Running title: Temperature responses of photosynthesis and respiration in wheat

Title: Exploring high temperature responses of photosynthesis and respiration to improve heat tolerance in wheat

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The high temperature responses of photosynthesis and respiration in wheat are an under-examined, yet potential avenue to improving heat tolerance and avoiding yield losses in a warming climate.

Abstract

High temperatures account for major wheat yield losses annually and, as the climate continues to warm, these losses will likely increase. Both photosynthesis and respiration are the main determinants of carbon balance and growth in wheat, and both are sensitive to high temperature. Wheat is able to acclimate photosynthesis and respiration to high temperature, and thus reduce the negative affects on growth. The capacity to adjust these processes to better suit warmer conditions stands as a potential avenue toward reducing heat-induced yield losses in the future. However, much remains to be learnt about such phenomena. Here, we review what is known of high temperature tolerance in wheat, particularly in respect to the high temperature responses of photosynthesis and respiration. We also identify the many unknowns that surround this area, particularly in respect to the high temperature response of wheat respiration and the consequences of this for growth and yield. It is concluded that further investigation into the response of photosynthesis and respiration to high temperature could present several methods of improving wheat high temperature tolerance. Extending our knowledge in this area could also lead to more immediate benefits, such as the enhancement of current crop models.

Key words: Abiotic stress, acclimation, carbon, heat, photosynthesis, respiration, stress, temperature, wheat

Abbreviations: Net photosynthesis, A; Photosynthetic assimilation, A_{net}; Heat shock proteins, HSPs; Maximum rate of electron transport, J_{max}; Photosystem II, PSII; Extent of increase in respiratory rate with an increase in temperature of 10 °C, Q_{10}; Dark respiration rate, R; Light respiration, R_{light}; Rubisco activase, Rca; Reactive oxygen species, ROS; Temperature of maximum respiration rate, T_{max}; Temperature of maximum photosynthetic rate, T_{opt}; Enzyme activity at 25°C, $V25$; Carboxylation rate of Rubisco, V_{c}; Maximum carboxylation rate of Rubisco, V_{cmax}; Oxygenation rate of Rubisco, V_{o}.

Introduction

The warming climate presents a pressing challenge to the global economy and food security, with food production required to increase by 60% to feed the growing world population (Ray *et al.*, 2013). Globally, the climate has been steadily warming over the past century, with the four decades from the 1970s to 2018 each warmer than their predecessor (CSIRO and The Bureau of Meteorology, 2018). Under a high emission scenario, global mean temperature will continue to rise by at least 4°C towards the end of this century (IPCC, 2014). In addition, an increase in frequency, intensity, and durations of heatwaves is predicted, as well as a diurnal asymmetry in the increase of temperatures, with mean daily minimum increasing more rapidly than mean daily maximum (Davy *et al.*, 2017; García *et al.*, 2015; Hatfield and Prueger, 2015; Lobell and Field, 2007). Considering the major role of temperature in determining the rate of plant growth and development (Berry and Raison, 1981; Hatfield and Prueger, 2015), and that exposure to supra-optimal temperatures can cause irreversible damage, and even death, in all plant species (Hoffmann *et al.*, 2013), increases in average temperatures and heatwaves are a considerable concern. High temperatures can cause delayed germination, disruption of metabolic processes, and reproductive failure (Machado and Paulsen, 2001; Wahid *et al.*, 2007). For an economically and culturally valuable crop like wheat, the effect of heat on yield is of particular importance.

Global wheat production exceeds 700 million tonnes annually, making it one of the most widely grown crops in the world (Food and Agriculture Organization of the United Nations, 2018). However, increases in temperatures over recent decades have reduced wheat yields in several regions worldwide, a trend that is predicted to continue (Al-Khatib and Paulsen, 1984; Alexander *et al.*, 2006; Asseng *et al.*, 2015; Barnabás *et al.*, 2008). An example of the global trend can be seen in Australia, where rising temperatures accounted for 17% of the observed 27% decline in average wheat yield potential between 1990 and 2015 (Hochman *et al.*, 2017). Increases in both mean daily maximum and minimum temperatures drive these high temperature-induced yield declines (Hunt *et al.*, 2018), with mean daily minimum temperatures exerting a proportionally greater influence on grain yields than mean daily maximums (Cossani and Reynolds, 2013; Martre *et al.*, 2017).

Teamed with the fact that mean night-time temperatures are rising at a faster rate than those during the daytime (Davy *et al.*, 2017), warming nights loom as a potential source of significant wheat yield reduction in the near future.

Effects of high temperature on wheat vary with development

Wheat is vulnerable to high temperature throughout its life cycle (Wardlaw *et al.*, 1989b), with the optimal temperature range varying across different phenological phases (Farooq *et al.*, 2011; Porter and Gawith, 1999; Slafer and Rawson, 1995). The consequences of heat stress also vary with development (Table 1). Around reproduction and flowering, high temperature reduces the number of grains per spikelet and thereby grains per unit area (when above-average temperature occurs prior to anthesis) (Ferris *et al.*, 1998; Prasad *et al.*, 2008; Wardlaw *et al.*, 1995; Wheeler *et al.*, 1996), and grain weight (when high temperature occurs following anthesis) (Stone and Nicolas, 1994; Wardlaw *et al.*, 1989a; Wardlaw *et al.*, 1989b). High temperature at anthesis is particularly detrimental to yield because of the narrow optimum temperature range of fertilisation. High temperature disrupts fertilisation (Prasad and Djanaguiraman, 2014) via the abnormal development of reproductive organs, such as the ovule or pollen tube, which in turn increases grain abortion (Saini *et al.*, 1983). It is for these reasons that the effects of high temperature at anthesis have been so heavily studied to date.

Wheat yields may also be adversely impacted by high temperatures occurring during developmental stages prior to and following anthesis (Porter and Gawith, 1999; Skylas *et al.*, 2002; Stone and Nicolas, 1994). High temperatures occurring as early as sowing can hamper both germination and seedling emergence (Rebetzke *et al.*, 2004). Supra-optimal temperatures during the vegetative stage speed up development (Al-Khatib and Paulsen, 1984; Asseng *et al.*, 2011; Harding *et al.*, 1990), causing plants to flower earlier in the season and leaving them vulnerable to substantial frost-induced yield losses (Hunt *et al.*, 2018). An acceleration of wheat development also reduces the window in which to capture resources (e.g. radiation and water) (Midmore *et al.*, 1982; Shpiler and Blum, 1986), thus reducing pre-anthesis biomass accumulation (Liu *et al.*, 2010). Up to 80% of total grain production can be drawn from carbohydrates accumulated and stored prior to flowering, and so less biomass at anthesis can reduce grain number (Prasad *et al.*, 2008; Slafer and Rawson, 1994) and overall yield (Blum *et al.*, 1994; Villegas *et al.*, 2001). Furthermore, a plant relies more heavily on stem carbohydrate reserves when experiencing stresses during the grain filling stage (Bidinger *et al.*, 1977). Thus, supra-optimal temperature earlier in development – prior to grain fill – will reduce the carbon supply that a plant is able to draw upon to later produce grain (Blum *et al.*, 1994). Coping with high temperature during vegetative growth thus requires that wheat be more efficient in the processes that control net carbon balance (i.e. photosynthesis and respiration) during vegetative growth. In this review, we explore what is known, and not known, about the impacts of heat on these two core carbon exchange processes in wheat.

High temperature responses of photosynthesis and respiration

Photosynthesis and respiration are both temperature sensitive. Net photosynthesis (A_{net}) increases as leaf temperature rises, peaking at an optimum temperature (T_{opt}), before then declining (see Fig. 1), reflecting the impact of temperature on photosynthetic CO_2 fixation, and CO_2 release by photorespiration and mitochondrial respiration. However, following sustained increases in growth temperature, most plants (including wheat) can adjust, or 'acclimate', their photosynthetic characteristics (Berry and Bjorkman, 1980; Yamori *et al.*, 2014). Thermal acclimation is a process by which plants adjust metabolic rates to compensate for a change in growth temperature, potentially resulting in metabolic homeostasis (i.e. identical metabolic rates in contrasting thermal regimes when measured *in situ*). As discussed in more detail in later sections, photosynthetic thermal acclimation likely involves altered activity of the enzyme responsible for CO_2 fixation – Rubisco, adjustments in electron transport through photosystem II (PSII) in chloroplasts (Yamasaki *et al.*, 2002), and changes in photo-inhibition susceptibility (Hurry and Huner, 1991, 1992; Oquist *et al.*, 1993). While the general temperature response of photosynthesis is well studied, little is known of genotypic variation in wheat photosynthetic thermal acclimation to high temperature, or of the mechanisms regulating it. This is important in the context of determining wheat yield under high temperature, as optimising photosynthesis serves to maximise net carbon gain in the daytime. Even less is known about the temperature-response of the other component of net carbon balance, respiration.

Wheat leaf respiration increases in response to short-term temperature rise (de Vries *et al.*, 1979), generally doubling with every 10°C increase in sub-optimal temperature (Table 2, Fig. 2), with the temperature dependence of respiration likely to be primarily driven by how temperature affects the processes of substrate supply (Azcón-Bieto *et al.*, 1983; Bingham and Stevenson, 1993) and demand for respiratory products, both locally and in remote tissues (Farrar, 1985; Farrar and Williams, 1991; O'Leary *et al.*, 2018). Energy demand is derived from processes such as phloem loading, protein turnover, ion gradient maintenance, and other metabolic activities in leaves and roots (Vos, 1981). Importantly, short-term changes in temperature have a greater effect on leaf respiration than on photosynthesis (Dusenge *et al.*, 2019), a factor with important consequences for leaf carbon economy. Some wheat varieties are able to thermally acclimate respiration to compensate for sustained increases in growth temperature, minimising respiratory carbon losses in leaves under hot growth conditions (Figure 2) (Gifford, 1995; Kurimoto *et al.*, 2004). In wheat, capacity to acclimate leaf respiration has also been linked to homeostasis of relative growth rate with varying growth temperature (Kurimoto *et al.*, 2004). Thus, it seems likely that the temperature response of leaf respiration, both over the short and long-term, is central in determining wheat net carbon balance and biomass accumulation following high temperature exposure. Despite this likelihood, our knowledge of the connection between respiratory thermal acclimation and wheat growth and yield remains limited.

Scope of review

In this review, we focus on short and long-term responses of wheat net carbon balance to high temperature. Specifically, we examine the high temperature responses of wheat photosynthesis and respiration, and their relationships in the context of crop production. While acknowledging that the effects of high temperature on wheat can depend on the presence of other stresses (abiotic and biotic) - including most notably with water stress, which can cause stomatal closure and increase leaf temperature (Reynolds *et al.*, 2010) - for the purposes of this review we focus solely to the effects of high-temperature. We begin with considering the general mechanisms likely to underpin heat tolerance in wheat, drawing on studies specific to this crop, as well as from other model systems. Thereafter, we discuss the roles of photosynthesis and respiration in determining leaf level and whole-plant net carbon balance. Next, we explore the response of wheat photosynthesis to short- and long-term high temperature exposure, including the biochemical mechanisms potentially underpinning this response. We then review factors that influence respiratory costs of growth and maintenance processes, and how temperature affects these processes, including changes associated with thermal acclimation of mitochondrial respiration. The importance of understanding how both wheat photosynthesis and respiration will respond to rising temperatures is highlighted throughout, particularly in the context of avoiding major yield reductions in a rapidly warming world.

Potential mechanisms underpinning heat tolerance in wheat leaves

Various biochemical mechanisms underpin heat tolerance in plants, including wheat, although the exact nature of these remain unclear. These mechanisms are related to lipid membrane thermostability, heat shock proteins (HSPs), reactive oxygen species (ROS), antioxidants, and the activities of important enzymes (e.g. Rubisco, starch synthase), among other factors. The thermostability of lipid membranes is controlled by the saturation or unsaturation of membrane fatty acids. Membranes with greater thermostability enhance protection against ROS, which are a by-product of increased respiration under high temperatures (Brestic *et al.*, 2012; Christiansen, 1978; Cossani and Reynolds, 2012; Mohammed and Tarpley, 2009). High temperature causes membranes to become overly fluid and permeable (Fig. 3) (Allakhverdiev *et al.*, 2008). The degree of saturation of membrane fatty acids regulates the structure of the membrane, with higher relative levels of saturated compared to unsaturated fatty acids in a membrane promoting rigidity (Los and Murata, 2004; Narayanan *et al.*, 2016). Therefore, plants that are more adept at increasing the ratio of saturated to unsaturated fatty acids in lipid membranes are likely to be more tolerant of heat stress (Murata and Los, 1997). PSII, a highly heat-susceptible component of the photosynthetic electron transport chain, is embedded in the thylakoid membrane. A higher degree of membrane thermostability is likely to promote heat tolerance of PSII, and thus result in a greater degree of photosynthetic thermal tolerance. Indeed, cell membrane thermostability has been observed to positively correlate with biomass and yield under high temperatures in field conditions, independent of drought or biotic stresses (Blum *et al.*, 2001; Reynolds *et al.*, 1994).

Heat shock proteins are another biochemical mechanism associated with plant thermal tolerance. These proteins are induced rapidly and in large quantities following the onset of heat stress, and are thought to assist other proteins to maintain functionality (Vierling, 1991; Wang *et al.*, 2004). Assistance may include acting as chaperones to other proteins to ensure that they are able to continue to function during bouts of high temperature, as well as preventing the aggregation of misfolded proteins(Trösch *et al.*, 2015). Despite persisting uncertainty about how specific HSPs may confer heat tolerance in wheat, studies in other species have found that they protect PSII during episodes of high temperature (Heckathorn *et al.*, 1998; Schroda *et al.*, 1999). Although no direct causal relationship was observed, Krishnan et al. (1989) found a positive correlation between thermal tolerance and the expression of small HSPs in two wheat varieties differing in susceptibility to heat stress. Small HSPs have also been associated with enhancing grain quality (Skylas *et al.*, 2002). Further research is needed to better understand how specific HSPs promote thermal tolerance in wheat, as well as the effect that the expression of these proteins may have on grain yield and quality. More specifically, the role of HSPs and membrane thermostability in protecting respiration and photosynthesis in wheat under high temperatures remains unclear, although it is likely that they number among the mechanisms that regulate the thermal tolerance of each of these processes.

Some of the potential biochemical explanations for heat-induced declines of chloroplast and mitochondrial function are presented in Fig. 3. High temperature has the effect of increasing the fluidity of cell and organelle lipid membranes, interfering with the membrane's ability to regulate what is allowed to pass in and out of the cell/organelle (Fig. 3). Membrane damage of this kind is common to both chloroplast and mitochondrial-located membranes(Niu and Xiang, 2018). In the context of the chloroplast, heat-induced membrane damage results mainly from the peroxidation of lipids (particularly polyunsaturated fatty acids), which interferes with the maintenance of the pH gradient required for ATP synthesis(Yadav and Pospíšil, 2012). Components of the PSII complex itself are also damaged by ROS under heat stress, most notably the D1 protein (Fig. 3)(Chan *et al.*, 2012). Heat stress to mitochondrial membranes has a similarly negative effect on ATP production. In mitochondria, this stems from the peroxidation of the phospholipid cardiolipin, which in turn inhibits cytochrome c oxidase activity, thus decreasing electron transport and, ultimately, ATP synthesis (Pan *et al.*, 2014; Paradies *et al.*, 1998). However, by increasing the relative amount of saturated fatty acids in cellular and organelle membranes, the membrane is able to preserve its optimal structure at higher temperatures. This fortification of membranes at high temperature offers membrane-bound electron transport greater protection from ROS, therefore enhancing the thermotolerance of photosynthesis and respiration.

Net carbon balance of wheat – importance of photosynthesis and respiration

The net carbon balance within plants is determined by a combination of both photosynthetic assimilation (A) and respiration (R). The general ratio of R/A in whole plants likely ranges between 0.35 – 0.80 (when measured at a common temperature), with the exact number varying based on both biotic and abiotic factors during plant growth (Amthor, 2000). For wheat, maize, and rice, the ratio of R/A generally falls between 0.3 – 0.6 (Amthor, 1989). Even small variations in this ratio can significantly affect plant growth, illustrating the importance of both A and R in determining overall productivity. The response of photosynthetic and respiratory carbon exchange to temperature is crucial in this respect, as R/A ratios of whole-plants typically increase with measurement temperature (Gifford, 1995). This reflects the fact that respiration is typically more sensitive to rising temperature than is net photosynthesis (Dusenge *et al.*, 2019). Looking ahead, one strategy to improve net carbon gain of wheat, then, could be to screen genotypes for variability in: (1) temperature-normalized R/A (i.e. of plants grown and measured at 25°C); (2) temperature-sensitive changes in R/A values (e.g. via having a lower differential in the short-term temperature sensitivity of R and A); and, (3) R/A values of hot-acclimated plants, where the target is to identify genotypes with lower R/A following acclimation to hot conditions.

A lower R/A could be achieved through improving the rate of photosynthetic CO_2 fixation (e.g. via increasing heat stability of Rubisco activity or improving PSII functionality), reducing the energy costs associated with cellular maintenance and/or biosynthesis (and thus limiting the rate of respiratory CO_2 release), and/or improving the efficiency of respiratory ATP synthesis per unit of CO_2 released. There is growing evidence of significant variation in net photosynthetic rate among field-grown wheat varieties (Reynolds *et al.*, 2000); similarly, a recent study (Scafaro *et al.*, 2017) using a high-throughput technique reported substantial genotypic variation in leaf respiration rates in wheat. Together, these observations point to the probability that R/A does differ among wheat lines. Moreover, there are reports of grain yields being higher in ryegrass, tomato and canola lines that exhibit lower respiratory rates (Hauben *et al.*, 2009; Nunes-Nesi *et al.*, 2005; Wilson and Jones, 1982). While the stability of such traits may vary depending on planting density (Kraus and Lambers, 2001), the possibility remains that variations in photosynthesis and/or respiration could influence wheat yields. More work needs to be done to understand how respiration influences growth and yield in wheat, how these relationships may be impacted by increased temperature, and whether measurement at the plant level extrapolates to field canopies. The capacity to identify varieties that maintain lower respiration rates under high temperatures could be invaluable to efforts to develop new wheat varieties better suited to a future climate that is increasingly warming and unpredictable.

Below, we outline possible ways of maintaining favourable net carbon balance in wheat. We start by focussing on mechanisms underpinning thermal acclimation of photosynthesis; we then consider factors that could influence respiratory costs associated with maintenance and growth, and finally, we consider what is known about thermal acclimation of respiration in wheat.

Thermal tolerance and acclimation of photosynthesis

Photosynthesis is a highly thermolabile process, which can be influenced or altered by high temperatures in a number of ways. The basic temperature response of photosynthesis has been well documented and, aside from variations based on species or biome differences, is largely conserved across plant species. It generally resembles a parabolic curve, with the photosynthetic rate initially increasing with temperature, before reaching a peak (T_{opt}) and then declining with further temperature increases (Fig. 1) (Berry and Bjorkman, 1980). This means that temperature extremes on either side of T_{opt} can inhibit photosynthesis. Temperatures significantly higher than T_{opt} can result in a reduction in photosynthesis in both wheat leaves and ears, which in turn impairs grain fill (Blum *et al.*, 1994). However, most plants are equipped to deal with non-optimal temperatures by acclimating their optimal temperature range of photosynthesis to better suit their new climate (Yamori *et al.*, 2014). When a plant experiences a temperature increase, acclimation allows it to become more efficient at fixing carbon at elevated temperatures. Wang et al. (2011) investigated the effects that pre-anthesis acclimation can have on photosynthetic characteristics later in winter wheat development. Following two 2-day exposures to 32/28 °C (day/night) pre-anthesis, plants were later exposed to further heat stress 7 days after anthesis. The plants that acclimated to high temperature pre-anthesis had smaller decreases in net photosynthesis, transpiration rate, and stomatal conductance in comparison to those that had not experienced pre-anthesis heat exposure (Wang *et al.*, 2011). Due to the inhibition of photosynthesis being directly associated with reduced yield (Scafaro and Atkin, 2016), the thermal tolerance and acclimation of photosynthesis in a valuable crop like wheat is a crucial area of study.

Rubisco activation is sensitive to moderate levels of heat stress

A key limiting factor of photosynthesis is the activity of the carbon-fixing protein Rubisco, and more specifically, its capacity for carboxylation (Demirevska-Kepova and Feller, 2004). Rubisco itself is a fairly thermostable enzyme, even in cold-adapted species (Salvucci and Crafts-Brandner, 2004; Yamori *et al.*, 2006). However, Rubisco activity has been observed to decline under high temperature, including in wheat (Feng *et al.*, 2014; Kobza and Edwards, 1987). Crafts-Brandner and Law (2000) suggested that the adverse effect of high temperature on Rubisco activation is caused by the inhibition of interactions between Rubisco and the enzyme Rubisco Activase (Rca). The main function of Rca is to clear Rubisco catalytic sites of sugar phosphates, allowing for more efficient activation (Robinson and Portis, 1988). During an episode of high temperature, the inhibition of Rubisco activation is thought to be due predominantly to the rate of Rca activity being outpaced by the rate at which Rubisco is being deactivated (Crafts-Brandner and Salvucci, 2000). It is reasonable to assume, then, that Rca plays an important role in determining the response of photosynthesis to increasing temperature. Ristic et al. (2009) indeed found that, in winter wheat, *Rca* expression was positively correlated with productivity following a 16-day heat stress over the anthesis period. Feller et al. (1998) observed a reduction in Rubisco activation in wheat leaf tissue following just 5 minutes of exposure to 30-35 °C. *Rca* also began to aggregate at high temperature, as well as becoming insoluble as temperatures rose above 37 °C (Feller *et al.*, 1998). Although investigations into the link between *Rca* and productivity in wheat have thus far been limited, findings such as these suggest that Rca plays a key role in the high temperature response of photosynthesis in wheat. Whether the expression and activity of this protein during periods of supra-optimal temperatures exerts a significant influence on growth and yield remains unknown.

Damage to photosystem II when leaves become very hot

Another way that high temperature can inhibit photosynthetic rate is by damaging PSII, a central component of the chloroplast electron transfer chain (Bukhov *et al.*, 1999). Specifically, it is thought that high temperature may lead to the loss of two manganese ions from the oxygen-evolving complex of PSII (Enami *et al.*, 1994). PSII is embedded in the chloroplast thylakoid membrane, which is itself also susceptible to heat-induced damage (Gounaris *et al.*, 1984), compounding the thermal sensitivity of PSII. Damage to PSII is a commonly used gauge of photosynthetic heat tolerance, as it is a trait that can be easily measured (Knight and Ackerly, 2002; O'Sullivan *et al.*, 2013; Zhu *et al.*, 2018). An increase in variable chlorophyll fluorescence indicates a decrease in the proportion of light energy used to drive electron transport, and thus an inhibition of the rate of photosynthesis (Atwell *et al.*, 1999). More specifically, there are a number of chlorophyll fluorescence parameters that are used to determine heat tolerance, including F_o (minimum fluorescence yield) and F_v/F_m (the maximum quantum efficiency of PSII). Both traits are commonly used as indicators of the heat tolerance of photosynthetic machinery in dark-adapted leaves and correlate strongly with each other (Sharma *et al.*, 2012), despite providing slightly different insights into the consequences of high temperature. F_o is the minimum fluorescence, achieved while all PSII reaction centres are open, and provides an indication of non-photochemical quenching (Maxwell and Johnson, 2000). The difference between F_o and the maximum fluorescence (F_m) is termed the variable fluorescence (F_v).The F_v/F_m ratio is taken following a high intensity pulse of light that causes PSII reaction centres to close. Decreases in this trait may reflect damage to PSII reaction centres or slowly relaxing quenching processes (Baker and Rosenqvist, 2004). The primary role that PSII plays in the electron transfer chain, along with the relative efficiency with which damage to this complex can be measured, make PSII thermostability a valuable indicator of photosynthetic thermal tolerance. As a result, a number of studies have employed these techniques when measuring high temperature tolerance in wheat (Brestic *et al.*, 2012; Haque *et al.*, 2014; Shanmugam *et al.*, 2013; Sharma *et al.*, 2012; Sharma *et al.*, 2015; Sharma *et al.*, 2014)

Understanding impact of high temperature on photosynthesis through modelling limitations in the maximum rates of electron transport and Rubisco activity

Two of the main limitations of photosynthesis are the maximum rate of electron transport (J_{max}), and the maximum carboxylation rate of Rubisco (V_{cmax}). These two processes determine the upper limit of the photosynthetic rate, assuming there are no limitations on vascular flow of water within the plant. In light saturated conditions and elevated CO_2, photosynthesis may be limited by the capacity to regenerate RuBP, which reflects J_{max} (Sage and Kubien, 2007). Alternatively, as temperature increases, V_{cmax} acts as the limiting factor on the rate of photosynthesis (Fig. 1). As mentioned previously, J_{max} may be inhibited by heat stress via damage incurred by the thermally-sensitive PSII. For V_{cmax}, temperature increases between approximately 15 – 30°C lead to an exponential increase; however, a rapid decline in V_{cmax} follows as temperatures continue to rise (Hikosaka *et al.*, 2005). This decline in V_{cmax} is likely due to the dysfunction of Rubisco Activase, resulting in a decline in Rubisco activity. The capacity to photosynthetically acclimate to high temperature in wheat is likely driven by the ability to adjust V_{cmax} and J_{max} in response to increasing temperature. Photosynthetic rate has been observed to correlate with leaf area index and yield (Chakrabarti *et al.*, 2013), meaning that limiting high temperature-induced reductions in photosynthesis and leaf area (likely symptoms of accelerated development) could potentially protect against yield losses in hot conditions. The capacity to maintain a high photosynthetic rate at high temperature could aid plants in compensating for a reduction in net carbon gain resulting from an acceleration in development. Research into the relationship between leaf-level photosynthesis and yield in wheat must be explored further in order to determine the influence of photosynthetic acclimation upon grain yield, as this link has yet to be demonstrated convincingly in the field.

Reducing the respiratory costs of maintenance and growth

As outlined earlier, one way of enhancing biomass accumulation (and thus yield) is through minimizing the ratio of respiratory carbon release compared to how much CO_2 is fixed by photosynthesis. From a respiratory perspective, this could be achieved by reducing the energy demands of growth and maintenance processes, both of which are crucial components of a plant's carbon economy (Wohl and James, 1942). Growth respiration refers to the respiratory products that are utilised in the conversion of existing materials into new plant structures (Amthor, 2000). Maintenance respiration encapsulates all respiration that contributes to the turnover of pre-existing plant proteins and the preservation of ionic gradients (Penning de Vries, 1975). In the context of improving yields in wheat and other crops, one strategy is to minimize the energy costs associated with cellular maintenance, while maintaining the allocation of respiratory products to growth processes. For such a strategy to work in field conditions, consideration needs to be given to the extent to which respiratory rates vary throughout development and among organs, as well as the factors that influence the amount of respiratory ATP produced per unit CO_2 released. The response of growth and maintenance respiration to short- and long-term changes in temperature – particularly high air temperatures - also needs to be characterised.

Developmental and organ-to-organ variation in respiration

Wheat respiration varies across developmental stages, and between different plant organs. Variation in leaf respiratory rates between developmental stages is unsurprising, given that a plant's energy demands change as it progresses through its life cycle. When measuring dark respiration in glasshouse-grown winter wheat, Todd (1982) observed lower shoot and leaf respiration rates in three week-old plants in the vegetative stage when compared with individuals in the midst of reproduction. Similarly, canopy respiration of Chinese winter wheat varieties increased following stem elongation, peaked at anthesis, and then decreased as the dough stage was approached (Shuting, 1994). Pinto et al. (2017) found leaf dark respiration decreased as spring wheat moved from booting and anthesis toward the latter stages of grain filling. These findings support the notion that wheat leaf respiration varies phenologically; increasing through the vegetative stage up until anthesis, then declining in subsequent stages. This trajectory mirrors the pattern of biomass accumulation throughout the life of many seasonal crops. Ontogenetic changes in respiration also parallel changes observed in tissue composition over time. McCullough and Hunt (1993) found that, between the early vegetative stage and anthesis, stores of structural and non-structural carbohydrates increased in spring and winter wheat, while protein and lipid levels declined over the same period. Such changes in substrate supply likely contribute to the observed variation in respiratory rates throughout wheat development.

As well as varying with phenological stage, wheat respiratory rates also differ across plant organs. Given the different physiological roles of leaves, shoots, and roots, it follows that respiratory rates would differ between these tissue types. While leaf respiration appears to increase through development up to anthesis, Mitchell et al. (1991) found that shoot respiration decreased as field-grown winter wheat approached anthesis. Developmental stage and leaf organ also play a role in determining the balance between growth and maintenance respiration. As wheat approaches maturity, ear respiration effectively accounts for the entirety of above-ground plant growth respiration (Mitchell *et al.*, 1991). This is likely typical of most domesticated cereals, having been selected for high yield over thousands of years. Considering the evidence that respiration varies across wheat developmental stage and plant organ, it is probable that the effect of high temperature on net carbon balance would differ in a similar fashion. However, to date there has been little work comparing the effects of high temperature on wheat respiration across leaves, shoots, and roots, as well as across phenological stages. Whether variations in wheat respiration rates are driven predominantly by substrate supply or energy demand is likely to depend on the extent to which environmental conditions regulate photosynthesis (influencing substrate supply), and/or influence the processes that use respiratory products.

Temperature dependence of growth and maintenance respiration

Temperature is one of the most important abiotic factors that influence plant respiration (Berry and Raison, 1981). When considering growth and maintenance respiration independently, both processes are responsive to changes in temperature; however, maintenance respiration is thought to be more sensitive to temperature change than growth respiration in mature tissue (Johnson and Thornley, 1985; Slot and Kitajima, 2015a; Vos, 1981). As ambient temperature rises, so too does the rate of activity of temperature-dependent plant processes, including growth, maintenance, and ion uptake. Along with this, enzymatic reactions are accelerated, and an increase in demand for respiratory products ensues. As a result, when measured at low to optimal temperatures, respiration rate rapidly increases in response to short-term increases in temperature (Fig. 2) (Penning de Vries *et al.*, 1979). In wheat, Penning De Vries et al. (1979) observed growth respiration increased with temperature from 10 °C, before reaching a maximal rate ($T_{\max}$) at just beyond 30 °C. Following this peak, growth respiration decreased sharply in those plants experiencing long-term exposure to temperatures above 30 °C (Penning de Vries *et al.*, 1979). Penning De Vries et al. (1979) also found leaf elongation responded to temperature increases in a similar fashion, perhaps indicative of restricted cell division rates as temperatures approached 30 °C, although this possibility was not investigated. A linear relationship was observed between whole plant above-ground respiration rate and temperature when measured between 10 – 20 °C (below the temperature at which growth respiration reaches its maximum rate) (Mitchell *et al.*, 1991). A similar relationship was observed for canopy respiration in both spring and winter wheat across the range of 5 – 35 °C (McCullough and Hunt, 1993). In both instances, the rate of respiration roughly doubled with every 10 °C increase in measurement temperature. Such relationships are reflected in numerous crop growth models that include a respiratory component (Table 3). These models generally represent the relationship between plant respiration and temperature as close to the assumption of $Q_{10} = 2$ (i.e. a doubling of respiration rate with a 10 °C increase in temperature). Along with the Arrhenius approach, Q_{10} has been the most commonly used way to model the temperature response of respiration in wheat (Table 2). However, models such as these often fail to capture the complexity inherent in the temperature response of respiration, notably overlooking the fact that: (1) respiration exhibits a decelerating function as leaves warm, reflecting a declining sensitivity to higher temperatures (Heskel *et al.*, 2016; Kruse and Adams, 2008); and (2) that respiration acclimates to sustained periods of warming (Atkin and Tjoelker, 2003; Reich *et al.*, 2016; Slot and Kitajima, 2015a).

Previous studies have found increasing daily minimum temperatures to drive yield loss in wheat and other crops (Cossani and Reynolds, 2012; Mohammed and Tarpley, 2009), and it is likely that higher respiration rates contribute to this. An increased respiration rate can increase carbon loss – and therefore, reduce yield – in a number of ways. Higher rates of night-time respiratory CO_2 release could negatively daily rates of net C gain (and biomass accumulation) during vegetative growth, and thus negatively affect yield. Thus, one strategy for improving wheat yields will be to select lines with reduced rates of respiratory CO_2 release during period of warmer nights. Another factor is the production of ROS, which damage cell and organelle membranes (Narayanan *et al.*, 2015). It has been suggested that one way that plants manage ROS is to use an alternative pathway of mitochondrial electron transport, one that uncouples respiratory oxidation from ATP production (Dahal and Vanlerberghe, 2017; O'Leary *et al.*, 2018; van Aken *et al.*, 2009; Vanlerberghe, 2013). It is posited that the use of the alternative cyanide-insensitive pathway may also fulfil other roles during abiotic stress, such as synthesising carbon skeletons as sources of phosphate or to aid in osmoregulation (Del-Saz *et al.*, 2018; O'Leary *et al.*, 2018). Our knowledge of the role that the alternative pathway plays in wheat during episodes of high temperature is still developing; however, recent studies have begun to explore this area. Results suggested that the activation of the alternative pathway protects wheat seedling photosynthetic machinery following short-term exposure to 42 °C (Batjuka *et al.*, 2017), and that the alternative pathway – specifically the alternative oxidase protein – assists in the acclimation of wheat seedlings to high temperature (Borovik and Grabelnych, 2018).

Thermal acclimation of respiration – general features

As the global climate becomes more erratic and the frequency and intensity of heatwaves increase, the trait of thermal acclimation is becoming increasingly relevant. Elevated growth temperatures – particularly night-time minimums – and exposure to heatwaves may elicit greater respiratory carbon losses in plants, so the capacity to thermally acclimate respiration rate will likely be important in determining wheat productivity going forward. High temperature acclimation is dynamic, and can refer to short-term, rapid responses to heat shock, as well as longer-term responses to prolonged exposure to elevated temperature. It is believed the biochemical mechanisms that underpin rapid acclimation likely differ from those that drive gradual thermal acclimation (Atkin and Tjoelker, 2003; O'Leary *et al.*, 2018; Zhu *et al.*, 2018), although understanding of these mechanisms remains limited. Thermal acclimation of respiration is characterised by a change in $T_{\max}$, or the intercept or slope of the respiratory temperature response curve in order to compensate for a shift in growth temperature (Fig. 2; (Atkin *et al.*, 2005; Atkin and Tjoelker, 2003). It has long been assumed that leaf respiration rates double for every 10 °C rise in temperature, however thermal acclimation prevents respiration from increasing to an inefficient level and causing excessive losses of carbon when there is no corresponding demand for such a large increase in ATP (Atkin *et al.*, 2000a; Covey-Crump *et al.*, 2002). An example of this is a Reich *et al*. (2016) field study of boreal and temperate trees, in which acclimation to a 3.4 °C increase in growth temperature resulted in an 80% reduction in the observed respiration rate compared to what was expected sans acclimation.

Atkin and Tjoelker (2003) suggested that long-term respiratory acclimation can occur in one of two ways. The first is 'type I' acclimation, in which the slope (Q_{10}) of a respiratory temperature response curve changes, but the intercept of the curve remains unchanged. In a high temperature situation, this would manifest as a decrease in the Q_{10} when plants acclimate to warmer conditions. In 'type II' acclimation, the intercept of the temperature response curve is shifted, resulting in altered respiration rates at both high and low measuring temperatures (Atkin and Tjoelker, 2003). Type II acclimation may also include a change in Q_{10}, although this is not necessary for this form of acclimation. Type I acclimation is thought to be driven by changes in the respiratory substrate supply, the restriction of adenylates to leaf respiration, and/or changes in protein abundance within existing organelles (Atkin and Tjoelker, 2003). Contrastingly, type II acclimation is more likely a product of altered leaf morphology and biochemistry in newly-developed leaves, leading to a change in respiratory capacity (Atkin and Tjoelker, 2003). Around the world, plants vary in their $T_{\max}$, and those from colder biomes exhibit greater leaf respiration rates and higher intercepts of their respiratory temperature response curves in comparison to warmer biomes (Heskel *et al.*, 2016; O'Sullivan *et al.*, 2017). It has been suggested that there are no systematic differences among species in acclimating root respiration (Atkinson *et al.*, 2007), or leaf respiration and photosynthesis (Campbell *et al.*, 2007). However, Atkin et al. (2007) and Loveys et al. (2002) both found that, while whole-plant R/A ratio remained constant at moderate growth temperatures, the ratio markedly increased at high growth temperatures due to increased respiratory costs associated with ion uptake and cellular maintenance.

Accounting for variability in the temperature response of respiration

A range of factors drive variation in the shape of the temperature response of plant respiration (i.e. variations in Q_{10} values), including temperature itself (Covey-Crump *et al.*, 2002; Loveys *et al.*, 2003; O'Sullivan *et al.*, 2013), water availability (Turnbull *et al.*, 2001), light availability , and soil nutrients (Turnbull *et al.*, 2005). In wheat, the effects of drought (Liu *et al.*, 2004), elevated CO_2 (Gifford, 1995), light (McCashin *et al.*, 1988; Vos, 1981), and N supply (Vos, 1981) on respiration have been investigated. However, the temperature sensitivity and response of wheat respiration remains largely unexplored. Variation in Q_{10} values may reflect the temperature sensitivity of respiratory enzymes, or a transition from enzymatic control to limitations imposed by adenylate or substrate demands (Atkin *et al.*, 2005; Atkin and Tjoelker, 2003). Respiration tends to be limited by enzyme capacity at lower temperatures, while the availability of substrates and adenylates limit respiration at high temperatures (Atkin *et al.*, 2005). As part of the energy demand that influences respiratory flux, adenylates can control respiration rates via the energy requirements of processes such as growth, maintenance, and ion uptake (van der Werf *et al.*, 1988). Therefore, temperature-driven changes in these processes can influence the extent to which respiration is regulated by adenylates, particularly at high temperatures. In fact, Slot and Kitajima (2015b) suggested that the observed decline in Q_{10} at high temperatures likely reflects the declining carbon pool which limits further increases in respiration. Similarly, given the large scope for adjustments of respiration rate via thermal acclimation, as well as the increasing variability of the climate, crop growth models should be improved to more accurately predict productivity in a future, warmer world. Current models (Table 3) should look to incorporate more realistic representations of the high temperature response of respiration, including a plant's capacity to thermally acclimate its respiration rate. This will require extending research into the high temperature response of, and variation in, respiration rates amongst wheat varieties, on which there has been little work to date. Assuming varieties do vary in their high temperature acclimation of respiration, it is still unknown whether this trait is associated with an increase in growth or yield in heat stressed wheat. However, considering that respiration is more sensitive to increases in temperature than is photosynthesis (Way and Yamori, 2014), the ability to minimise respiratory carbon loss under high temperature would likely have a direct impact on growth and yield. By minimising respiratory carbon losses, particularly at night, the R/A ratio could be prevented from moving past the point at which the plant experiences net carbon losses induced by high temperature.

Conclusions and future directions

Despite growing awareness of the negative impacts of high temperature on both respiration and photosynthesis, as well as the continued warming of the climate, understanding of how these processes respond to high temperature in wheat remains limited. In addition, the response of wheat net carbon balance to increases in daily maximum and minimum temperature looms as a crucial, yet poorly understood area. Given that the diurnal asymmetry in climate warming favours night-time temperature rises, there is potential for increased night-time carbon loss via respiration amongst wheat lines and other major crops going forward. When combined with the possibility of increasing daily maximum temperatures leading to a reduction in carbon fixed during the day, wheat biomass accumulation will likely be compromised in a future warming climate. A better understanding of how plants protect photosynthetic processes against high temperature may contribute to maintaining net carbon gain over a 24-hour period, and ultimately productivity. However, because of the more rapid rate of increase of night time temperatures, the higher thermal sensitivity of respiration, and the previously observed links between high night temperatures and yield loss, the thermal response of leaf respiration will likely be even more influential in determining heat-induced decreases in wheat biomass accumulation. Plants with a greater capacity for respiratory acclimation to high temperature could stand to lose 1.5 times less carbon via CO_2 efflux (Atkin *et al.*, 2000b). Because of this, the ability to adjust respiratory rates in the face of supra-optimal temperatures is a highly desirable trait for future wheat varieties. Such varieties could potentially compensate for a reduced period of biomass accumulation via greater efficiency in managing net carbon balance under high temperature (i.e. maximising photosynthetic carbon gain through the day and minimising respiratory carbon losses at night). Developing new varieties that are more adept at thermally acclimating respiration and photosynthesis may therefore help to avoid the yield losses that are projected with increasing average day and night-time temperatures. In order to successfully develop varieties equipped for high temperature acclimation, identifying the extent of genetic variation that exists for these traits in wheat is a necessity.

In pursuit of this, future work must determine the extent to which wheat thermal acclimation of net carbon balance is associated with increased production in hot conditions. By identifying the biochemical mechanisms that confer chloroplast and mitochondrial heat tolerance and acclimation, we could then seek to quantify the effect of these on growth and yield. Screening large numbers of varieties for variability in acclimation potential and respiratory thermal tolerance (i.e. screening for T_{max}, see Fig. 2) will also be valuable moving forward, with genome wide association studies a potential option for understanding the genetic basis of such traits. The benefits of better thermally acclimating varieties could also be enhanced by delayed-flowering mechanisms. The combination of increasing net carbon gain over a 24-hour period with a delay in flowering time could aid plants in maximizing their resource capture, particularly when high temperatures have accelerated phenological development. Finally, incorporating this knowledge into current crop growth models would also allow for more accurate predictions of wheat productivity in a future warmer climate. The increasing volatility of the climate means that high resolution predictions of crop growth and yield will likely become more difficult. Models of greater accuracy may better inform growers about which varieties are more suited to cope with either warmer growth temperatures, or the sudden onset of heatwaves. Such models could also improve yield estimates for wheat varieties during growing seasons, including when heatwaves have been experienced, or are anticipated.

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References

Al-Khatib K, Paulsen G. 1984. Mode of high temperature injury to wheat during grain development. Physiologia Plantarum **61**, 363-368.

Alexander L, Zhang X, Peterson T, Caesar J, Gleason B, Klein Tank A, Haylock M, Collins D, Trewin B, Rahimzadeh F. 2006. Global observed changes in daily climate extremes of temperature and precipitation. Journal of Geophysical Research: Atmospheres **111**.

Allakhverdiev SI, Kreslavski VD, Klimov VV, Los DA, Carpentier R, Mohanty P. 2008. Heat stress: an overview of molecular responses in photosynthesis. Photosynthesis Research **98**, 541-550.

Amthor JS. 1989. *Respiration and crop productivity*. New York, NY: Springer-Verlag.

Amthor JS. 2000. The McCree-de Wit-Penning de Vries-Thornley respiration paradigms: 30 years later. Annals of Botany **86**, 1-20.

Asseng S, Ewert F, Martre P, Rotter RP, Lobell DB, Cammarano D, Kimball BA, Ottman MJ, Wall GW, White JW, Reynolds MP, Alderman PD, Prasad PVV, Aggarwal PK, Anothai J, Basso B, Biernath C, Challinor AJ, De Sanctis G, Doltra J, Fereres E, Garcia-Vila M, Gayler S, Hoogenboom G, Hunt LA, Izaurralde RC, Jabloun M, Jones CD, Kersebaum KC, Koehler AK, Muller C, Naresh Kumar S, Nendel C, O'Leary G, Olesen JE, Palosuo T, Priesack E, Eyshi Rezaei E, Ruane AC, Semenov MA, Shcherbak I, Stockle C, Stratonovitch P, Streck T, Supit I, Tao F, Thorburn PJ, Waha K, Wang E, Wallach D, Wolf J, Zhao Z, Zhu Y. 2015. Rising temperatures reduce global wheat production. Nature Climate Change **5**, 143-147.

Asseng S, Foster I, Turner NC. 2011. The impact of temperature variability on wheat yields. Global Change Biology **17**, 997-1012.

Atkin O, Holly C, Ball M. 2000a. Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. Plant, Cell & Environment **23**, 15-26.

Atkin O, Scheurwater I, Pons T. 2007. Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures. New Phytologist **174**, 367-380.

Atkin OK, Bruhn D, Tjoelker MG. 2005. Response of plant respiration to changes in temperature: mechanisms and consequences of variations in Q_{10} values and acclimation. In: Lambers H, Ribas-Carbo M, eds. *Plant Respiration: From Cell to Ecosystem*. Dordrecht: Springer Netherlands, 95-135.

Atkin OK, Edwards EJ, Loveys BR. 2000b. Response of root respiration to changes in temperature and its relevance to global warming. The New Phytologist **147**, 141-154.

Atkin OK, Tjoelker MG. 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. Trends in plant science **8**, 343-351.

Atkinson LJ, Hellicar MA, Fitter AH, Atkin OK. 2007. Impact of temperature on the relationship between respiration and nitrogen concentration in roots: an analysis of scaling relationships, Q_{10} values and thermal acclimation ratios. New Phytologist **173**, 110-120.

Atwell B, Kriedemann P, Turnbull C. 1999. *Plants in Action: Adaptation in Nature, Performance in Cultivation*. Melbourne, Australia: Macmillan Education Austalia Pty Ltd.

Azcón-Bieto J, Lambers H, Day DA. 1983. Effect of photosynthesis and carbohydrate status on respiratory rates and the involvement of the alternative pathway in leaf respiration. Plant Physiology **72**, 598-603.

Azcón-Bieto J, Osmond CB. 1983. Relationship between photosynthesis and respiration. The effect of carbohydrate status on the rate of CO_2 production by respiration in darkened and illuminated wheat leaves. Plant Physiology **71**, 574-581.

Baker NR, Rosenqvist E. 2004. Applications of chlorophyll fluorescence can improve crop production strategies: an examination of future possibilities. Journal of Experimental Botany **55**, 1607-1621.

Barnabás B, Jäger K, Fehér A. 2008. The effect of drought and heat stress on reproductive processes in cereals. Plant, Cell & Environment **31**, 11-38.

Batjuka A, Škute N, Petjukevičs A. 2017. The influence of antimycin A on pigment composition and functional activity of photosynthetic apparatus in *Triticum aestivum* L. under high temperature. Photosynthetica **55**, 251-263.

Berry J, Bjorkman O. 1980. Photosynthetic response and adaptation to temperature in higher plants. Annual Review of Plant Physiology **31**, 491-543.

Berry J, Raison J. 1981. Responses of macrophytes to temperature. *Physiological plant ecology I*: Springer, 277-338.

Bidinger F, Musgrave R, Fischer R. 1977. Contribution of stored pre-anthesis assimilate to grain yield in wheat and barley. Nature **270**, 431.

Bingham I, Stevenson E. 1993. Control of root growth: effects of carbohydrates on the extension, branching and rate of respiration of different fractions of wheat roots. Physiologia Plantarum **88**, 149-158.

Blum A, Klueva N, Nguyen H. 2001. Wheat cellular thermotolerance is related to yield under heat stress. Euphytica **117**, 117-123.

Blum A, Sinmena B, Mayer J, Golan G, Shpiler L. 1994. Stem reserve mobilisation supports wheat-grain filling under heat stress. Functional Plant Biology **21**, 771-781.

Borovik OA, Grabelnych OI. 2018. Mitochondrial alternative cyanide-resistant oxidase is involved in an increase of heat stress tolerance in spring wheat. Journal of plant physiology **231**, 310-317.

Brestic M, Zivcak M, Kalaji HM, Carpentier R, Allakhverdiev SI. 2012. Photosystem II thermostability *in situ*: environmentally induced acclimation and genotype-specific reactions in *Triticum aestivum* L. Plant Physiology and Biochemistry **57**, 93-105.

Bukhov NG, Wiese C, Neimanis S, Heber U. 1999. Heat sensitivity of chloroplasts and leaves: leakage of protons from thylakoids and reversible activation of cyclic electron transport. Photosynthesis Research **59**, 81-93.

Campbell C, Atkinson L, Zaragoza-Castells J, Lundmark M, Atkin O, Hurry V. 2007. Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional group. New Phytologist **176**, 375-389.

Chakrabarti B, Singh S, Kumar V, Harit R, Misra S. 2013. Growth and yield response of wheat and chickpea crops under high temperature. Indian Journal of Plant Physiology **18**, 7-14.

Challinor A, Wheeler T, Craufurd P, Slingo J. 2005. Simulation of the impact of high temperature stress on annual crop yields. Agricultural and Forest Meteorology **135**, 180-189.

Chan T, Shimizu Y, Pospíšil P, Nijo N, Fujiwara A, Taninaka Y, Ishikawa T, Hori H, Nanba D, Imai A. 2012. Quality control of photosystem II: lipid peroxidation accelerates photoinhibition under excessive illumination. PLoS ONE **7**, e52100.

Christiansen M. 1978. The physiology of plant tolerance to temperature extremes. In: Jung G, ed. *Crop tolerance to suboptimal land conditions*. Madison, WI.: ASA, 173-191.

Cossani CM, Reynolds MP. 2012. Physiological traits for improving heat tolerance in wheat. Plant Physiology **160**, 1710-1718.

Cossani CM, Reynolds MP. 2013. What physiological traits should we focus on in breeding for heat tolerance? In: Alderman PD, Quilligan E, Asseng S, Ewert F, Reynolds MP, eds. *Modeling Wheat Response to High Temperature*. CIMMYT, El Batan, Texcoco, Mexico, 24.

Covey-Crump E, Attwood R, Atkin O. 2002. Regulation of root respiration in two species of Plantago that differ in relative growth rate: the effect of short-and long-term changes in temperature. Plant, Cell & Environment **25**, 1501-1513.

Crafts-Brandner S, Law R. 2000. Effect of heat stress on the inhibition and recovery of the ribulose-1, 5-bisphosphate carboxylase/oxygenase activation state. Planta **212**, 67-74.

Crafts-Brandner SJ, Salvucci ME. 2000. Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO_2. Proceedings of the National Academy of Sciences of the United States of America **97**, 13430-13435.

CSIRO, The Bureau of Meteorology. 2018. *State of the Climate 2018*. Canberra, Australia: Australian Government.

Dahal K, Vanlerberghe GC. 2017. Alternative oxidase respiration maintains both mitochondrial and chloroplast function during drought. New Phytologist **213**, 560-571.

Davy R, Esau I, Chernokulsky A, Outten S, Zilitinkevich S. 2017. Diurnal asymmetry to the observed global warming. International Journal of Climatology **37**, 79-93.

de Vries F, Witlage J, Kremer D. 1979. Rates of respiration and of increase in structural dry matter in young wheat, ryegrass and maize plants in relation to temperature, to water stress and to their sugar content. Annals of Botany **44**, 595-609.

de Wit A, Boogaard H, Fumagalli D, Janssen S, Knapen R, van Kraalingen D, Supit I, van der Wijngaart R, van Diepen K. 2018. 25 years of the WOFOST cropping systems model. Agricultural Systems **168**, 154-167.

Del-Saz NF, Ribas-Carbo M, McDonald AE, Lambers H, Fernie AR, Florez-Sarasa I. 2018. An *in vivo* perspective of the role(s) of the alternative oxidase pathway. Trends in plant science **23**, 206-219.

Demirevska-Kepova K, Feller U. 2004. Heat sensitivity of Rubisco, Rubisco activase and Rubisco binding protein in higher plants. Acta Physiologiae Plantarum **26**, 103-114.

Dias A, Lidon F. 2009. Evaluation of grain filling rate and duration in bread and durum wheat, under heat stress after anthesis. Journal of Agronomy and Crop Science **195**, 137-147.

Dusenge ME, Duarte AG, Way DA. 2019. Plant carbon metabolism and climate change: elevated CO_2 and temperature impacts on photosynthesis, photorespiration and respiration. New Phytologist **221**, 32-49.

Enami I, Kitamura M, Tomo T, Isokawa Y, Ohta H, Katoh S. 1994. Is the primary cause of thermal inactivation of oxygen evolution in spinach PSII membranes release of the extrinsic 33 kDa protein or of Mn? Biochimica et Biophysica Acta (BBA)-Bioenergetics **1186**, 52-58.

Farooq M, Bramley H, Palta JA, Siddique KH. 2011. Heat stress in wheat during reproductive and grain-filling phases. Critical Reviews in Plant Sciences **30**, 491-507.

Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta **149**, 78-90.

Farrar J. 1985. The respiratory source of CO_2. Plant, Cell & Environment **8**, 427-438.

Farrar J, Williams M. 1991. The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. Plant, Cell & Environment **14**, 819-830.

Feller U, Crafts-Brandner SJ, Salvucci ME. 1998. Moderately high temperatures inhibit ribulose-1, 5-bisphosphate carboxylase/oxygenase (Rubisco) activase-mediated activation of Rubisco. Plant Physiology **116**, 539-546.

Feng B, Liu P, Li G, Dong S, Wang F, Kong L, Zhang J. 2014. Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. Journal of Agronomy and Crop Science **200**, 143-155.

Ferris R, Ellis R, Wheeler T, Hadley P. 1998. Effect of high temperature stress at anthesis on grain yield and biomass of field-grown crops of wheat. Annals of Botany **82**, 631-639.

Food and Agriculture Organization of the United Nations. 2018. *FAO Cereal Supply and Demand Brief*. Vol. 2018.

García GA, Dreccer MF, Miralles DJ, Serrago RA. 2015. High night temperatures during grain number determination reduce wheat and barley grain yield: a field study. Global Change Biology **21**, 4153-4164.

Gifford RM. 1995. Whole plant respiration and photosynthesis of wheat under increased CO_2 concentration and temperature: long-term vs. short-term distinctions for modelling. Global Change Biology **1**, 385-396.

Gounaris K, Brain A, Quinn P, Williams W. 1984. Structural reorganisation of chloroplast thylakoid membranes in response to heat-stress. Biochimica et Biophysica Acta (BBA)-Bioenergetics **766**, 198-208.

Hansen S, Jensen H, Nielsen N, Svendsen H. 1991. Simulation of nitrogen dynamics and biomass production in winter wheat using the Danish simulation model DAISY. Fertilizer research **27**, 245-259.

Haque MS, Kjaer KH, Rosenqvist E, Sharma DK, Ottosen C-O. 2014. Heat stress and recovery of photosystem II efficiency in wheat (*Triticum aestivum* L.) cultivars acclimated to different growth temperatures. Environmental and Experimental Botany **99**, 1-8.

Harding SA, Guikema JA, Paulsen GM. 1990. Photosynthetic decline from high temperature stress during maturation of wheat I. Interaction with senescence processes. Plant Physiology **92**, 648-653.

Hatfield JL, Prueger JH. 2015. Temperature extremes: effect on plant growth and development. Weather and Climate Extremes **10, Part A**, 4-10.

Hauben M, Haesendonckx B, Standaert E, Van Der Kelen K, Azmi A, Akpo H, Van Breusegem F, Guisez Y, Bots M, Lambert B, Laga B, De Block M. 2009. Energy use efficiency is characterized by an epigenetic component that can be directed through artificial selection to increase yield. Proceedings of the National Academy of Sciences of the United States of America **106**, 20109-20114.

Heckathorn SA, Downs CA, Sharkey TD, Coleman JS. 1998. The small, methionine-rich chloroplast heat-shock protein protects photosystem II electron transport during heat stress. Plant Physiology **116**, 439-444.

Heskel MA, O'Sullivan OS, Reich PB, Tjoelker MG, Weerasinghe LK, Penillard A, Egerton JJ, Creek D, Bloomfield KJ, Xiang J. 2016. Convergence in the temperature response of leaf respiration across biomes and plant functional types. Proceedings of the National Academy of Sciences of the United States of America **113**, 3832-3837.

Hikosaka K, Ishikawa K, Borjigidai A, Muller O, Onoda Y. 2005. Temperature acclimation of photosynthesis: mechanisms involved in the changes in temperature dependence of photosynthetic rate. Journal of Experimental Botany **57**, 291-302.

Hochman Z, Gobbett DL, Horan H. 2017. Climate trends account for stalled wheat yields in Australia since 1990. Global Change Biology, n/a-n/a.

Hoffmann AA, Chown SL, Clusella-Trullas S. 2013. Upper thermal limits in terrestrial ectotherms: how constrained are they? Functional Ecology **27**, 934-949.

Hunt JR, Hayman PT, Richards RA, Passioura JB. 2018. Opportunities to reduce heat damage in rain-fed wheat crops based on plant breeding and agronomic management. Field Crops Research **224**, 126-138.

Hurry V, Huner N. 1991. Low growth temperature effects a differential inhibition of photosynthesis in spring and winter wheat. Plant Physiology **96**, 491-497.

Hurry V, Huner N. 1992. Effect of cold hardening on sensitivity of winter and spring wheat leaves to short-term photoinhibition and recovery of photosynthesis. Plant Physiology **100**, 1283-1290.

IPCC. 2014. *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. In: R.K. P, L.A. M, eds. Geneva, Switzerland: IPCC, 151.

Johnson I, Thornley J. 1985. Temperature dependence of plant and crop process. Annals of Botany **55**, 1-24.

Knight CA, Ackerly DD. 2002. An ecological and evolutionary analysis of photosynthetic thermotolerance using the temperature-dependent increase in fluorescence. Oecologia **130**, 505-514.

Kobza J, Edwards GE. 1987. Influences of leaf temperature on photosynthetic carbon metabolism in wheat. Plant Physiology **83**, 69-74.

Kraus E, Lambers H. 2001. Leaf and root respiration of *Lolium perenne* populations selected for contrasting leaf respiration rates are affected by intra-and interpopulation interactions. Plant and Soil **231**, 267-274.

Krishnan M, Nguyen HT, Burke JJ. 1989. Heat shock protein synthesis and thermal tolerance in wheat. Plant Physiology **90**, 140-145.

Kruse J, Adams MA. 2008. Three parameters comprehensively describe the temperature response of respiratory oxygen reduction. Plant, Cell & Environment **31**, 954-967.

Kurimoto K, Day DA, Lambers H, Noguchi K. 2004. Effect of respiratory homeostasis on plant growth in cultivars of wheat and rice. Plant Cell and Environment **27**, 853-862.

Liu H-S, Li F-M, Xu H. 2004. Deficiency of water can enhance root respiration rate of drought-sensitive but not drought-tolerant spring wheat. Agricultural water management **64**, 41-48.

Liu Y, Wang E, Yang X, Wang J. 2010. Contributions of climatic and crop varietal changes to crop production in the North China Plain, since 1980s. Global Change Biology **16**, 2287-2299.

Lobell DB, Field CB. 2007. Global scale climate–crop yield relationships and the impacts of recent warming. Environmental research letters **2**, 014002.

Los DA, Murata N. 2004. Membrane fluidity and its roles in the perception of environmental signals. Biochimica et Biophysica Acta (BBA)-Biomembranes **1666**, 142-157.

Loveys B, Atkinson LJ, Sherlock D, Roberts RL, Fitter AH, Atkin OK. 2003. Thermal acclimation of leaf and root respiration: an investigation comparing inherently fast-and slow-growing plant species. Global Change Biology **9**, 895-910.

Loveys B, Scheurwater I, Pons T, Fitter A, Atkin O. 2002. Growth temperature influences the underlying components of relative growth rate: an investigation using inherently fast-and slow-growing plant species. Plant, Cell & Environment **25**, 975-988.

Machado S, Paulsen GM. 2001. Combined effects of drought and high temperature on water relations of wheat and sorghum. Plant and Soil **233**, 179-187.

Martre P, Reynolds MP, Asseng S, Ewert F, Alderman PD, Cammarano D, Maiorano A, Ruane AC, Aggarwal PK, Anothai J. 2017. The International Heat Stress Genotype Experiment for modeling wheat response to heat: field experiments and AgMIP-Wheat multi-model simulations. Open Data Journal for Agricultural Research **3**, 23-28.

Maxwell K, Johnson GN. 2000. Chlorophyll fluorescence—a practical guide. Journal of Experimental Botany **51**, 659-668.

McCaig T, Hill R. 1977. Cyanide-insensitive respiration in wheat: cultivar differences and effects of temperature, carbon dioxide, and oxygen. Canadian Journal of Botany **55**, 549-555.

McCashin BG, Cossins EA, Canvin DT. 1988. Dark respiration during photosynthesis in wheat leaf slices. Plant Physiology **87**, 155-161.

McCullough D, Hunt L. 1993. Mature tissue and crop canopy respiratory characteristics of rye, triticale and wheat. Annals of Botany **72**, 269-282.

Midmore D, Cartwright P, Fischer R. 1982. Wheat in tropical environments. I. Phasic development and spike size. Field Crops Research **5**, 185-200.

Mirschel W, Wenkel K-O. 2007. Modelling soil–crop interactions with AGROSIM model family. *Modelling water and nutrient dynamics in soil–crop systems*: Springer, 59-73.

Mitchell RA, Lawlor DW, Young AT. 1991. Dark respiration of winter wheat crops in relation to temperature and simulated photosynthesis. Annals of Botany **67**, 7-16.

Mohammed A-R, Tarpley L. 2009. Impact of high nighttime temperature on respiration, membrane stability, antioxidant capacity, and yield of rice plants. Crop Science **49**, 313-322.

Murata N, Los DA. 1997. Membrane fluidity and temperature perception. Plant Physiology **115**, 875.

Narayanan S, Prasad P, Fritz A, Boyle D, Gill B. 2015. Impact of high night-time and high daytime temperature stress on winter wheat. Journal of Agronomy and Crop Science **201**, 206-218.

Narayanan S, Tamura PJ, Roth MR, Prasad P, Welti R. 2016. Wheat leaf lipids during heat stress: I. High day and night temperatures result in major lipid alterations. Plant, Cell & Environment **39**, 787-803.

Nendel C, Berg M, Kersebaum K, Mirschel W, Specka X, Wegehenkel M, Wenkel K, Wieland R. 2011. The MONICA model: Testing predictability for crop growth, soil moisture and nitrogen dynamics. Ecological Modelling **222**, 1614-1625.

Niu Y, Xiang Y. 2018. An overview of biomembrane functions in plant responses to high-temperature stress. Frontiers in plant science **9**, 915.

Nunes-Nesi A, Carrari F, Lytovchenko A, Smith AM, Loureiro ME, Ratcliffe RG, Sweetlove LJ, Fernie AR. 2005. Enhanced photosynthetic performance and growth as a consequence of decreasing mitochondrial malate dehydrogenase activity in transgenic tomato plants. Plant Physiology **137**, 611-622.

O'Leary BM, Asao S, Millar AH, Atkin OK. 2018. Core principles which explain variation in respiration across biological scales. New Phytologist.

O'Sullivan OS, Heskel MA, Reich PB, Tjoelker MG, Weerasinghe LK, Penillard A, Zhu L, Egerton JJG, Bloomfield KJ, Creek D, Bahar NHA, Griffin KL, Hurry V, Meir P, Turnbull MH, Atkin OK. 2017. Thermal limits of leaf metabolism across biomes. Global Change Biology **23**, 209-223.

O'Sullivan OS, Weerasinghe KLK, Evans JR, Egerton JJ, Tjoelker MG, Atkin OK. 2013. High-resolution temperature responses of leaf respiration in snow gum (*Eucalyptus pauciflora*) reveal high-temperature limits to respiratory function. Plant, Cell & Environment **36**, 1268-1284.

Oquist G, Hurry V, Huner N. 1993. Low-temperature effects on photosynthesis and correlation with freezing tolerance in spring and winter cultivars of wheat and rye. Plant Physiology **101**, 245-250.

Pan R, Jones AD, Hu J. 2014. Cardiolipin-mediated mitochondrial dynamics and stress response in Arabidopsis. The Plant Cell, tpc. 113.121095.

Paradies G, Ruggiero FM, Petrosillo G, Quagliariello E. 1998. Peroxidative damage to cardiac mitochondria: cytochrome oxidase and cardiolipin alterations. FEBS letters **424**, 155-158.

Penning de Vries F. 1975. The cost of maintenance processes in plant cells. Annals of Botany **39**, 77-92.

Penning de Vries F, Witlage J, Kremer D. 1979. Rates of respiration and of increase in structural dry matter in young wheat, ryegrass and maize plants in relation to temperature, to water stress and to their sugar content. Annals of Botany **44**, 595-609.

Pinto RS, Molero G, Reynolds MP. 2017. Identification of heat tolerant wheat lines showing genetic variation in leaf respiration and other physiological traits. Euphytica **213**, 76.

Pomeroy MK, Andrews CJ. 1975. Effect of temperature on respiration of mitochondria and shoot segments from cold-hardended and nonhardened wheat and rye seedlings. Plant Physiology **56**, 703-706.

Porter JR, Gawith M. 1999. Temperatures and the growth and development of wheat: a review. European Journal of Agronomy **10**, 23-36.

Pradhan GP, Prasad PV. 2015. Evaluation of wheat chromosome translocation lines for high temperature stress tolerance at grain filling stage. PLoS ONE **10**, e0116620.

Prasad PV, Djanaguiraman M. 2014. Response of floret fertility and individual grain weight of wheat to high temperature stress: sensitive stages and thresholds for temperature and duration. Functional Plant Biology **41**, 1261-1269.

Prasad PV, Pisipati S, Ristic Z, Bukovnik U, Fritz A. 2008. Impact of nighttime temperature on physiology and growth of spring wheat. Crop Science **48**, 2372-2380.

Rahman M, Wilson J. 1978. Determination of spikelet number in wheat. III.* Effect of varying temperature on ear development. Australian Journal of Agricultural Research **29**, 459-467.

Raison JK, Chapman EA, White P. 1977. Wheat mitochondria oxidative activity and membrane lipid structure as a function of temperature. Plant Physiology **59**, 623-627.

Ray DK, Mueller ND, West PC, Foley JA. 2013. Yield trends are insufficient to double global crop production by 2050. PLoS ONE **8**, e66428.

Rebetzke G, Richards R, Sirault X, Morrison A. 2004. Genetic analysis of coleoptile length and diameter in wheat. Australian Journal of Agricultural Research **55**, 733-743.

Reich PB, Sendall KM, Stefanski A, Wei X, Rich RL, Montgomery RA. 2016. Boreal and temperate trees show strong acclimation of respiration to warming. Nature **531**, 633-636.

Reynolds M, Balota M, Delgado M, Amani I, Fischer R. 1994. Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. Functional Plant Biology **21**, 717-730.

Reynolds M, Gutiérrez-Rodríguez M, Larqué-Saavedra A. 2000. Photosynthesis of wheat in a warm, irrigated environment: I: genetic diversity and crop productivity. Field Crops Research **66**, 37-50.

Reynolds MP, Hays D, Chapman S. 2010. Breeding for adaptation to heat and drought stress. Climate change and crop production **1**, 71-91.

Ristic Z, Momčilović I, Bukovnik U, Prasad PV, Fu J, DeRidder BP, Elthon TE, Mladenov N. 2009. Rubisco activase and wheat productivity under heat-stress conditions. Journal of Experimental Botany **60**, 4003-4014.

Robinson SP, Portis AR. 1988. Release of the nocturnal inhibitor, carboxyarabinitol-1-phosphate, from ribulose bisphosphate carboxylase/oxygenase by rubisco activase. FEBS letters **233**, 413-416.

Sage RF, Kubien DS. 2007. The temperature response of C_3 and C_4 photosynthesis. Plant, Cell & Environment **30**, 1086-1106.

Saini H, Sedgley M, Aspinall D. 1983. Effect of heat stress during floral development on pollen tube growth and ovary anatomy in wheat (*Triticum aestivum* L.). Functional Plant Biology **10**, 137-144.

Salvucci ME, Crafts-Brandner SJ. 2004. Relationship between the heat tolerance of photosynthesis and the thermal stability of Rubisco activase in plants from contrasting thermal environments. Plant Physiology **134**, 1460-1470.

Scafaro AP, Atkin OK. 2016. The Impact of Heat Stress on the Proteome of Crop Species. In: Salekdeh GH, ed. *Agricultural Proteomics Volume 2: Environmental Stresses*. Cham: Springer International Publishing, 155-175.

Scafaro AP, Negrini ACA, O'Leary B, Rashid FAA, Hayes L, Fan Y, Zhang Y, Chochois V, Badger MR, Millar AH. 2017. The combination of gas-phase fluorophore technology and automation to enable high-throughput analysis of plant respiration. Plant Methods **13**, 16.

Schoolfield R, Sharpe P, Magnuson C. 1981. Non-linear regression of biological temperature-dependent rate models based on absolute reaction-rate theory. Journal of theoretical biology **88**, 719-731.

Schroda M, Vallon O, Wollman F-A, Beck CF. 1999. A chloroplast-targeted heat shock protein 70 (HSP70) contributes to the photoprotection and repair of photosystem II during and after photoinhibition. The Plant Cell **11**, 1165-1178.

Shanmugam S, Kjaer KH, Ottosen CO, Rosenqvist E, Kumari Sharma D, Wollenweber B. 2013. The Alleviating effect of elevated CO_2 on heat stress susceptibility of two wheat (*Triticum aestivum* L.) cultivars. Journal of Agronomy and Crop Science **199**, 340-350.

Sharma DK, Andersen SB, Ottosen C-O, Rosenqvist E. 2012. Phenotyping of wheat cultivars for heat tolerance using chlorophyll a fluorescence. Functional Plant Biology **39**, 936-947.

Sharma DK, Andersen SB, Ottosen CO, Rosenqvist E. 2015. Wheat cultivars selected for high Fv/Fm under heat stress maintain high photosynthesis, total chlorophyll, stomatal conductance, transpiration and dry matter. Physiologia Plantarum **153**, 284-298.

Sharma DK, Fernández JO, Rosenqvist E, Ottosen C-O, Andersen SB. 2014. Genotypic response of detached leaves versus intact plants for chlorophyll fluorescence parameters under high temperature stress in wheat. Journal of plant physiology **171**, 576-586.

Shpiler L, Blum A. 1986. Differential reaction of wheat cultivars to hot environments. Euphytica **35**, 483-492.

Shuting D. 1994. Canopy apparent photosynthesis, respiration and yield in wheat. The Journal of Agricultural Science **122**, 7-12.

Skylas D, Cordwell S, Hains P, Larsen M, Basseal D, Walsh B, Blumenthal C, Rathmell W, Copeland L, Wrigley C. 2002. Heat shock of wheat during grain filling: proteins associated with heat-tolerance. Journal of Cereal Science **35**, 175-188.

Slafer G, Rawson H. 1995. Base and optimum temperatures vary with genotype and stage of development in wheat. Plant, Cell & Environment **18**, 671-679.

Slafer GA, Rawson H. 1994. Sensitivity of wheat phasic development to major environmental factors: a re-examination of some assumptions made by physiologists and modellers. Functional Plant Biology **21**, 393-426.

Slot M, Kitajima K. 2015a. General patterns of acclimation of leaf respiration to elevated temperatures across biomes and plant types. Oecologia **177**, 885-900.

Slot M, Kitajima K. 2015b. Whole-plant respiration and its temperature sensitivity during progressive carbon starvation. Functional Plant Biology **42**, 579-588.

Stöckle CO, Donatelli M, Nelson R. 2003. CropSyst, a cropping systems simulation model. European Journal of Agronomy **18**, 289-307.

Stone P, Nicolas M. 1994. Wheat cultivars vary widely in their responses of grain yield and quality to short periods of post-anthesis heat stress. Functional Plant Biology **21**, 887-900.

Tan K, Zhou G, Ren S. 2013. Response of leaf dark respiration of winter wheat to changes in CO 2 concentration and temperature. Chinese Science Bulletin **58**, 1795-1800.

Todd GW. 1982. Photosynthesis and respiration of vegetative and reproductive parts of wheat and barley plants in response to increasing temperature. Proceedings of the Oklahoma Academy of Science **62**, 57-62.

Trösch R, Mühlhaus T, Schroda M, Willmund F. 2015. ATP-dependent molecular chaperones in plastids—More complex than expected. Biochimica et Biophysica Acta (BBA)-Bioenergetics **1847**, 872-888.

Turnbull MH, Tissue DT, Griffin KL, Richardson SJ, Peltzer DA, Whitehead D. 2005. Respiration characteristics in temperate rainforest tree species differ along a long-term soil-development chronosequence. Oecologia **143**, 271-279.

Turnbull MH, Whitehead D, Tissue DT, Schuster WS, Brown KJ, Griffin KL. 2001. Responses of leaf respiration to temperature and leaf characteristics in three deciduous tree species vary with site water availability. Tree physiology **21**, 571-578.

van Aken O, Giraud E, Clifton R, Whelan J. 2009. Alternative oxidase: a target and regulator of stress responses. Physiologia Plantarum **137**, 354-361.

van der Werf A, Kooijman A, Welschen R, Lambers H. 1988. Respiratory energy costs for the maintenance of biomass, for growth and for ion uptake in roots of *Carex diandra* and *Carex acutiformis*. Physiologia Plantarum **72**, 483-491.

van Keulen H, Penning de Vries F, Drees E. 1982. A summary model for crop growth. *Simulation of plant growth and crop production*: Pudoc, 87-97.

Vanlerberghe GC. 2013. Alternative oxidase: a mitochondrial respiratory pathway to maintain metabolic and signaling homeostasis during abiotic and biotic stress in plants. International Journal of Molecular Sciences **14**, 6805-6847.

Vierling E. 1991. The roles of heat shock proteins in plants. Annual review of plant biology **42**, 579-620.

Villegas D, Aparicio N, Blanco R, Royo C. 2001. Biomass accumulation and main stem elongation of durum wheat grown under Mediterranean conditions. Annals of Botany **88**, 617-627.

Vos J. 1981. Effects of temperature and nitrogen supply on post-floral growth of wheat: measurements and simulations, Pudoc.

Wahid A, Gelani S, Ashraf M, Foolad MR. 2007. Heat tolerance in plants: An overview. Environmental and Experimental Botany **61**, 199-223.

Wang W, Vinocur B, Shoseyov O, Altman A. 2004. Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. Trends in plant science **9**, 244-252.
Wang X, Cai J, Jiang D, Liu F, Dai T, Cao W. 2011. Pre-anthesis high-temperature acclimation alleviates damage to the flag leaf caused by post-anthesis heat stress in wheat. Journal of plant physiology **168**, 585-593.
Wardlaw I, Dawson I, Munibi P. 1989a. The tolerance of wheat to hight temperatures during reproductive growth. 2. Grain development. Crop and Pasture Science **40**, 15-24.
Wardlaw I, Dawson I, Munibi P, Fewster R. 1989b. The tolerance of wheat to high temperatures during reproductive growth. I. Survey procedures and general response patterns. Australian Journal of Agricultural Research **40**, 1-13.
Wardlaw I, Moncur L. 1995. The response of wheat to high temperature following anthesis. I. The rate and duration of kernel filling. Functional Plant Biology **22**, 391-397.
Wardlaw I, Moncur L, Patrick J. 1995. The response of wheat to high temperature following anthesis. II. Sucrose accumulation and metabolism by isolated kernels. Functional Plant Biology **22**, 399-407.
Way DA, Yamori W. 2014. Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. Photosynthesis Research **119**, 89-100.
Wheeler T, Hong T, Ellis R, Batts G, Morison J, Hadley P. 1996. The duration and rate of grain growth, and harvest index, of wheat (*Triticum aestivum* L.) in response to temperature and CO_2. Journal of Experimental Botany **47**, 623-630.
White JW. 2001. Modeling temperature response in wheat and maize. In: White JW, ed. *Modeling Temperature Response in Wheat and Maize*. El Batan, Mexico.
Wilson D, Jones JG. 1982. Effect of selection for dark respiration rate of mature leaves on crop yields of *Lolium perenne* cv. S23. Annals of Botany **49**, 313-320.
Wohl K, James W. 1942. The energy changes associated with plant respiration. New Phytologist **41**, 230-256.
Yadav DK, Pospíšil P. 2012. Role of chloride ion in hydroxyl radical production in photosystem II under heat stress: electron paramagnetic resonance spin-trapping study. Journal of bioenergetics and biomembranes **44**, 365-372.
Yamasaki T, Yamakawa T, Yamane Y, Koike H, Satoh K, Katoh S. 2002. Temperature acclimation of photosynthesis and related changes in photosystem II electron transport in winter wheat. Plant Physiology **128**, 1087-1097.
Yamori W, Hikosaka K, Way DA. 2014. Temperature response of photosynthesis in C_3, C_4, and CAM plants: temperature acclimation and temperature adaptation. Photosynthesis Research **119**, 101-117.
Yamori W, Suzuki K, Noguchi K, Nakai M, Terashima I. 2006. Effects of Rubisco kinetics and Rubisco activation state on the temperature dependence of the photosynthetic rate in spinach leaves from contrasting growth temperatures. Plant, Cell & Environment **29**, 1659-1670.
Zhao H, Dai T, Jing Q, Jiang D, Cao W. 2007. Leaf senescence and grain filling affected by post-anthesis high temperatures in two different wheat cultivars. Plant Growth Regulation **51**, 149-158.
Zheng B, Chenu K, Doherty A, Chapman S. 2014. The APSIM-Wheat module (7.5 R3008). *Agricultural Production Systems Simulator (APSIM) Initiative*.
Zhu L, Bloomfield KJ, Hocart CH, Egerton JJ, O'Sullivan OS, Penillard A, Weerasinghe LK, Atkin OK. 2018. Plasticity of photosynthetic heat tolerance in plants adapted to thermally contrasting biomes. Plant, Cell & Environment.

Table 1: Negative effects of high temperature on wheat across development stages

Developmental stage when heat treatment occurred(approximate Zadok's growth stages)^1	Temperature treatment	Key findings of effects of high temperature	Reference
Pre-anthesis			
Includes Z10 – 60	Natural warming throughout vegetative stage	Shortened pre-anthesis stage, reduced biomass at anthesis	Liu *et al.* (2010)
No stage listed – model	Increased maximum temperatures during vegetative growth (modeled)	Increased crop evapotranspiration leading to reduced soil moisture later in seasons	(Asseng *et al.*, 2011)
Z0 – 59	30/23°C for duration of vegetative growth until ear emergence	Decreased duration of vegetative, spikelet, and elongation phases, decreased number of spikelets per ear	Rahman and Wilson (1978)
Anthesis			
~Z41	30°C for 3 days	Greatly decreased grain set, reduced female fertility	Saini *et al.* (1983)
~Z61 – 91	31/20°C, from anthesis to maturity	Reduced duration of grain filling period	Dias and Lidon (2009)
~Z59 – 65	12 days, max temp +31°C	Decreased root biomass, grain number and yield	Ferris *et al.* (1998)
~Z51 – 65	5 days, 36/26°C	Decreased floret fertility	Prasad and Djanaguiraman (2014)
Post-anthesis			
~Z69 – 83	3 days, max temp 40°C	Reduced individual grain mass	Stone and Nicolas (1994)
~Z69 – 91	24/19°C or 30/25°C from anthesis to maturity	Reduced grain mass at maturity	Wardlaw and Moncur (1995)
~Z69 - 75	34/26°C for 16 days, beginning 10 days after anthesis	Reduced quantum yield of PSII, reduced individual grain mass and yield	Pradhan and Prasad (2015)
~Z69 – 91	34°C/22°C, 32°C/24°C, 26°C/14°C, and 24°C/16°C from 7 days after anthesis to maturity	Accelerated leaf senescence, reduced single grain mass, increased lipid peroxidation	Zhao *et al.* (2007)

[1] Zadok's growth stages provided are estimates based on methodology provided in respective papers. Most studies did not provide any kind of growth scoring for their plants, and estimates with large ranges of growth stage reflect this.

Table 2: Summary of past approaches used to quantify the response of wheat respiration to short-term increases in temperature.

Approach used to measure short term temperature sensitivity[1]	**Scope of the study relevant to the present review**	**Growth stage considered for measurements**	**Organ/organelle used for** respiration **measurements**	**Findings**	**Reference**
Arrhenius plots					
	To study the effect of temperature on mitochondrial and shoot segment respiration in three wheat varieties grown at 2 and 18°C	Compared germinating seedling at common morphological stage i.e. seedlings grown at 24°C for 2 days with seedlings at 2°C for 4 weeks in the dark	Shoot segments and isolated mitochondria	Respiration decreased sharply beyond the transition temperature of 6-10°C for shoot segments and 10-14°C for isolated mitochondria indicating increased activation energy (E_a) for respiration	Pomeroy and Andrews (1975)
	To explore the cyanide-insensitive respiration among wheat genotypes and the effects of temperature	Etiolated coleoptiles at 20-22°C for 3-4 days in the dark	Isolated mitochondria	Relatively linear increase in respiration increasing temperature. A distinct break noted at ~17.5 °C and alternative respiration was maximal around this point as the state of mitochondrial membrane influenced the alternative oxidase in germinating wheat. Also, respiration declined following this point partly owing to decreased solubility of oxygen when increasing temperature	McCaig and Hill (1977)

	To test whether the E_a of wheat mitochondrial oxidative activity is constant across the physiological range of temperature and to explore any phase transition in membrane lipids within this temperature range.	Germinating seedling at 24°C for 24 to 36 hours in the dark	Isolated mitochondria	The E_a for the oxidation of both succinate, α-ketoglutarate and succinate-cytochrome c oxidoreductase activity were constant across the temperature range of 3-27°C and a phase transition has been noted about 0 and 30°C for wheat membrane lipids in chilling resistant varieties being similar to their chilling sensitive counterparts.	Raison *et al.* (1977)
	To explore the effect of carbohydrate status on temperature dependence of respiration in darkened and illuminated wheat leaves	Mature leaves of 30-day-old plants grown at 25/20°C and at day length of 13 hours. Measurement temperatures began at 20°C and increased rapidly up to 42°C	Mature leaves	CO_2 efflux increased following photosynthetic activity due to carbohydrate accumulation and a dramatic change observed in the shape of respiration-temperature showing different E_a above and below 20°C.	Azcón-Bieto and Osmond (1983)
Q_{10}	The temperature coefficient of respiration in the short term	Instantaneous temperature response of respiration was measured between 14 and 27°C	Various organs including shoot, roots, stem, sheath, leaf laminae and ears	The Q_{10} remained closer to 2.2 yet varied from 1.8 to 2.4 when tested between 14-27°C. A representative Q_{10} value of 2.2 has been suggested by authors for vegetative organs of wheat irrespective of the treatment, age, organ, and temperature range.	(Vos, 1981)
	Effect of temperature on dark respiration and temperature sensitivity of wheat varieties in vegetative stage	14 hour photoperiod and measurement temperatures ranged from 5 - 35°C, with exposure for between 30 – 60 minutes.	Shoots during vegetative stage	Respiration increased when increasing temperature up to 35°C. Q_{10} was 1.89 at 15/5°C (day/night), 1.37 at 25/15°C, and 1.98 at 35/25°C. Respiration rate at 35°C was higher in vegetative stage than at reproductive stage.	(Todd, 1982)
	Effect of temperature on dark respiration and temperature sensitivity of wheat varieties in reproductive stage.	14 hour photoperiod and measurement temperatures ranged from 5 - 35°C, with	Flag leaf and spike during reproductive stage	Respiration gradually increased when increasing temperature from 5°C to 35°C. Consistently higher	(Todd, 1982)

		exposure for between 30 – 60 minutes.		respiration values than vegetative stage at same measuring temperatures. Q_{10} value decreased from 3.74 for plants at 15/5°C (day/night) to 2.04 at 35/25°C	
	Observe response of leaf dark respiration in winter wheat to natural variations in night temperature	Plants experienced ambient night-time temperature fluctuations (10 -21°C), leaf dark respiration measured at four time points throughout one night during booting stage	Mature flag leaves	From four measurements taken throughout one night, Q_{10} value was 1.977	(Tan *et al.*, 2013)
1	Measure relationship between dark respiration of shoots and ears with N, water availability, temperature, and simulated photosynthesis	Shoots measured through vegetative stage to anthesis, ears measured from anthesis to maturity.	Main shoots and ears	Although not explicitly provided by the authors, Q_{10} could be estimated from figure. Q_{10} for shoots was roughly 2; for ears, Q_{10} was approximately 2 when measured near anthesis, yet less than 2 when measured closer to maturity	(Mitchell *et al.*, 1991)[2]
Arrhenius plot and Q_{10}	Compare short and long term effects of temperature on dark respiration, its components and its relationship to the ratio of respiration to net assimilation	Plants were grown at 15, 20, 25 and 30°C and then exposed to 15, 20, 25, or 35°C for 4 hours.	Whole plants	Arrhenius coefficients of $1.2\text{x}10^6$, 46 $\text{x}10^3$, $5\text{x}10^3$, $0.3\text{x}10^3$ and Q_{10} values of 1.80, 1.59, 1.49 and 1.32 were found at 15, 20, 25, 30°C, respectively. The absolute sensitivity of specific respiration was independent of temperature across 15-25°C and then declined at 30°C	(Gifford, 1995)

[1] Q_{10}, extent of increase in respiratory rate with an increase in temperature of 10 °C; [2] the authors do not mention the term Q_{10}, but they provided results that allow for the calculation of Q_{10}

Table 3: Selection of popular crop growth models and how these models incorporate photosynthesis, respiration, and the temperature responses of each.

Model	Species modelled	Incorporation of respiration (R)	Incorporation of CO_2 assimilation (A)	Temperature responses of R & A	References
APSIM	Wheat, maize, rice, and others	When modelling transpiration demand for wheat, potential biomass accumulation is intercepted radiation minus R, divided by transpiration efficiency. Assumes R is 0.	A represented as potential biomass accumulation resulting from radiation interception, accounting for stress factors.	Includes temperature factor in models of biomass accumulation, calculated based on mean daily temperature. No temperature response of R included.	(Zheng *et al.*, 2014)
CERES-wheat	Over 42 crops (mainly annual crops such as wheat, rice, maize, and grain legumes)	R is calculated as proportional to A rather than calculated individually. It is assumed to increase exponentially with temperature up until the maximal rate is reached.	Represented as potential daily carbohydrate production, minus low temperature, water stress, and N stress.	Temperature stress component of photosynthesis calculation is based on weighted mean of daily maximum and minimum temperatures. The optimum daytime temperature for photosynthesis is considered to be 18°C.	(White, 2001)
DAISY	Spring barley, winter wheat	Respiration considered as a combination of growth respiration and temperature dependent maintenance respiration.	Daily gross canopy photosynthesis based on assumptions that gross leaf photosynthesis is described as a single light response curve, and that Beer's law describes crop canopy light distribution.	Assumes Q_{10} of maintenance respiration is 2, and therefore a constant relationship between R/T (i.e. for every 10°C increase, R doubles).	(Hansen *et al.*, 1991)
MONICA (derived from HERMES)	Wheat and eight crops	Maintenance respiration is calculated separately for day and night periods using AGROSIM algorithms.	A based on gross canopy CO_2 assimilation, consisting of light response curve of leaves, green area of canopy, leaf arrangement, and incident irradiation.	Estimations of impacts of extreme heat on growth and yield via reduction of biomass accumulation based on Challinor *et al.* (2005). Maintenance R Q_{10} = 2.	(Mirschel and Wenkel, 2007; Nendel *et al.*, 2011; van Keulen *et al.*, 1982)

WOFOST	Wheat, barley, rice, maize and others	Maintenance R calculation based on plant organ dry weight and chemical composition. Assumes maintenance R cannot outstrip gross A.	Calculation of daily gross CO_2-assimilation rate is based on absorbed radiation (incoming radiation and leaf area) and photosynthesis-light response curve of leaves. Leaf age and temperature also influence A.	Maintenance R $Q_{10} = 2$. Daily minimum temperature can reduce A, based on low temperature inhibiting transition of assimilates to structural biomass in the night.	(de Wit *et al.*, 2018)
CropSyst	Most crops (including wheat)	Has no respiration component. Daily biomass accumulation is mediated only by N, transpiration, and temperature factors.	Represents A as unstressed biomass accumulation, calculated as intercepted PAR-dependent biomass growth, which comprises of RUE, intercepted PAR.	The RUE component of A is limited by low temperature during early growth. RUE is assumed to linearly increase with increases in air temperature from base temperature for development to an optimum temperature for early growth. There are no high temperature limitations on growth.	(Stöckle *et al.*, 2003)

Abbreviations: Respiration rate, R*; photosynthetic rate,* A*; nitrogen, N; radiation use efficiency, RUE; photosynthetically active radiation, PAR;* Q_{10}*, extent of increase in respiratory rate with an increase in temperature of 1*

Box: High temperature tolerance and acclimation of photosynthesis and respiration

Box Text: Figures 1 and 2 depicts the typical temperature responses of net CO_2 assimilation (A_{net}) and leaf dark respiration (R), respectively, with a focus on what occurs at high temperatures when these processes peak (i.e. at the temperature of maximum photosynthetic rate – $T_{opt,}$ and respiration rate – T_{max})and then begin to fall. Figure 1 compares the temperature response of light-saturated A_{net} in a cold-acclimated and hot-acclimated plant. A_{net} increases with measuring temperature, until it reaches a maximum rate of assimilation (T_{opt}). A_{net} reflects the balance between photosynthetic carbon gain and photorespiratory carbon loss. Thus, T_{opt} is not necessarily an optimum temperature for photosynthetic carbon gain, but rather the point at which photosynthetic carbon gain is maximized in respect to respiratory carbon loss. Increases in temperature beyond T_{opt} result in A_{net} sharply declining. A_{net} is determined by a combination of the carboxylation rate of Rubisco (V_c), the oxygenation rate of Rubisco (V_o), and respiration in the light (R_{light}). The equation for this comes from Farquhar *et al.* (1980):

$$A_{\mathrm{net}} = V_{\mathrm{c}} - 0.5V_{\mathrm{o}} - R_{\mathrm{light}}$$

The effects of these factors on A_{net} change with temperature, as is represented in the bars below Fig. 1. The increase in A_{net} prior to reaching T_{opt} is driven by the rise in V_c outpacing that of V_o or R_{light}. However, beyond T_{opt} V_o and R_{light} begin to increase with temperature at a rate greater than that of V_c. This results in carbon loss outpacing carbon gain, and thus the observed decrease in A_{net}.

At low temperatures in light saturated conditions carbon assimilation is limited by the rate of electron transport. When temperatures approach and exceed T_{opt} the maximum rate of carboxylation by Rubisco (V_{cmax}) becomes the predominant factor limiting assimilation. Therefore, T_{opt} is partly a reflection of V_{cmax}, and so a higher T_{opt} may be indicative of a greater V_{cmax}. Applying this to Fig. 1, it is likely that the V_{cmax} of the cold-acclimated plant is greater than that of the hot-acclimated plant at temperatures below and around its T_{opt}. However, as temperatures increase beyond this point, the V_{cmax} of the hot-acclimated plant continues to increase, while that of the cold-acclimated plant falls. The difference in A_{net} at high measuring temperatures between the cold- and hot-acclimated genotypes in Fig. 1 therefore reflects the difference in V_{cmax} between the two plants. Because of the important role of Rubisco Activase (Rca) in maintaining Rubisco function at high temperatures, V_{cmax} represents the capacity of Rca to continually activate Rubisco under heat stress. The higher T_{opt} of the hot-acclimated plant in Fig. 1 suggests that it has a greater V_{cmax} at high measuring temperatures, and thus likely a greater abundance of and/or a more thermally stabile Rca.

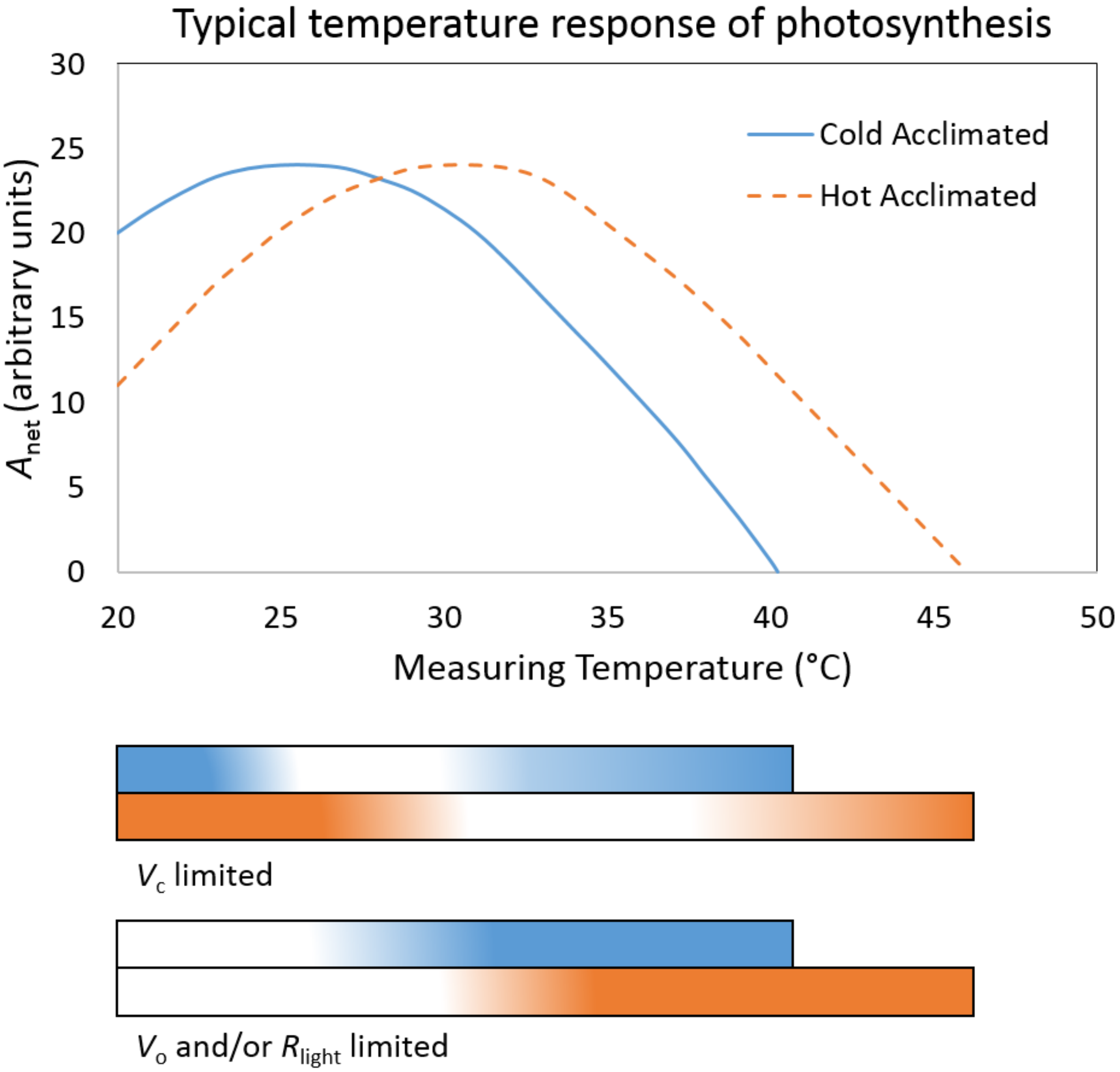
Figure 2 shows dark respiration plotted against measurement temperature for a hot acclimated and a cold acclimated plant. This figure was generated using the Schoolfield model of temperature-dependent enzyme activity (Schoolfield *et al.*, 1981). The acclimation effect observed was generated within the model by increasing the high temperature tolerance of enzyme activity and decreasing the rate of enzyme activity at 25°C in the hot-acclimated plant when compared to the cold-acclimated plant. As is the case for A_{net} in Fig. 1, respiration increases with temperature until it peaks at T_{max}, at which point respiration rate decreases with subsequent increases in temperature. The thermal acclimation of respiration can be seen when comparing the curves of the two plants at different measuring temperatures. Respiration in the hot-acclimated plant is lower than the cold-acclimated plant at lower measuring temperatures. T_{max} also occurs at a higher temperature in the hot-acclimated plant, and so respiration begins to fall at lower temperatures in the cold-acclimated plant than in the hot-acclimated one. At 30°C, R is greater in the cold-acclimated plant than the hot-acclimated one. This corresponds to what is occurring at the same temperature in Fig. 1, where A_{net} is lower in the cold-acclimated than the hot-acclimated plant. The decrease in A_{net} in the cold-acclimated plant at 30°C is likely driven in part by an increase in carbon loss via R. Similarly, the hot-acclimated plant's ability to maintain A_{net} at higher temperatures than the cold-acclimated plant is aided by a comparatively lower respiratory rate at these temperatures.

Figure Legends

Figure 1: Typical temperature response curves of net CO_2 assimilation (A_{net}) for a cold-acclimated plant (blue, solid line) and hot-acclimated plant (orange, dotted line). Bars underneath plot indicate factors limiting A_{net} as temperature increases. A_{net} is predominantly limited by Rubisco capacity (V_c) at sub-optimal temperatures and by the rates of oxygenation of Rubisco (V_o) and respiration in the light (R_{light}) at supra-optimal temperatures.

Figure 2: Typical high temperature responses of leaf dark respiration in a cold acclimated (blue solid line) and hot-acclimated (orange dashed line) plant. Figure was generated using the Schoolfield model of temperature-dependent enzyme activity (Schoolfield *et al.*, 1981). The parameters of the model that were altered to achieve the acclimation response pictured were enzyme activity (arbitrary units) at 25°C (V25) and the high temperature tolerance (in K) of enzyme activity (T_H). For the cold acclimated plant, V25 = 14, T_H = 337 K; for the hot-acclimated plant, V25 = 18, T_H = 347 K.

Figure 3: Schematic diagrams of thylakoid membrane and inner mitochondrial membrane following heat shock exposure. In both organelles, high temperature-generated reactive oxygen species damage membrane-bound proteins and inhibit electron transfer. In each case this has the effect of decreasing ATP synthesis, and contributes to the falling rates of A_{net} and R that are observed at high temperatures in Figures 1 and 2. In the case of the mitochondrial membrane, the plant can also activate an alternative pathway for oxidation when experiencing heat stress. This alternative pathway (represented by the membrane components in white – external dehydrogenase, *ED*; internal dehydrogenase, *ID*; alternative oxidase, *AOX*) uncouples ATP synthesis from oxidation by not including any of the proton pumping characteristic of Complexes III – IV. This is thought to curb the production of toxic reactive oxygen species (ROS; like $^1O_2$). The membrane also contains uncoupling proteins which serve to limit the buildup of ROS. The negative effects of ROS are also counteracted by the induction of small HSPs, which assist proteins in maintaining their structure under high temperatures.



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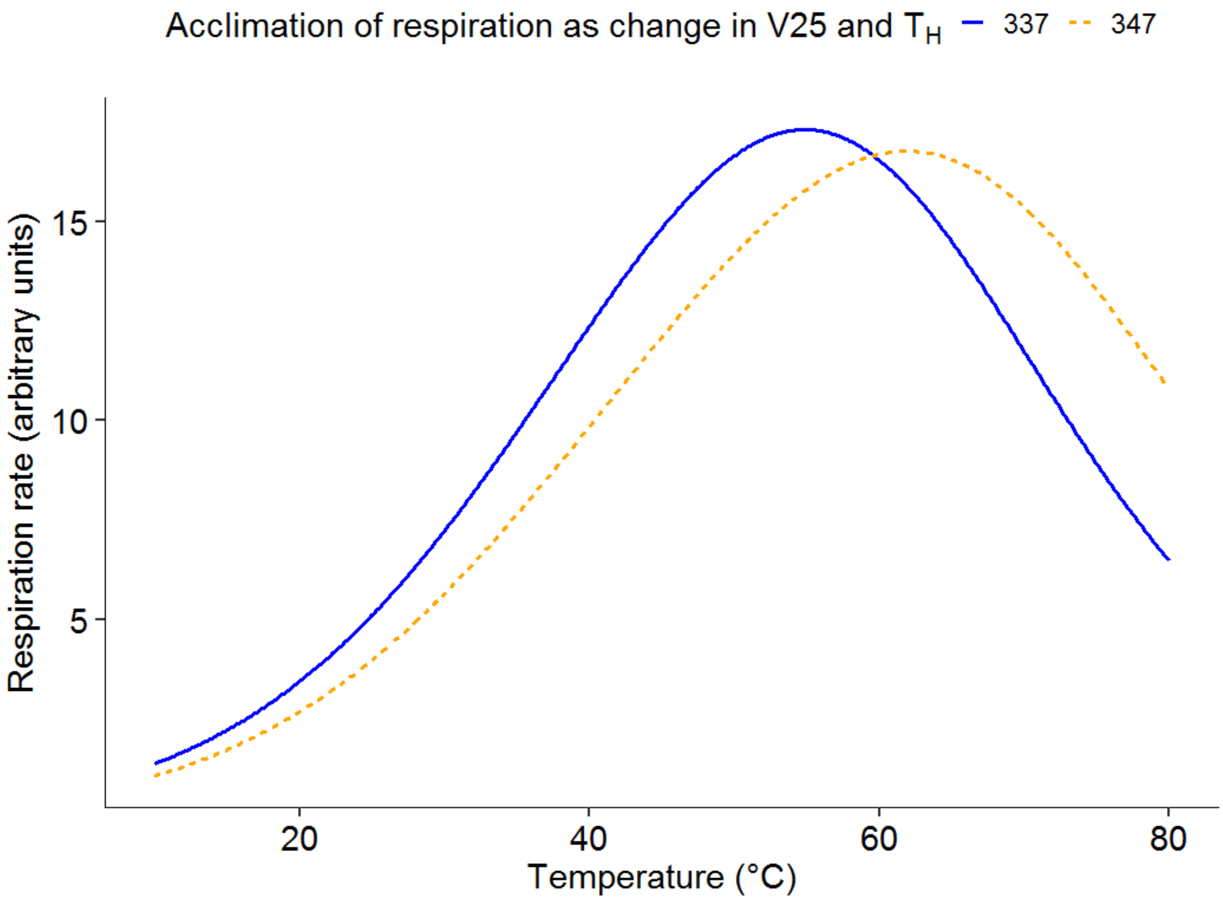

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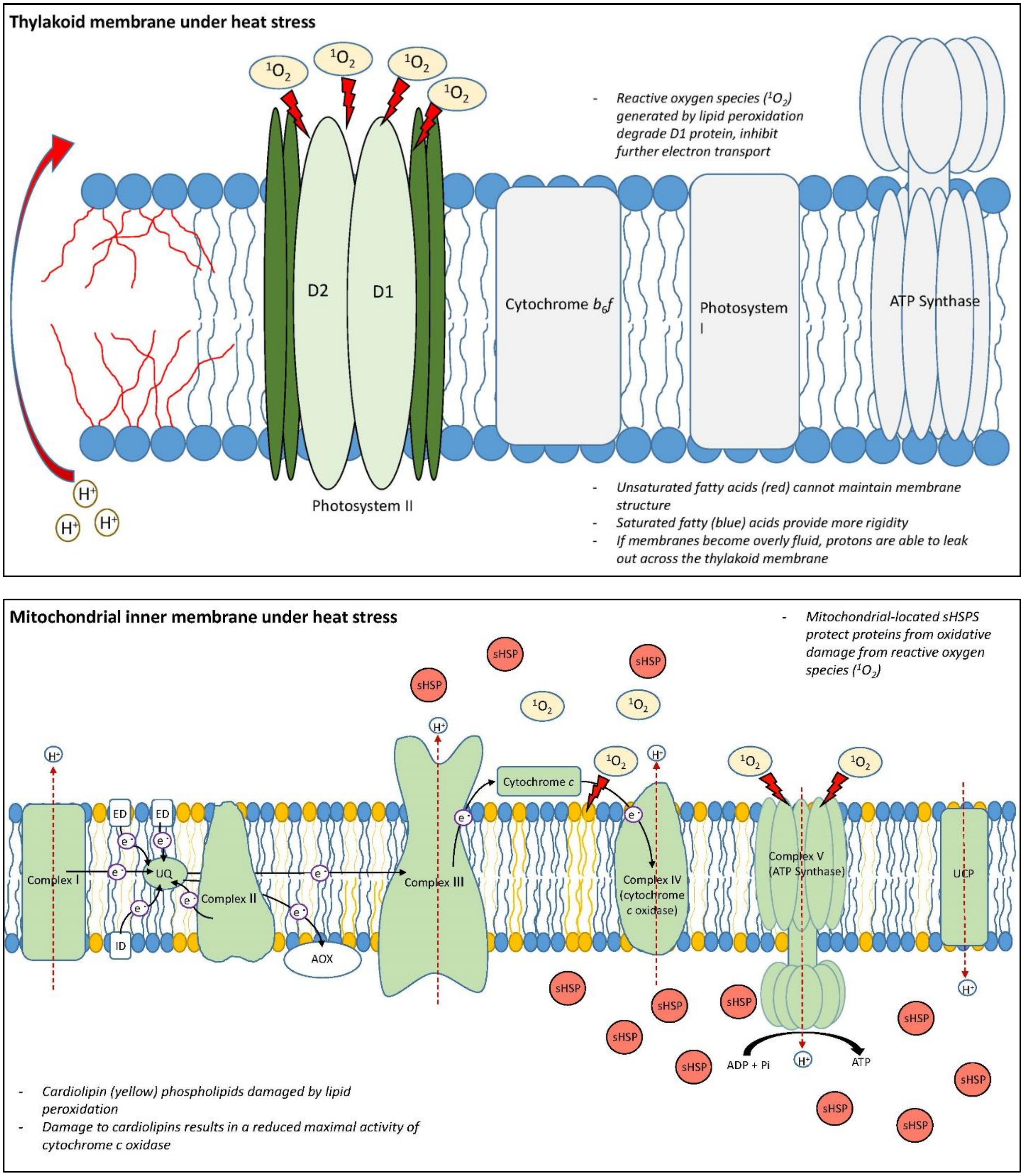

- *Reactive oxygen species ($^1O_2$) generated by lipid peroxidation degrade D1 protein, inhibit further electron transport*

- *Unsaturated fatty acids (red) cannot maintain membrane structure*
- *Saturated fatty (blue) acids provide more rigidity*
- *If membranes become overly fluid, protons are able to leak out across the thylakoid membrane*

- *Mitochondrial-located sHSPS protect proteins from oxidative damage from reactive oxygen species ($^1O_2$)*

- *Cardiolipin (yellow) phospholipids damaged by lipid peroxidation*
- *Damage to cardiolipins results in a reduced maximal activity of cytochrome c oxidase*

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