive around anthesis to early grain filling (Wardlaw et al., 1989; Blumenthal et al., 1991; Stone and Nicolas, 1994). Blumenthal et al. (1991) found a highly significant correlation between heat stress (hours above 35 °C) during grain filling and grain yield using 27 years of trial data. Heat shock triggers specific physiological responses (Stone et al., 1995) which ultimately result in a significant reduction in grain yield. During grain filling heat shock triggers many processes including premature senescence, decreased leaf chlorophyll, inhibited kernel development through reduced translocation of photosynthates to the grain as well as starch synthesis and deposition in the developing grain (Wardlaw and Wrigley, 1994; Stone and Nicolas, 1995; Acevedo et al., 2002; Pradhan et al., 2012). Heat shock also triggers the production of heat shock proteins which have been linked to heat stress tolerance mechanisms (Acevedo et al., 2002).

Heat shock during the reproductive phase of wheat decreases grain set by adversely affecting ovary development and pollen germination (Pradhan et al., 2012). Tashiro and Wardlaw (1990) showed that the number of sterile grains produced by a heat shock event was greatest two days prior to anthesis and reduced down to low levels about two days after anthesis. Stone and Nicolas (1995) showed no significant reduction in grain number when heat shock was applied 10–30 days after anthesis (across the 75 cultivars), although heat shock at 10 days after anthesis did result in a significant response in 5 individual cultivars (12–22% reduction in grain number). Similarly, Hays et al. (2007) found 25% grain abortion in one wheat cultivar and no response in another in response to a heat shock event 10 days after pollination. These differences are attributed to genetic variation in heat tolerance (discussed in more detail below) (Stone and Nicolas, 1995; Hays et al., 2007; Farooq et al., 2011).

Heat shock also produces wheat kernels that are small, notched, and split (Tashiro and Wardlaw, 1990) that also significantly affect crop yield and quality. The production of small and shrivelled grains is a response to a range of factors including abnormal nuclear cell division after fertilisation, and variable rates of starch granule deposition (Tashiro and Wardlaw, 1990). Tashiro and Wardlaw (1990) showed that the frequency of small, damaged grains appeared to be greatest (up to 30%) when heat shock occurred between 2 and 10 days after anthesis.

Heat shock significantly affects the duration of grain filling (Lobell et al., 2012) and therefore the size of grains (Wardlaw et al., 1989; Ferris et al., 1998). Using MODIS satellite data to measure advanced rates of senescence in India, Lobell et al. (2012) showed a shortening of the growing season of up to 8 days due to high temperatures. High temperatures have been shown to reduce the grain filling period by 45–60% (Yang et al., 2002; Shah and Paulsen, 2003), however there is significant genetic variability in the actual degree to which the grain filling period is affected (Harding et al., 1990). Heat stress appears to alter the regulation of senescence processes, reducing photosynthesis and leaf chlorophyll content and resulting in accelerated senescence (Harding et al., 1990; Yang et al., 2002; Zhao et al., 2007). Importantly, the study of heat impacts on senescence and the grain filling period often utilise a

Table 2
The key physiological damage to wheat in response to a heat shock event (>33 °C).

Damage observed	Process	Days pre/post 50% anthesis (Z65)		Potential yield impact
		Max[a]	Range[b]	
Reduced grain number	Sterility	−2	−3 to 2	45% sterility (−3 days), 58% sterility (−2 days), 5% sterility (2 days) (Tashiro and Wardlaw, 1990)[c]
	Abortion of grains		10	10–25% reduction in kernel number (Hays et al., 2007)[d] and also (Stone and Nicolas, 1995)[e] in 5 out of 75 cultivars
			−1 to 3	4% abortion at 1 day (Tashiro and Wardlaw, 1990)[c]
	Abortion and sterility		0–16	35–62% reduction in grain number (Pradhan et al., 2012)[f]
Reduced grain size	Grain filling duration: days (senescence and rate of development)		Around anthesis to maturity	30–45% reduction (Wardlaw and Moncur, 1995)[g]
				45–62% reduction (Yang et al., 2002)[h]
				50% reduction (Shah and Paulsen, 2003)[i]
				10–20% reduction (Stone et al., 1995)[j]
	Grain filling duration: thermal time		15–20	10–15% reduction in cumulative degree days (Stone et al., 1995)[j]

[a] Day pre/post anthesis that a heat shock event resulted in the maximum reduction in yield.
[b] Range of days pre/post anthesis where a heat shock event resulted in a yield reduction.
[c] 36/31 °C for two days.
[d] 38/25 °C for one day.
[e] 3 days with 40 °C maximum temperature.
[f] 36/30 °C for 16 days from anthesis.
[g] 24/19 °C or 30/25 °C anthesis to maturity.
[h] 20/15 °C and 30/25 °C 10 DAA to maturity.
[i] 15/10 °C to 35/30 °C anthesis to maturity
[j] 21/16 °C or 40/16 °C between 15-19 DAA and then 21/16 °C, 27/22 °C or 30/25 °C from 20 DAA to maturity.

constant temperature treatment from around anthesis to maturity, rather than a short term exposure to extreme temperatures even when temperatures greater than 30 °C are utilised. Exposing wheat plants to a heat shock event during early grain filling reduces both the duration and the cumulative degree days during grain filling resulting in smaller grains at harvest (Stone et al., 1995). Stone et al. (1995) suggest that very high temperature enhanced the rate of development, resulting in a breakdown of the asymptotic relationship between temperature and duration of grain filling (Marcellos and Single, 1972), but does not speculate on the cause. The impact of heat shock observed by Stone et al. (1995) highlights the need to consider maximum temperatures not just the daily average temperature in determining the duration of the grain filling period.

Heat shock can also significantly alter the rate of grain filling (Stone et al., 1995). Increased rates of grain filling have been reported in response to high temperatures up to 30 °C (Sofield et al., 1977; Wardlaw and Moncur, 1995; Calderini et al., 1999), however these studies did not account for heat shock. In contrast, a decreased rate of grain filling was reported in response to heat shock in other studies (Stone et al., 1995; Talukder et al., 2010). While, Zhao et al. (2007) showed an initial increase in the rate of grain filling, followed by a reduced rate from 12 days after anthesis. However, despite reported differences in the rate of grain filling, the significantly reduced duration of the grain filling period appears to be the dominant factor in determining grain yield response. As research has shown that even an increased rate of grain filling cannot compensate for the reduced duration (Pradhan et al., 2012).

Wheat plants appear to have some capacity to acclimate to heat events. Warmer temperatures prior to heat shock have been shown to reduce the impact of the heat shock event on grain yield. For example Spiertz et al. (2006) showed that across all genotypes the effect of heat stress was larger when plants were grown at 18/13 °C compared to 25/20 °C. In addition, a heat shock event may reduce the impact of high temperatures after the heat shock (Stone et al., 1995). This increase in thermo-tolerance has been correlated with the development of a group of proteins known as heat shock proteins (Blumenthal et al., 1994; Wardlaw and Wrigley, 1994).

Wheat genotypes have been shown to vary significantly in their sensitivity to heat (Slafer and Rawson, 1994) and heat shock events (Stone and Nicolas, 1995; Hays et al., 2007; Farooq et al., 2011). For example Calderini et al. (1999) showed both linear and curvilinear relationships between heat and the rate of grain filling depending on the cultivar. While Schapendonk et al. (2007) suggest that genetic variation in storage processes (grain fill) may be more important in determining heat shock impacts than photosynthesis-linked processes. While research has shown significant genotype x temperature interactions it is still not known what factors determine the large differences (Spiertz et al., 2006). However, the differences in heat tolerance may be associated with multiple processes including leaf rolling and transpirational cooling (Farooq et al., 2011) as well as mechanisms involving heat shock proteins, transcription factors and other stress related genes (Qin et al., 2008).

In addition to acclimation and genetic variability, the impact of heat shock on grain number is also affected by other confounding factors including water status (drought), variations in canopy temperatures and relative humidity. Pradhan et al. (2012) report a decrease in leaf chlorophyll, individual grain weight, and grain yield in an increasing magnitude of drought < high temperature < combined stress. While drought conditions have a direct influence on the plant they can also affect relative humidity within the crop and canopy temperature depression (Balota et al., 2007). For example, greater sterility from a heat shock at anthesis has been observed at high relative humidity (>50% RH) compared to low relative humidity (35% RH) (Tashiro and Wardlaw, 1990) as the floret temperature was 1.8 °C cooler under the low relative humidity compared to the higher relative humidity conditions.

2.2.1. Key physiological responses to heat shock

Heat shock results in a range of physiological impacts on wheat, crop models need to capture the physiological responses which have the greatest impacts on production. Based on the literature we conclude that the greatest impacts on production from a heat shock event for grain number and grain size are:

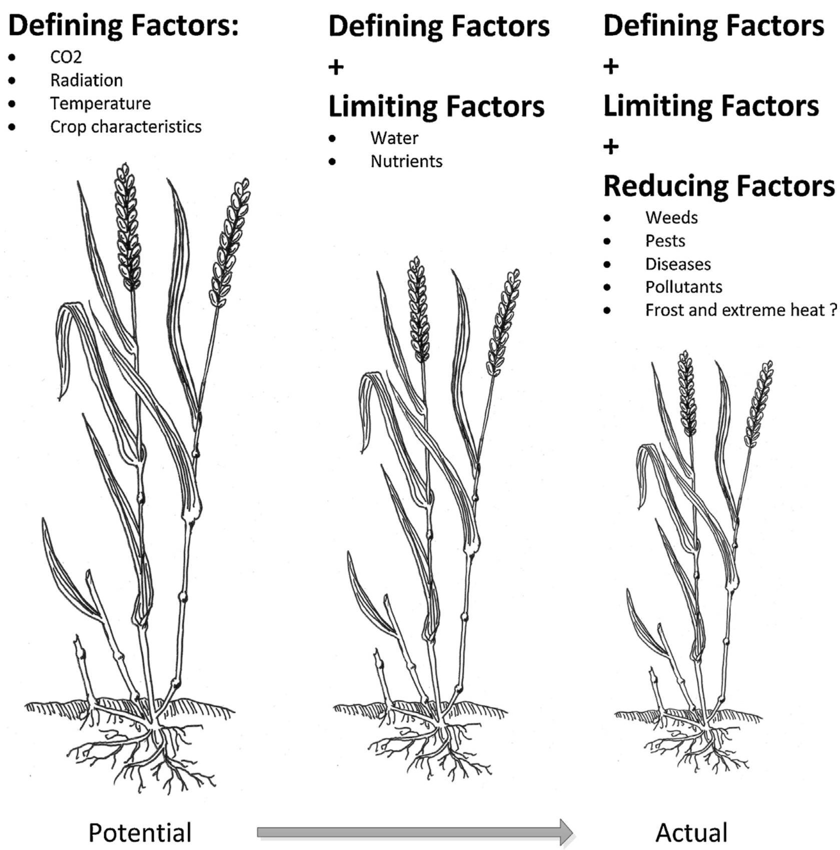

Fig. 2. A conceptual representation of a systematic hierarchy of growth factors and associated production levels typically used in crop models adapted from van Ittersum et al. (2003).

- Grain number is largely affected by sterility and abortion of grains in a period from just before anthesis to at least 10 days after anthesis, depending on the cultivar selected (Table 2). Sterility and the abortion of grains results in a non-recoverable reduction in the potential yield of the crop, which cannot be compensated for in the future growth of the crop (for example: Spiertz, 1974).
- Grain size is affected by cellular damage which results in shrunken, notched and split grains (Tashiro and Wardlaw, 1990). Cellular damage is related to the timing of heat stress with a maximum sensitivity around booting (Ugarte et al., 2007) through to 8 days after anthesis (Stone et al., 1995). After this grain size is a response to the rate (Stone et al., 1995) and duration (Lobell et al., 2012) of grain filling. In terms of heat shock impacts, one of the most important processes to capture in terms of grain size appears to be the duration of grain filling which is affected by the rate of crop development and accelerated senescence (Ugarte et al., 2007).

The extent to which these processes are considered within crop models is considered in Section 3.

3. How current models account for extreme heat and frost

Crop models can conceptually be presented using a hierarchy of growth factors and associated production levels (Fig. 2, adapted from van Ittersum et al. (2003)). In this conceptual structure the *Potential Yield* is defined by environmental and crop specific factors that are managed through tactical decisions including sowing date, sowing density and cultivar selection. These *Defining Factors* include temperature, solar radiation and other environmental factors including CO_2 and VPD. There are a range of factors that can limit growth and yield such as water and nutrient supply which result in significant reductions in yield by limiting daily growth. These *Limiting Factors* can be partly managed by irrigation and fertiliser regimes. The harvestable product yielded from crops is grain and this is modelled by either simple harvest ratios (harvest index approach) or more complex partitioning driven by dynamics of mean grain numbers per unit area and grain growth rates. Either approach usually reduces daily biomass production and grain growth or the harvest index and therefore accumulated yield, in response to *Limiting Factors* including water and nitrogen supplies. In addition to the *Defining* and *Limiting Factors* some crop models, depending on their targeted application, may also include *Reducing Factors* such as weeds, pests and disease (Fig. 2).

Defining factors are often a cumulative response to daily conditions over all or part of the season (van Ittersum et al., 2003). Temperature as a *Defining Factor* within crop models is essential in terms of crop development, growth and the prediction of final yields. The major components of temperature which drive crop development are low temperatures (vernalisation) and temperature per se (to drive development) (Slafer and Rawson, 1994). It is widely recognised that development accelerates as temperature increases (Slafer and Rawson, 1994) and this relationship is used in calculations such as the accumulation of thermal time to *Define* crop development. Temperature also has a *Defining* role in terms of biomass production, for example the temperature effect on radiation use efficiency which drives biomass production (e.g. APSIM, CERES-Wheat), this relationship between temperature and radiation (the photothermal quotient) is also important in *Defining* grain number (Fischer, 1985). Temperature also helps *Define* the prediction of the rate of grain filling and senescence (e.g. APSIM, STICS).

Frost and heat shock could be considered as either *Defining* or *Reducing Factors* within crop models. While frost and heat shock are temperature effects, they are not a cumulative response to daily conditions over the season as is the case for *Defining* and *Limiting Factors*. Instead, the main impacts appear to be a response to between one and three days of extreme temperatures at key development stages which result in a step reduction in yield potential. As such we believe that frost and heat shock need to be considered as *Reducing Factors* within a model.

From reviewing the crop responses to both frost and heat shock (Section 2), it is evident that both climate extremes can result in a disproportionate reduction in grain number through sterility and abortion, as well as more cumulative impacts on crop yield through advanced senescence and the reduced rates/duration during grain filling. While these yield impacts, specifically from a reduction in grain number, may be partially compensated for through the potential growth of higher order florets which would naturally abort (Spiertz, 1974) as well as through slightly increased grain size (Rawson and Evans, 1970) this compensation is not always observed (Zhang et al., 2010; Wu et al., 2014).

Crop models simplify the processes being represented by necessity and disregard some constraints on yield. However, from this review there are some significant impacts from climate extremes which need to be incorporated within crop models. This section of the review investigates how contemporary processed-based crop models deal with heat shock and frost impacts on crop yield.

3.1. Modelling frost impacts

Models currently account for frost damage to varying degrees using a range of strategies including crop death, as well as reducing seedling density, crop biomass or leaf area. The direct impacts of frost around anthesis on grain number are not widely captured in contemporary process based crop models. Some examples of modelled frost impacts within the literature include:

- CERES-Wheat (Jones et al., 2003) and CAT (DPI, 2009) contain a winter-kill function which is applied at any growth stage prior to anthesis. When it is applied, 100% of the crop dies. Similarly, EPIC (Williams, 2002) includes a frost kill function which is linked to a snow cover factor.
- EPIC also incorporates a frost function which reduces total biomass by a percentage for each day below a certain temperature, with frost damage greatest in seedlings and approaching zero at maturity. This approach does not reflect the greater sensitivity of wheat to frost damage around anthesis and is more appropriate to winter dormancy and snow cover which may be more significant in some environments than radiant frosts in spring (Williams, 2002).
- CropSyst (Stockle et al., 2003) incorporates a number of freezing parameters but these influence soil freezing and hydrology rather than having a direct biological impact on grain yield.
- APSIM incorporates a frost stress function which results in leaf senescence. In this model leaf area senescence is the maximum of five factors (age, water stress, light intensity, frost and heat). While frost is included as a factor in APSIM the default value is zero which means there is no frost stress (Zheng et al., 2014). The function for leaf area senescence caused by frost ($\Delta\mathrm{LAI}_{\mathrm{sen\_frost}}$) is:

$$\Delta\mathrm{LAI}_{\mathrm{sen\_frost}} = k_{\mathrm{sen\_frost}} \times \mathrm{LAI} \tag{1}$$

where $k_{\mathrm{sen\_frost}}$ is a function of daily minimum temperature and is defined by the linear interpolation between two parameters $x_{\mathrm{temp\_senescence}}$ and $y_{\mathrm{senescence\_fac}}$ which are linearly interpolated by APSIM.

- InfoCrop, a dynamic simulation model developed for tropical environments incorporates a frost function (Aggarwal et al., 2006). This function reduces leaf area in proportion to the crops sensitivity. The impact of frost is reduced when the available soil water fraction of the surface exceeds 0.9, which simulates an ability of irrigation to reduce frost impacts.
- Wheatman (Woodruff, 1992), a decision support tool incorporates the risk of frost damage by overlapping a risk of a 0 °C screen temperature with ear emergence. However, it does not calculate a yield impact. As a decision support tool it allows the user to modify their frost risk based on their knowledge of their properties susceptibility to frost and whether they are generally colder/warmer than the nearest weather station.

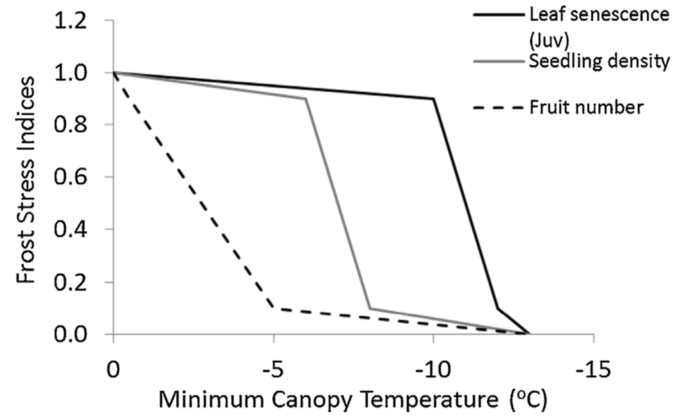

Fig. 3. An example of the Frost Stress Indices calculated in STICS using minimum crop temperature and four cardinal temperatures to describe each stress function. Adapted from Brisson et al. (2008).

Typically models such as CERES-Wheat, EPIC and CropSyst were designed to account for very cold temperatures such as in continental Europe and northern America, however they are not necessarily suited to more temperate climates, where spring radiant frosts are the primary risk. Whilst these models, incorporate a reduction in yield due to one or two frost events through reduced biomass or advanced senescence, none of these frost models account for the sterility and loss of florets around anthesis.

Of more interest is the STICS model which includes a frost impact on seedling density, leaf senescence and fruit number which have a flow on effect to yield (Brisson et al., 2003). For all of these stages, a frost stress indices (0–1) is calculated within the model which is defined as a function of four minimum crop temperatures (for example Fig. 3). In the application of the frost stress indices for seedling density it is applied in a multiplicative way which reduces plant density. Of particular interest in this model is the allowance for a step reduction in fruit/grain number consistent with the literature presented in Section 2.1. Brisson et al. (2008) acknowledge that the cardinal temperatures (threshold values) may need to be adjusted as a function of genetic tolerance.

3.2. Modelling extreme heat impacts

Modelling heat shock can be considered in terms of five physiological processes which need to be considered: (1) reduced duration of grain filling, (2) accelerated senescence, (3) reduced grain growth rate, (4) reduced grain number in response to sterility and abortion of grains, and (5) production of small and shrivelled grains.

Temperature is the main factor determining the duration of grain filling (anthesis to physiological maturity) (Slafer and Rawson, 1994). This is accounted for by all crop models through the calculation of thermal time, with the duration of grain filling reduced by higher temperatures. Some models (e.g. APSIM (Zheng et al., 2014)) also alter the rate of grain filling in response to

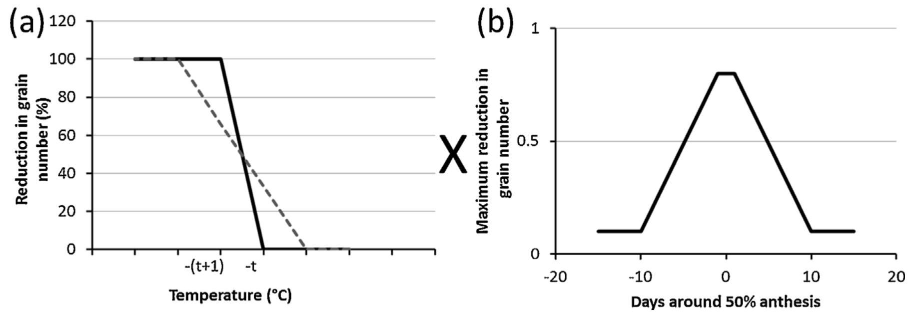

Fig. 4. Proposed relationships to describe the reduction in grain number to a radiant frost event (as defined by canopy temperature), (a) the reduction in grain number observed at anthesis at either a single point (▬▬▬) or across a paddock which needs to account for the distribution in temperature and therefore damage (▬ ▬ ▬ ▬), and (b) the distribution of anthesis around the predicted date of 50% anthesis.

temperature. However, none of the crop models appear to specifically alter the calculation of the duration or rate of grain filling in response to heat shock. Nor do they alter the cumulative degree days for the grain filling period in response to a heat shock event despite some evidence in the literature (Stone et al., 1995), although there is limited data to support the development of a response curve.

In terms of advanced senescence, all of the models have some link between high temperature and the rate at which leaves senescence and accordingly a decline in photosynthesis and grain filling rate (Lobell et al., 2012). The senescence function in APSIM-Nwheat was modified to specifically account for extreme heat events, by introducing a stress function which starts at 34 °C (Asseng et al., 2011) based on controlled environment and field studies (Asseng et al., 2011). This model introduces a discontinuity at the 34 °C threshold with a step increase in the 'factor to accelerate senescence' from 1 to 3, followed by a linear increase with increasing temperature. Each day an additional change in leaf area index (LAI) is calculated in response to extreme heat as a 'fraction of LAI senescence' multiplied by LAI. Where the 'fraction of LAI senescence' due to heat ranges from 0 at 34 °C to 0.4 at 45 °C. This relationship reduces LAI incrementally each day. This reduction in LAI, translates to an impact on the percentage of final grain yield, with a resultant 60% reduction in grain yield when temperatures greater than 34 °C occur every day during grain filling. This relationship has also been incorporated into the APSIM wheat module (Zheng et al., 2014). This model by Asseng et al. (2011) captures a non-linear response of plant senescence to extreme heat, however it does not account for the significant reduction in grain number which has been observed in response to a shorter time period (1–2 days) of heat shock.

Few models incorporate functions to reduce grain number in response to heat stress or heat shock around anthesis. Of the literature searched only GLAM (parameterised for groundnuts: Challinor et al., 2005) and MONICA (including cereals: Nendel et al., 2011), account for high temperature heat stress effects on grain number and yield. The heat stress function in GLAM (Challinor et al., 2005) and MONICA calculates an average daytime temperature (T_{photo}; Eq. (2)) during a defined period around anthesis. The model calculates a reduced grain number (G) on day (t) during this period using a linear interpolation between a critical temperature (T_{crit}) at which pod-set/grain number begins to be affected and a temperature (T_{lim}) at which zero pod-set/grain number occurs (Eq. (3)). The greatest temperature (T_{photo}) over the period of interest (e.g. anthesis) is used to modify the grain number.

$$T_{photo} = T_{max} - \frac{T_{max} - T_{min}}{4} \tag{2}$$

$$G(t) = 1 - \left(\frac{T_{photo} - T_{crit}}{T_{lim} - T_{crit}} \right) \tag{3}$$

4. Discussion

Our review showed that contemporary processed-based crop models do not adequately account for the impact of climate extremes on crop growth. Our findings are consistent with a number of model comparison studies which compared model predictions under various climate scenarios (e.g. Zheng et al., 2012). Sanchez et al. (2014) highlighted the need to define response functions for extreme temperatures, with a priority on the response during anthesis and grain filling.

We conclude from the literature presented in this review that a reduction in grain number has the greatest impact on yield from a short term (1–3 days) extreme heat or frost event. The reduction in grain number due to floret sterility and/or abortion of grains resets the potential yield of the crop, resulting in a non-linear response (Sanchez et al., 2014). This leads to a significant reduction in overall yield, but also affects the distribution of resources within the plants. For crop models to have greater utility they will need to consider the reduction in grain number which occurs in response to frost and extreme heat events.

In this discussion we suggest an approach for modelling the impacts of extreme heat and frost on grain number and yield. We identify the challenge in defining canopy temperatures at a point and across the landscape as important considerations in the application of these component modules. We also identify some of the key knowledge gaps which reduce the accuracy with which the impacts of heat shock and frost can be predicted.

4.1. Proposed frost module

Consistent with the observed reduction in grain number to a frost event (e.g. Fig. 1) and similar to the STICS model (Fig. 3) Our proposed structure for modelling radiant frost within crop models (Fig. 4) includes a calculation of the percentage reduction in grain number in response to a frost event around anthesis; and a distribution of impact over time. This approach could be used to determine a yield reduction through either a reduced grain number, or a reduced harvest index approach depending on the crop model.

We propose that the reduction in grain number is based on the relationship shown in Fig. 4. In this approach a minimum canopy temperature is set at which frost damage starts to occur, using a predicted canopy temperature of around −4 to −5 °C (Marcellos and Single, 1984). When the model is applied at a point the reduction in grain number would drop from 0% loss at −5 °C to 100% loss at −6 °C (Fig. 4a). However, across a paddock temperature may vary by up to 4 °C (Rebbeck and Knell, 2007). We submit that this variability, could be incorporated conceptually by increasing the temperature range over which damage occurs to account for parts

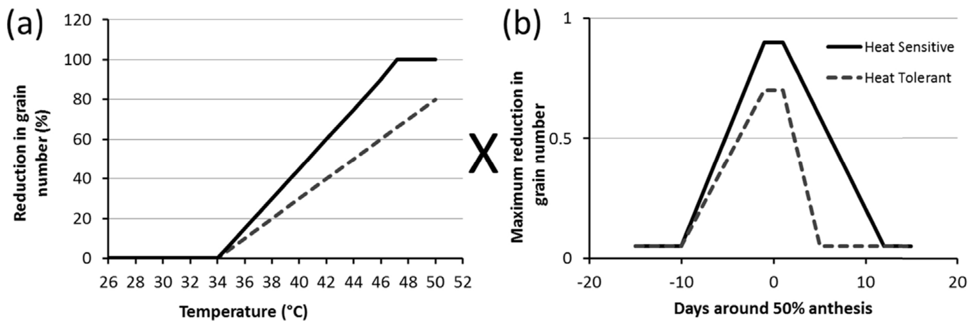

Fig. 5. Proposed generic relationships to describe the reduction in grain number to a heat shock event (values are indicative rather than being prescriptive).

of the paddock being warmer and/or cooler than the point source measurement (Fig. 4a).

Finally we suggest the use of a stochastic distribution around 50% anthesis to scale the yield reduction. This would ensure that the maximum reduction in grain number only occurs around 50% anthesis (consistent with greatest sensitivity of crops during the reproductive phase) but the losses are scaled around this due to the variation in the timing of anthesis within a single plant as well as across a paddock (Fig. 4b). This is distinct from the STICS model which appears to apply its frost function as a single step function over a development phase.

These two response functions would be multiplicative and used together to predict the reduction in yield. With the potential to modify either the critical temperatures (Fig. 4a) or the distribution of damage (Fig. 4b) in response to genetic differences in frost tolerance which are currently being investigated (Juttner, 2014). These relationships could be used to determine the reduction in grain number for models which explicitly predict grain number. Alternatively they could be included as one of a number of stress factors which reduce the harvest index of the crop to define total yield.

While there is sufficient data within the literature to develop a frost crop module some key gaps have been identified. These gaps need to be addressed, to allow refinement and greater accuracy in the crop modules. Some of the key gaps identified were: (1) the duration of time below a critical temperature for frost damage to occur; (2) the distribution of frost sensitivity around anthesis, as the literature clearly shows that anthesis is the most sensitive time, but how this sensitivity varies around anthesis and how the variation in anthesis within the crop affect whole crop impacts is less clear; (3) the cumulative effect of multiple frost events over the anthesis window; and finally (4) how large are the potential compensatory effects in the translocation of resources due to partial sterility of the wheat head (Rawson and Evans, 1970).

4.2. Proposed heat shock module

Based on the literature presented we conclude that a heat shock module needs to account for the reduction in grain number around anthesis, as well as advanced senescence and reduced rate/duration of grain filling from cumulative heat load during grain filling. Temperature along with crop development are primary factors in determining the crop response to heat shock events.

The reduction in grain number could be modelled using the procedure of GLAM/MONICA (Challinor et al., 2005; Nendel et al., 2011) which, similar to the proposed frost module calculates the potential reduction based on temperature a distribution of impact around anthesis. Alternatively, the same module that was developed for frost could be applied to the impacts of heat shock on grain number with different parameterisation (Fig. 5). The percentage reduction in grain number is a function of temperature (Fig. 5a) which may be different between heat sensitive and tolerant cultivars. This reduction can then be multiplied by a distribution of risk, whether the risk is centred around 50% anthesis as the most sensitive time of wheat to sterility and abortion of grains still needs to be determined (Table 2). However, the distribution of risk (Fig. 5b), reflects the fact that the impact of heat shock on grain number varies with crop development stage and cultivar and that there is a distribution of development within a crop which will potentially affect the heat shock impacts across a paddock. Such a model would be consistent with the literature, for example: Stone and Nicolas (1995) showed no significant reduction in grain number with heat shock at 10 days after anthesis, with the exception of 5 heat sensitive cultivars which showed a 12–22% reduction in grain number.

A heat shock model also needs to account for the reduced duration of the grain filling period and advanced senescence. While, all of the models have a link between temperature stress and the rate at which leaves senescence they do not capture such non-linear response to heat shock. We propose that a similar approach to that presented in APSIM-Nwheat (Asseng et al., 2011) would allow models to account for heat shock impacts on senescence and therefore also influence the duration of grain filling. Finally, there is a need to validate whether there is a change in thermal time accumulation (anthesis to maturity/harvest) due to heat shock as suggested by the results of Stone et al. (1995).

Quantifying the impacts of extreme heat on yield and defining the yield temperature relationships for heat shock is difficult. This difficulty is a response to the large variability in experimental conditions in the literature. In particular, more comprehensive data sets are required which define the combination of heat wave conditions encountered i.e. various combination of timing, temperature and duration on grain set and subsequent growth of wheat. Experiments are needed to measure any cumulative effects. How the rate of temperature change affects reductions in grain yield is also unclear. For example, Stone and Nicolas (1994) used a gradual increase in temperature over approximately 5 h but notes that other studies use a sudden temperature change which may exaggerate the temperature effect on yield and quality. Caution is therefore needed not to expound an unrealistic model of stress.

4.3. Temperature

Temperature is a key factor in determining the impact of heat shock and frost events on wheat production. As noted previously canopy temperature can differ significantly from air temperature (e.g. 1.2 m Stevenson Screen). These differences are not a constant and may be affected by a range of factors, including soil water content, soil type, crop density, canopy height and stubble retention as well as minor variations in topography and aspect.

All contemporary process based crop models utilise commonly available climate data as key inputs into models, including daily maximum/minimum temperatures. The models range in terms of the complexity with which they deal with the variation between canopy and air temperature. For example, APSIM uses an empirical calculation of average crown temperature for the calculation of thermal time using daily maximum/minimum air temperatures, as well as a mean daily air temperature for the calculation of temperature stress (Zheng et al., 2014). In contrast, STICS uses either an empirical or energy balance approach (based on available climate date) to determine a maximum and minimum crop temperature (Brisson et al., 2008). While the mathematical approach for estimating temperature may vary, what is consistent is the use of daily climate data.

The proposed heat shock and frost crop modules (Sections 4.1 and 4.2) use daily maximum and minimum temperatures. In the case of frost the critical temperature in the module is defined by the minimum canopy temperature (Section 4.1), whilst the critical temperatures for extreme heat is defined by the maximum standard air temperatures (Section 4.2), with these temperatures selected based on the available experimental data. Where a crop model uses a calculated canopy temperature, then the critical temperatures identified from the literature for frost can be used directly. However, many models use the standard climate data as driving factors (Brisson et al., 2006); in which case either the critical canopy temperatures identified within the literature would need to be scaled (e.g. assuming canopy minimum temperature is a standard 2 °C cooler than air temperature) or a canopy maximum and minimum temperature would need to be calculated using either an empirical or energy balance approach.

Although the proposed heat shock and frost crop modules utilise daily maximum and minimum temperatures an important consideration within the literature was the duration of exposure to either a heat shock or frost event. For example, the degree of damage would realistically be different if the crop was exposed to a critical temperature for half an hour versus 6 h. While the duration of exposure will have an impact we found limited data directly relating the hours of exposure to crop damage, suggesting that there would be insufficient data to support the complexity of incorporating hourly climate data. However, future work could investigate whether minimum/maximum temperatures could be used to approximate a heat load. In the case of heat shock there is some evidence to support the calculation of a thermal load (hours over a certain temperature) rather than just a maximum temperature (Blumenthal et al., 1991).

Similarly, the impact of consecutive/multiple days of frost or extreme heat needs to be considered within the model. It is unlikely to be sufficient to assume the maximum impact of multiple events. This suggests that the estimation of a heat or frost load not only from a single event but also over a key period (i.e. 10–90% anthesis) may be of value. However, further work would be required to try and quantify a heat/frost load based on daily maximum/minimum air temperatures and to quantify the relationship with the physiological impact on the crop and therefore crop yield.

4.4. Future work

In developing studies to determine the impacts of extreme heat and frost events to inform and validate model development, the combined effects of different abiotic stresses need to be considered (Barnabas et al., 2008). Previous studies (Rizhsky et al., 2004; Mittler, 2006) have shown that the molecular and metabolic responses of plants to a combination of multiple abiotic stresses is unique and cannot be directly extrapolated from the response of plants to each of the different stresses individually. One combination of stressors which may be of particular relevance to some regions is the potential for both frost and heat shock events to occur together. It is also important that future research considers the implications of spatial variability in temperature extremes (especially frost) and therefore crop damage. Understanding of this spatial variation could be facilitated through airborne and satellite sensors (Rodriguez et al., 2005; Lobell et al., 2012), with the topographic effects properly considered.

In the development and testing of frost and heat shock models there are three key steps which need to be considered in more detail. First is further analysis of temperature data, both canopy and Stevenson screen to determine potential relationships between maximum/minimum temperatures and heat/frost loads especially around anthesis. Second is the validation of the response functions with experimental data. Third is a sensitivity analysis to validate the interaction between yield reduction and sowing time under a range of environmental conditions.

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