

1 **Running title: Temperature responses of photosynthesis and respiration in wheat**

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

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

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39

40 **Abstract**

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

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

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

73

74 **Introduction**

75 The warming climate presents a pressing challenge to the global economy and food
76 security, with food production required to increase by 60% to feed the growing world
77 population (Ray *et al.*, 2013). Globally, the climate has been steadily warming over the past
78 century, with the four decades from the 1970s to 2018 each warmer than their predecessor
79 (CSIRO and The Bureau of Meteorology, 2018). Under a high emission scenario, global
80 mean temperature will continue to rise by at least 4°C towards the end of this century
81 (IPCC, 2014). In addition, an increase in frequency, intensity, and durations of heatwaves is
82 predicted, as well as a diurnal asymmetry in the increase of temperatures, with mean daily
83 minimum increasing more rapidly than mean daily maximum (Davy *et al.*, 2017; García *et*
84 *al.*, 2015; Hatfield and Prueger, 2015; Lobell and Field, 2007). Considering the major role of
85 temperature in determining the rate of plant growth and development (Berry and Raison,
86 1981; Hatfield and Prueger, 2015), and that exposure to supra-optimal temperatures can
87 cause irreversible damage, and even death, in all plant species (Hoffmann *et al.*, 2013),
88 increases in average temperatures and heatwaves are a considerable concern. High
89 temperatures can cause delayed germination, disruption of metabolic processes, and
90 reproductive failure (Machado and Paulsen, 2001; Wahid *et al.*, 2007). For an economically
91 and culturally valuable crop like wheat, the effect of heat on yield is of particular
92 importance.

93 Global wheat production exceeds 700 million tonnes annually, making it one of the
94 most widely grown crops in the world (Food and Agriculture Organization of the United
95 Nations, 2018). However, increases in temperatures over recent decades have reduced
96 wheat yields in several regions worldwide, a trend that is predicted to continue (Al-Khatib
97 and Paulsen, 1984; Alexander *et al.*, 2006; Asseng *et al.*, 2015; Barnabás *et al.*, 2008). An
98 example of the global trend can be seen in Australia, where rising temperatures accounted
99 for 17% of the observed 27% decline in average wheat yield potential between 1990 and
100 2015 (Hochman *et al.*, 2017). Increases in both mean daily maximum and minimum
101 temperatures drive these high temperature-induced yield declines (Hunt *et al.*, 2018), with
102 mean daily minimum temperatures exerting a proportionally greater influence on grain
103 yields than mean daily maximums (Cossani and Reynolds, 2013; Martre *et al.*, 2017).

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

107 [Effects of high temperature on wheat vary with development](#)

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

122 Wheat yields may also be adversely impacted by high temperatures occurring
123 during developmental stages prior to and following anthesis (Porter and Gawith, 1999;
124 Skylas *et al.*, 2002; Stone and Nicolas, 1994). High temperatures occurring as early as
125 sowing can hamper both germination and seedling emergence (Rebetzke *et al.*, 2004).
126 Supra-optimal temperatures during the vegetative stage speed up development (Al-Khatib
127 and Paulsen, 1984; Asseng *et al.*, 2011; Harding *et al.*, 1990), causing plants to flower
128 earlier in the season and leaving them vulnerable to substantial frost-induced yield losses
129 (Hunt *et al.*, 2018). An acceleration of wheat development also reduces the window in
130 which to capture resources (e.g. radiation and water) (Midmore *et al.*, 1982; Shpiler and
131 Blum, 1986), thus reducing pre-anthesis biomass accumulation (Liu *et al.*, 2010). Up to
132 80% of total grain production can be drawn from carbohydrates accumulated and stored
133 prior to flowering, and so less biomass at anthesis can reduce grain number (Prasad *et al.*,

134 2008; Slafer and Rawson, 1994) and overall yield (Blum *et al.*, 1994; Villegas *et al.*, 2001).
135 Furthermore, a plant relies more heavily on stem carbohydrate reserves when
136 experiencing stresses during the grain filling stage (Bidinger *et al.*, 1977). Thus, supra-
137 optimal temperature earlier in development – prior to grain fill – will reduce the carbon
138 supply that a plant is able to draw upon to later produce grain (Blum *et al.*, 1994). Coping
139 with high temperature during vegetative growth thus requires that wheat be more efficient
140 in the processes that control net carbon balance (i.e. photosynthesis and respiration)
141 during vegetative growth. In this review, we explore what is known, and not known, about
142 the impacts of heat on these two core carbon exchange processes in wheat.

143 High temperature responses of photosynthesis and respiration

144 Photosynthesis and respiration are both temperature sensitive. Net photosynthesis (A_{net})
145 increases as leaf temperature rises, peaking at an optimum temperature (T_{opt}), before then
146 declining (see Fig. 1), reflecting the impact of temperature on photosynthetic CO₂ fixation,
147 and CO₂ release by photorespiration and mitochondrial respiration. However, following
148 sustained increases in growth temperature, most plants (including wheat) can adjust, or
149 ‘acclimate’, their photosynthetic characteristics (Berry and Bjorkman, 1980; Yamori *et al.*,
150 2014). Thermal acclimation is a process by which plants adjust metabolic rates to
151 compensate for a change in growth temperature, potentially resulting in metabolic
152 homeostasis (i.e. identical metabolic rates in contrasting thermal regimes when measured
153 *in situ*). As discussed in more detail in later sections, photosynthetic thermal acclimation
154 likely involves altered activity of the enzyme responsible for CO₂ fixation – Rubisco,
155 adjustments in electron transport through photosystem II (PSII) in chloroplasts (Yamasaki
156 *et al.*, 2002), and changes in photo-inhibition susceptibility (Hurry and Huner, 1991, 1992;
157 Oquist *et al.*, 1993). While the general temperature response of photosynthesis is well
158 studied, little is known of genotypic variation in wheat photosynthetic thermal acclimation
159 to high temperature, or of the mechanisms regulating it. This is important in the context of
160 determining wheat yield under high temperature, as optimising photosynthesis serves to
161 maximise net carbon gain in the daytime. Even less is known about the temperature-
162 response of the other component of net carbon balance, respiration.

163 Wheat leaf respiration increases in response to short-term temperature rise (de
164 Vries *et al.*, 1979), generally doubling with every 10°C increase in sub-optimal temperature
165 (Table 2, Fig. 2), with the temperature dependence of respiration likely to be primarily
166 driven by how temperature affects the processes of substrate supply (Azcón-Bieto *et al.*,
167 1983; Bingham and Stevenson, 1993) and demand for respiratory products, both locally
168 and in remote tissues (Farrar, 1985; Farrar and Williams, 1991; O'Leary *et al.*, 2018).
169 Energy demand is derived from processes such as phloem loading, protein turnover, ion
170 gradient maintenance, and other metabolic activities in leaves and roots (Vos, 1981).
171 Importantly, short-term changes in temperature have a greater effect on leaf respiration
172 than on photosynthesis (Dusenge *et al.*, 2019), a factor with important consequences for
173 leaf carbon economy. Some wheat varieties are able to thermally acclimate respiration to
174 compensate for sustained increases in growth temperature, minimising respiratory carbon
175 losses in leaves under hot growth conditions (Figure 2) (Gifford, 1995; Kurimoto *et al.*,
176 2004). In wheat, capacity to acclimate leaf respiration has also been linked to homeostasis
177 of relative growth rate with varying growth temperature (Kurimoto *et al.*, 2004). Thus, it
178 seems likely that the temperature response of leaf respiration, both over the short and
179 long-term, is central in determining wheat net carbon balance and biomass accumulation
180 following high temperature exposure. Despite this likelihood, our knowledge of the
181 connection between respiratory thermal acclimation and wheat growth and yield remains
182 limited.

183 [Scope of review](#)

184 In this review, we focus on short and long-term responses of wheat net carbon balance to
185 high temperature. Specifically, we examine the high temperature responses of wheat
186 photosynthesis and respiration, and their relationships in the context of crop production.
187 While acknowledging that the effects of high temperature on wheat can depend on the
188 presence of other stresses (abiotic and biotic) - including most notably with water stress,
189 which can cause stomatal closure and increase leaf temperature (Reynolds *et al.*, 2010) -
190 for the purposes of this review we focus solely to the effects of high-temperature. We begin
191 with considering the general mechanisms likely to underpin heat tolerance in wheat,
192 drawing on studies specific to this crop, as well as from other model systems. Thereafter,

193 we discuss the roles of photosynthesis and respiration in determining leaf level and whole-
194 plant net carbon balance. Next, we explore the response of wheat photosynthesis to short-
195 and long-term high temperature exposure, including the biochemical mechanisms
196 potentially underpinning this response. We then review factors that influence respiratory
197 costs of growth and maintenance processes, and how temperature affects these processes,
198 including changes associated with thermal acclimation of mitochondrial respiration. The
199 importance of understanding how both wheat photosynthesis and respiration will respond
200 to rising temperatures is highlighted throughout, particularly in the context of avoiding
201 major yield reductions in a rapidly warming world.

202 **Potential mechanisms underpinning heat tolerance in wheat leaves**

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

222 with biomass and yield under high temperatures in field conditions, independent of
223 drought or biotic stresses (Blum *et al.*, 2001; Reynolds *et al.*, 1994).

224 Heat shock proteins are another biochemical mechanism associated with plant
225 thermal tolerance. These proteins are induced rapidly and in large quantities following the
226 onset of heat stress, and are thought to assist other proteins to maintain functionality
227 (Vierling, 1991; Wang *et al.*, 2004). Assistance may include acting as chaperones to other
228 proteins to ensure that they are able to continue to function during bouts of high
229 temperature, as well as preventing the aggregation of misfolded proteins (Trösch *et al.*,
230 2015). Despite persisting uncertainty about how specific HSPs may confer heat tolerance in
231 wheat, studies in other species have found that they protect PSII during episodes of high
232 temperature (Heckathorn *et al.*, 1998; Schroda *et al.*, 1999). Although no direct causal
233 relationship was observed, Krishnan *et al.* (1989) found a positive correlation between
234 thermal tolerance and the expression of small HSPs in two wheat varieties differing in
235 susceptibility to heat stress. Small HSPs have also been associated with enhancing grain
236 quality (Skylas *et al.*, 2002). Further research is needed to better understand how specific
237 HSPs promote thermal tolerance in wheat, as well as the effect that the expression of these
238 proteins may have on grain yield and quality. More specifically, the role of HSPs and
239 membrane thermostability in protecting respiration and photosynthesis in wheat under
240 high temperatures remains unclear, although it is likely that they number among the
241 mechanisms that regulate the thermal tolerance of each of these processes.

242 Some of the potential biochemical explanations for heat-induced declines of
243 chloroplast and mitochondrial function are presented in Fig. 3. High temperature has the
244 effect of increasing the fluidity of cell and organelle lipid membranes, interfering with the
245 membrane's ability to regulate what is allowed to pass in and out of the cell/organelle (Fig.
246 3). Membrane damage of this kind is common to both chloroplast and mitochondrial-
247 located membranes (Niu and Xiang, 2018). In the context of the chloroplast, heat-induced
248 membrane damage results mainly from the peroxidation of lipids (particularly
249 polyunsaturated fatty acids), which interferes with the maintenance of the pH gradient
250 required for ATP synthesis (Yadav and Pospíšil, 2012). Components of the PSII complex
251 itself are also damaged by ROS under heat stress, most notably the D1 protein (Fig. 3) (Chan

252 *et al.*, 2012). Heat stress to mitochondrial membranes has a similarly negative effect on
253 ATP production. In mitochondria, this stems from the peroxidation of the phospholipid
254 cardiolipin, which in turn inhibits cytochrome c oxidase activity, thus decreasing electron
255 transport and, ultimately, ATP synthesis (Pan *et al.*, 2014; Paradies *et al.*, 1998). However,
256 by increasing the relative amount of saturated fatty acids in cellular and organelle
257 membranes, the membrane is able to preserve its optimal structure at higher
258 temperatures. This fortification of membranes at high temperature offers membrane-
259 bound electron transport greater protection from ROS, therefore enhancing the
260 thermotolerance of photosynthesis and respiration.

261 **Net carbon balance of wheat – importance of photosynthesis and respiration**

262 The net carbon balance within plants is determined by a combination of both
263 photosynthetic assimilation (A) and respiration (R). The general ratio of R/A in whole
264 plants likely ranges between 0.35 – 0.80 (when measured at a common temperature), with
265 the exact number varying based on both biotic and abiotic factors during plant growth
266 (Amthor, 2000). For wheat, maize, and rice, the ratio of R/A generally falls between 0.3 –
267 0.6 (Amthor, 1989). Even small variations in this ratio can significantly affect plant growth,
268 illustrating the importance of both A and R in determining overall productivity. The
269 response of photosynthetic and respiratory carbon exchange to temperature is crucial in
270 this respect, as R/A ratios of whole-plants typically increase with measurement
271 temperature (Gifford, 1995). This reflects the fact that respiration is typically more
272 sensitive to rising temperature than is net photosynthesis (Dusenge *et al.*, 2019). Looking
273 ahead, one strategy to improve net carbon gain of wheat, then, could be to screen
274 genotypes for variability in: (1) temperature-normalized R/A (i.e. of plants grown and
275 measured at 25°C); (2) temperature-sensitive changes in R/A values (e.g. via having a
276 lower differential in the short-term temperature sensitivity of R and A); and, (3) R/A values
277 of hot-acclimated plants, where the target is to identify genotypes with lower R/A following
278 acclimation to hot conditions.

279 A lower R/A could be achieved through improving the rate of photosynthetic CO₂
280 fixation (e.g. via increasing heat stability of Rubisco activity or improving PSII

281 functionality), reducing the energy costs associated with cellular maintenance and/or
282 biosynthesis (and thus limiting the rate of respiratory CO₂ release), and/or improving the
283 efficiency of respiratory ATP synthesis per unit of CO₂ released. There is growing evidence
284 of significant variation in net photosynthetic rate among field-grown wheat varieties
285 (Reynolds *et al.*, 2000); similarly, a recent study (Scafaro *et al.*, 2017) using a high-
286 throughput technique reported substantial genotypic variation in leaf respiration rates in
287 wheat. Together, these observations point to the probability that *R/A* does differ among
288 wheat lines. Moreover, there are reports of grain yields being higher in ryegrass, tomato
289 and canola lines that exhibit lower respiratory rates (Hauben *et al.*, 2009; Nunes-Nesi *et al.*,
290 2005; Wilson and Jones, 1982). While the stability of such traits may vary depending on
291 planting density (Kraus and Lambers, 2001), the possibility remains that variations in
292 photosynthesis and/or respiration could influence wheat yields. More work needs to be
293 done to understand how respiration influences growth and yield in wheat, how these
294 relationships may be impacted by increased temperature, and whether measurement at the
295 plant level extrapolates to field canopies. The capacity to identify varieties that maintain
296 lower respiration rates under high temperatures could be invaluable to efforts to develop
297 new wheat varieties better suited to a future climate that is increasingly warming and
298 unpredictable.

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

304 Thermal tolerance and acclimation of photosynthesis

305 Photosynthesis is a highly thermolabile process, which can be influenced or altered by high
306 temperatures in a number of ways. The basic temperature response of photosynthesis has
307 been well documented and, aside from variations based on species or biome differences, is
308 largely conserved across plant species. It generally resembles a parabolic curve, with the
309 photosynthetic rate initially increasing with temperature, before reaching a peak (T_{opt}) and

310 then declining with further temperature increases (Fig. 1) (Berry and Bjorkman, 1980).
311 This means that temperature extremes on either side of T_{opt} can inhibit photosynthesis.
312 Temperatures significantly higher than T_{opt} can result in a reduction in photosynthesis in
313 both wheat leaves and ears, which in turn impairs grain fill (Blum *et al.*, 1994). However,
314 most plants are equipped to deal with non-optimal temperatures by acclimating their
315 optimal temperature range of photosynthesis to better suit their new climate (Yamori *et al.*,
316 2014). When a plant experiences a temperature increase, acclimation allows it to become
317 more efficient at fixing carbon at elevated temperatures. Wang *et al.* (2011) investigated
318 the effects that pre-anthesis acclimation can have on photosynthetic characteristics later in
319 winter wheat development. Following two 2-day exposures to 32/28 °C (day/night) pre-
320 anthesis, plants were later exposed to further heat stress 7 days after anthesis. The plants
321 that acclimated to high temperature pre-anthesis had smaller decreases in net
322 photosynthesis, transpiration rate, and stomatal conductance in comparison to those that
323 had not experienced pre-anthesis heat exposure (Wang *et al.*, 2011). Due to the inhibition
324 of photosynthesis being directly associated with reduced yield (Scafaro and Atkin, 2016),
325 the thermal tolerance and acclimation of photosynthesis in a valuable crop like wheat is a
326 crucial area of study.

327 Rubisco activation is sensitive to moderate levels of heat stress

328 A key limiting factor of photosynthesis is the activity of the carbon-fixing protein Rubisco,
329 and more specifically, its capacity for carboxylation (Demirevska-Kepova and Feller, 2004).
330 Rubisco itself is a fairly thermostable enzyme, even in cold-adapted species (Salvucci and
331 Crafts-Brandner, 2004; Yamori *et al.*, 2006). However, Rubisco activity has been observed
332 to decline under high temperature, including in wheat (Feng *et al.*, 2014; Kobza and
333 Edwards, 1987). Crafts-Brandner and Law (2000) suggested that the adverse effect of high
334 temperature on Rubisco activation is caused by the inhibition of interactions between
335 Rubisco and the enzyme Rubisco Activase (Rca). The main function of Rca is to clear
336 Rubisco catalytic sites of sugar phosphates, allowing for more efficient activation
337 (Robinson and Portis, 1988). During an episode of high temperature, the inhibition of
338 Rubisco activation is thought to be due predominantly to the rate of Rca activity being
339 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_0 (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_0 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_0 and the

370 maximum fluorescence (F_m) is termed the variable fluorescence (F_v). The F_v/F_m ratio is
371 taken following a high intensity pulse of light that causes PSII reaction centres to close.
372 Decreases in this trait may reflect damage to PSII reaction centres or slowly relaxing
373 quenching processes (Baker and Rosenqvist, 2004). The primary role that PSII plays in the
374 electron transfer chain, along with the relative efficiency with which damage to this
375 complex can be measured, make PSII thermostability a valuable indicator of photosynthetic
376 thermal tolerance. As a result, a number of studies have employed these techniques when
377 measuring high temperature tolerance in wheat (Brestic *et al.*, 2012; Haque *et al.*, 2014;
378 Shanmugam *et al.*, 2013; Sharma *et al.*, 2012; Sharma *et al.*, 2015; Sharma *et al.*, 2014)

379 Understanding impact of high temperature on photosynthesis through modelling 380 limitations in the maximum rates of electron transport and Rubisco activity

381 Two of the main limitations of photosynthesis are the maximum rate of electron transport
382 (J_{max}), and the maximum carboxylation rate of Rubisco (V_{cmax}). These two processes
383 determine the upper limit of the photosynthetic rate, assuming there are no limitations on
384 vascular flow of water within the plant. In light saturated conditions and elevated CO₂,
385 photosynthesis may be limited by the capacity to regenerate RuBP, which reflects J_{max} (Sage
386 and Kubien, 2007). Alternatively, as temperature increases, V_{cmax} acts as the limiting factor
387 on the rate of photosynthesis (Fig. 1). As mentioned previously, J_{max} may be inhibited by
388 heat stress via damage incurred by the thermally-sensitive PSII. For V_{cmax} , temperature
389 increases between approximately 15 – 30°C lead to an exponential increase; however, a
390 rapid decline in V_{cmax} follows as temperatures continue to rise (Hikosaka *et al.*, 2005). This
391 decline in V_{cmax} is likely due to the dysfunction of Rubisco Activase, resulting in a decline in
392 Rubisco activity. The capacity to photosynthetically acclimate to high temperature in wheat
393 is likely driven by the ability to adjust V_{cmax} and J_{max} in response to increasing temperature.
394 Photosynthetic rate has been observed to correlate with leaf area index and yield
395 (Chakrabarti *et al.*, 2013), meaning that limiting high temperature-induced reductions in
396 photosynthesis and leaf area (likely symptoms of accelerated development) could
397 potentially protect against yield losses in hot conditions. The capacity to maintain a high
398 photosynthetic rate at high temperature could aid plants in compensating for a reduction in
399 net carbon gain resulting from an acceleration in development. Research into the

400 relationship between leaf-level photosynthesis and yield in wheat must be explored further
401 in order to determine the influence of photosynthetic acclimation upon grain yield, as this
402 link has yet to be demonstrated convincingly in the field.

403 [Reducing the respiratory costs of maintenance and growth](#)

404 As outlined earlier, one way of enhancing biomass accumulation (and thus yield) is through
405 minimizing the ratio of respiratory carbon release compared to how much CO₂ is fixed by
406 photosynthesis. From a respiratory perspective, this could be achieved by reducing the
407 energy demands of growth and maintenance processes, both of which are crucial
408 components of a plant's carbon economy (Wohl and James, 1942). Growth respiration
409 refers to the respiratory products that are utilised in the conversion of existing materials
410 into new plant structures (Amthor, 2000). Maintenance respiration encapsulates all
411 respiration that contributes to the turnover of pre-existing plant proteins and the
412 preservation of ionic gradients (Penning de Vries, 1975). In the context of improving yields
413 in wheat and other crops, one strategy is to minimize the energy costs associated with
414 cellular maintenance, while maintaining the allocation of respiratory products to growth
415 processes. For such a strategy to work in field conditions, consideration needs to be given
416 to the extent to which respiratory rates vary throughout development and among organs,
417 as well as the factors that influence the amount of respiratory ATP produced per unit CO₂
418 released. The response of growth and maintenance respiration to short- and long-term
419 changes in temperature – particularly high air temperatures - also needs to be
420 characterised.

421 [Developmental and organ-to-organ variation in respiration](#)

422 Wheat respiration varies across developmental stages, and between different plant organs.
423 Variation in leaf respiratory rates between developmental stages is unsurprising, given that
424 a plant's energy demands change as it progresses through its life cycle. When measuring
425 dark respiration in glasshouse-grown winter wheat, Todd (1982) observed lower shoot
426 and leaf respiration rates in three week-old plants in the vegetative stage when compared
427 with individuals in the midst of reproduction. Similarly, canopy respiration of Chinese
428 winter wheat varieties increased following stem elongation, peaked at anthesis, and then

429 decreased as the dough stage was approached (Shuting, 1994). Pinto et al. (2017) found
430 leaf dark respiration decreased as spring wheat moved from booting and anthesis toward
431 the latter stages of grain filling. These findings support the notion that wheat leaf
432 respiration varies phenologically; increasing through the vegetative stage up until anthesis,
433 then declining in subsequent stages. This trajectory mirrors the pattern of biomass
434 accumulation throughout the life of many seasonal crops. Ontogenetic changes in
435 respiration also parallel changes observed in tissue composition over time. McCullough and
436 Hunt (1993) found that, between the early vegetative stage and anthesis, stores of
437 structural and non-structural carbohydrates increased in spring and winter wheat, while
438 protein and lipid levels declined over the same period. Such changes in substrate supply
439 likely contribute to the observed variation in respiratory rates throughout wheat
440 development.

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

459 Temperature dependence of growth and maintenance respiration

460 Temperature is one of the most important abiotic factors that influence plant respiration
461 (Berry and Raison, 1981). When considering growth and maintenance respiration
462 independently, both processes are responsive to changes in temperature; however,
463 maintenance respiration is thought to be more sensitive to temperature change than
464 growth respiration in mature tissue (Johnson and Thornley, 1985; Slot and Kitajima,
465 2015a; Vos, 1981). As ambient temperature rises, so too does the rate of activity of
466 temperature-dependent plant processes, including growth, maintenance, and ion uptake.
467 Along with this, enzymatic reactions are accelerated, and an increase in demand for
468 respiratory products ensues. As a result, when measured at low to optimal temperatures,
469 respiration rate rapidly increases in response to short-term increases in temperature (Fig.
470 2) (Penning de Vries *et al.*, 1979). In wheat, Penning De Vries *et al.* (1979) observed growth
471 respiration increased with temperature from 10 °C, before reaching a maximal rate (T_{max})
472 at just beyond 30 °C. Following this peak, growth respiration decreased sharply in those
473 plants experiencing long-term exposure to temperatures above 30 °C (Penning de Vries *et al.*
474 *et al.*, 1979). Penning De Vries *et al.* (1979) also found leaf elongation responded to
475 temperature increases in a similar fashion, perhaps indicative of restricted cell division
476 rates as temperatures approached 30 °C, although this possibility was not investigated. A
477 linear relationship was observed between whole plant above-ground respiration rate and
478 temperature when measured between 10 – 20 °C (below the temperature at which growth
479 respiration reaches its maximum rate) (Mitchell *et al.*, 1991). A similar relationship was
480 observed for canopy respiration in both spring and winter wheat across the range of 5 – 35
481 °C (McCullough and Hunt, 1993). In both instances, the rate of respiration roughly doubled
482 with every 10 °C increase in measurement temperature. Such relationships are reflected in
483 numerous crop growth models that include a respiratory component (Table 3). These
484 models generally represent the relationship between plant respiration and temperature as
485 close to the assumption of $Q_{10} = 2$ (i.e. a doubling of respiration rate with a 10 °C increase in
486 temperature). Along with the Arrhenius approach, Q_{10} has been the most commonly used
487 way to model the temperature response of respiration in wheat (Table 2). However,
488 models such as these often fail to capture the complexity inherent in the temperature
489 response of respiration, notably overlooking the fact that: (1) respiration exhibits a

490 decelerating function as leaves warm, reflecting a declining sensitivity to higher
491 temperatures (Heskel *et al.*, 2016; Kruse and Adams, 2008); and (2) that respiration
492 acclimates to sustained periods of warming (Atkin and Tjoelker, 2003; Reich *et al.*, 2016;
493 Slot and Kitajima, 2015a).

494 Previous studies have found increasing daily minimum temperatures to drive yield
495 loss in wheat and other crops (Cossani and Reynolds, 2012; Mohammed and Tarpley,
496 2009), and it is likely that higher respiration rates contribute to this. An increased
497 respiration rate can increase carbon loss – and therefore, reduce yield – in a number of
498 ways. Higher rates of night-time respiratory CO₂ release could negatively daily rates of net
499 C gain (and biomass accumulation) during vegetative growth, and thus negatively affect
500 yield. Thus, one strategy for improving wheat yields will be to select lines with reduced
501 rates of respiratory CO₂ release during period of warmer nights. Another factor is the
502 production of ROS, which damage cell and organelle membranes (Narayanan *et al.*, 2015).
503 It has been suggested that one way that plants manage ROS is to use an alternative pathway
504 of mitochondrial electron transport, one that uncouples respiratory oxidation from ATP
505 production (Dahal and Vanlerberghe, 2017; O'Leary *et al.*, 2018; van Aken *et al.*, 2009;
506 Vanlerberghe, 2013). It is posited that the use of the alternative cyanide-insensitive
507 pathway may also fulfil other roles during abiotic stress, such as synthesising carbon
508 skeletons as sources of phosphate or to aid in osmoregulation (Del-Saz *et al.*, 2018; O'Leary
509 *et al.*, 2018). Our knowledge of the role that the alternative pathway plays in wheat during
510 episodes of high temperature is still developing; however, recent studies have begun to
511 explore this area. Results suggested that the activation of the alternative pathway protects
512 wheat seedling photosynthetic machinery following short-term exposure to 42 °C (Batjuka
513 *et al.*, 2017), and that the alternative pathway – specifically the alternative oxidase protein
514 – assists in the acclimation of wheat seedlings to high temperature (Borovik and
515 Gabelnych, 2018).

516 Thermal acclimation of respiration – general features

517 As the global climate becomes more erratic and the frequency and intensity of heatwaves
518 increase, the trait of thermal acclimation is becoming increasingly relevant. Elevated

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

537 Atkin and Tjoelker (2003) suggested that long-term respiratory acclimation can
538 occur in one of two ways. The first is 'type I' acclimation, in which the slope (Q_{10}) of a
539 respiratory temperature response curve changes, but the intercept of the curve remains
540 unchanged. In a high temperature situation, this would manifest as a decrease in the Q_{10}
541 when plants acclimate to warmer conditions. In 'type II' acclimation, the intercept of the
542 temperature response curve is shifted, resulting in altered respiration rates at both high
543 and low measuring temperatures (Atkin and Tjoelker, 2003). Type II acclimation may also
544 include a change in Q_{10} , although this is not necessary for this form of acclimation. Type I
545 acclimation is thought to be driven by changes in the respiratory substrate supply, the
546 restriction of adenylates to leaf respiration, and/or changes in protein abundance within
547 existing organelles (Atkin and Tjoelker, 2003). Contrastingly, type II acclimation is more
548 likely a product of altered leaf morphology and biochemistry in newly-developed leaves,

549 leading to a change in respiratory capacity (Atkin and Tjoelker, 2003). Around the world,
550 plants vary in their T_{\max} , and those from colder biomes exhibit greater leaf respiration rates
551 and higher intercepts of their respiratory temperature response curves in comparison to
552 warmer biomes (Heskel *et al.*, 2016; O'Sullivan *et al.*, 2017). It has been suggested that
553 there are no systematic differences among species in acclimating root respiration
554 (Atkinson *et al.*, 2007), or leaf respiration and photosynthesis (Campbell *et al.*, 2007).
555 However, Atkin *et al.* (2007) and Loveys *et al.* (2002) both found that, while whole-plant
556 R/A ratio remained constant at moderate growth temperatures, the ratio markedly
557 increased at high growth temperatures due to increased respiratory costs associated with
558 ion uptake and cellular maintenance.

559 Accounting for variability in the temperature response of respiration

560 A range of factors drive variation in the shape of the temperature response of plant
561 respiration (i.e. variations in Q_{10} values), including temperature itself (Covey-Crump *et al.*,
562 2002; Loveys *et al.*, 2003; O'Sullivan *et al.*, 2013), water availability (Turnbull *et al.*, 2001),
563 light availability, and soil nutrients (Turnbull *et al.*, 2005). In wheat, the effects of drought
564 (Liu *et al.*, 2004), elevated CO_2 (Gifford, 1995), light (McCashin *et al.*, 1988; Vos, 1981), and
565 N supply (Vos, 1981) on respiration have been investigated. However, the temperature
566 sensitivity and response of wheat respiration remains largely unexplored. Variation in Q_{10}
567 values may reflect the temperature sensitivity of respiratory enzymes, or a transition from
568 enzymatic control to limitations imposed by adenylate or substrate demands (Atkin *et al.*,
569 2005; Atkin and Tjoelker, 2003). Respiration tends to be limited by enzyme capacity at
570 lower temperatures, while the availability of substrates and adenylates limit respiration at
571 high temperatures (Atkin *et al.*, 2005). As part of the energy demand that influences
572 respiratory flux, adenylates can control respiration rates via the energy requirements of
573 processes such as growth, maintenance, and ion uptake (van der Werf *et al.*, 1988).
574 Therefore, temperature-driven changes in these processes can influence the extent to
575 which respiration is regulated by adenylates, particularly at high temperatures. In fact, Slot
576 and Kitajima (2015b) suggested that the observed decline in Q_{10} at high temperatures
577 likely reflects the declining carbon pool which limits further increases in respiration.
578 Similarly, given the large scope for adjustments of respiration rate via thermal acclimation,

579 as well as the increasing variability of the climate, crop growth models should be improved
580 to more accurately predict productivity in a future, warmer world. Current models (Table
581 3) should look to incorporate more realistic representations of the high temperature
582 response of respiration, including a plant's capacity to thermally acclimate its respiration
583 rate. This will require extending research into the high temperature response of, and
584 variation in, respiration rates amongst wheat varieties, on which there has been little work
585 to date. Assuming varieties do vary in their high temperature acclimation of respiration, it
586 is still unknown whether this trait is associated with an increase in growth or yield in heat
587 stressed wheat. However, considering that respiration is more sensitive to increases in
588 temperature than is photosynthesis (Way and Yamori, 2014), the ability to minimise
589 respiratory carbon loss under high temperature would likely have a direct impact on
590 growth and yield. By minimising respiratory carbon losses, particularly at night, the R/A
591 ratio could be prevented from moving past the point at which the plant experiences net
592 carbon losses induced by high temperature.

593 **Conclusions and future directions**

594 Despite growing awareness of the negative impacts of high temperature on both
595 respiration and photosynthesis, as well as the continued warming of the climate,
596 understanding of how these processes respond to high temperature in wheat remains
597 limited. In addition, the response of wheat net carbon balance to increases in daily
598 maximum and minimum temperature looms as a crucial, yet poorly understood area. Given
599 that the diurnal asymmetry in climate warming favours night-time temperature rises, there
600 is potential for increased night-time carbon loss via respiration amongst wheat lines and
601 other major crops going forward. When combined with the possibility of increasing daily
602 maximum temperatures leading to a reduction in carbon fixed during the day, wheat
603 biomass accumulation will likely be compromised in a future warming climate. A better
604 understanding of how plants protect photosynthetic processes against high temperature
605 may contribute to maintaining net carbon gain over a 24-hour period, and ultimately
606 productivity. However, because of the more rapid rate of increase of night time
607 temperatures, the higher thermal sensitivity of respiration, and the previously observed
608 links between high night temperatures and yield loss, the thermal response of leaf

609 respiration will likely be even more influential in determining heat-induced decreases in
610 wheat biomass accumulation. Plants with a greater capacity for respiratory acclimation to
611 high temperature could stand to lose 1.5 times less carbon via CO₂ efflux (Atkin *et al.*,
612 2000b). Because of this, the ability to adjust respiratory rates in the face of supra-optimal
613 temperatures is a highly desirable trait for future wheat varieties. Such varieties could
614 potentially compensate for a reduced period of biomass accumulation via greater efficiency
615 in managing net carbon balance under high temperature (i.e. maximising photosynthetic
616 carbon gain through the day and minimising respiratory carbon losses at night).
617 Developing new varieties that are more adept at thermally acclimating respiration and
618 photosynthesis may therefore help to avoid the yield losses that are projected with
619 increasing average day and night-time temperatures. In order to successfully develop
620 varieties equipped for high temperature acclimation, identifying the extent of genetic
621 variation that exists for these traits in wheat is a necessity.

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

639 onset of heatwaves. Such models could also improve yield estimates for wheat varieties
640 during growing seasons, including when heatwaves have been experienced, or are
641 anticipated.

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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
<u>Pre-anthesis</u>			
_Includes Z10 – 60	Natural warming throughout vegetative stage	Shortened pre-anthesis stage, reduced biomass at anthesis	Liu <i>et al.</i> (2010)
No stage listed – model	Increased maximum temperatures during vegetative growth (modeled)	Increased crop evapotranspiration leading to reduced soil moisture later in seasons	(Asseng <i>et al.</i> , 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)
<u>Anthesis</u>			
_~Z41	30°C for 3 days	Greatly decreased grain set, reduced female fertility	Saini <i>et al.</i> (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 <i>et al.</i> (1998)
~Z51 – 65	5 days, 36/26°C	Decreased floret fertility	Prasad and Djanaguiraman (2014)
<u>Post-anthesis</u>			
_~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 <i>et al.</i> (2007)

¹Zadok'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 sensitivity¹	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)

Q_{10}

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 <i>et al.</i> (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)
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)

	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	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 From four measurements taken throughout one night, Q_{10} value was 1.977	(Tan <i>et al.</i> , 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 <i>et al.</i> , 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 1.2×10^6 , 46×10^3 , 5×10^3 , 0.3×10^3 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 <i>et al.</i> , 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 <i>et al.</i> , 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 <i>et al.</i> (2005). Maintenance R $Q_{10} = 2$.	(Mirschel and Wenkel, 2007; Nendel <i>et al.</i> , 2011; van Keulen <i>et al.</i> , 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 <i>et al.</i> , 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 <i>et al.</i> , 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 CO₂ 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):

$$A_{\text{net}} = V_c - 0.5V_o - R_{\text{light}}$$

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 stable 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 CO₂ 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 (V_{25}) and the high temperature tolerance (in K) of enzyme activity (T_H). For the cold acclimated plant, $V_{25} = 14$, $T_H = 337$ K; for the hot-acclimated plant, $V_{25} = 18$, $T_H = 347$ 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 ¹O₂). 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.

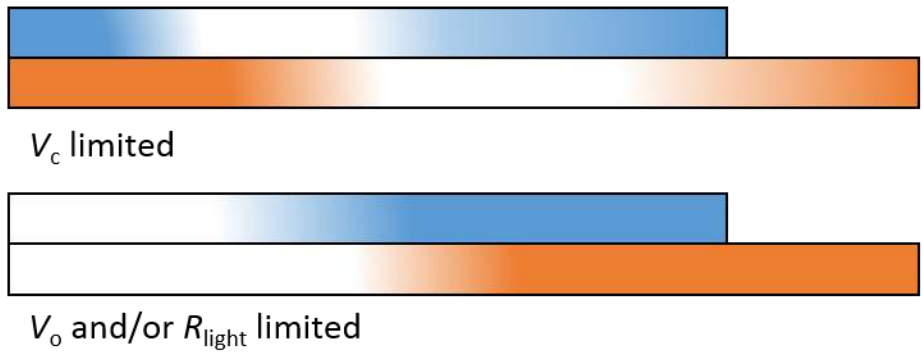
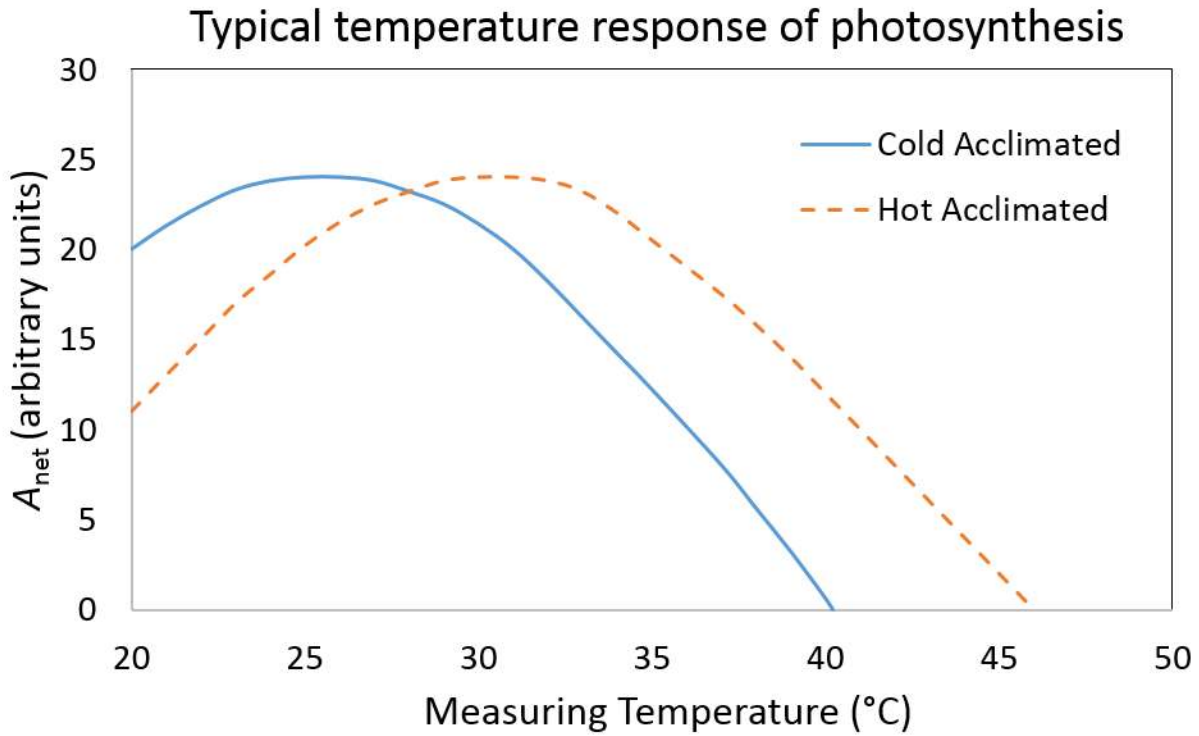


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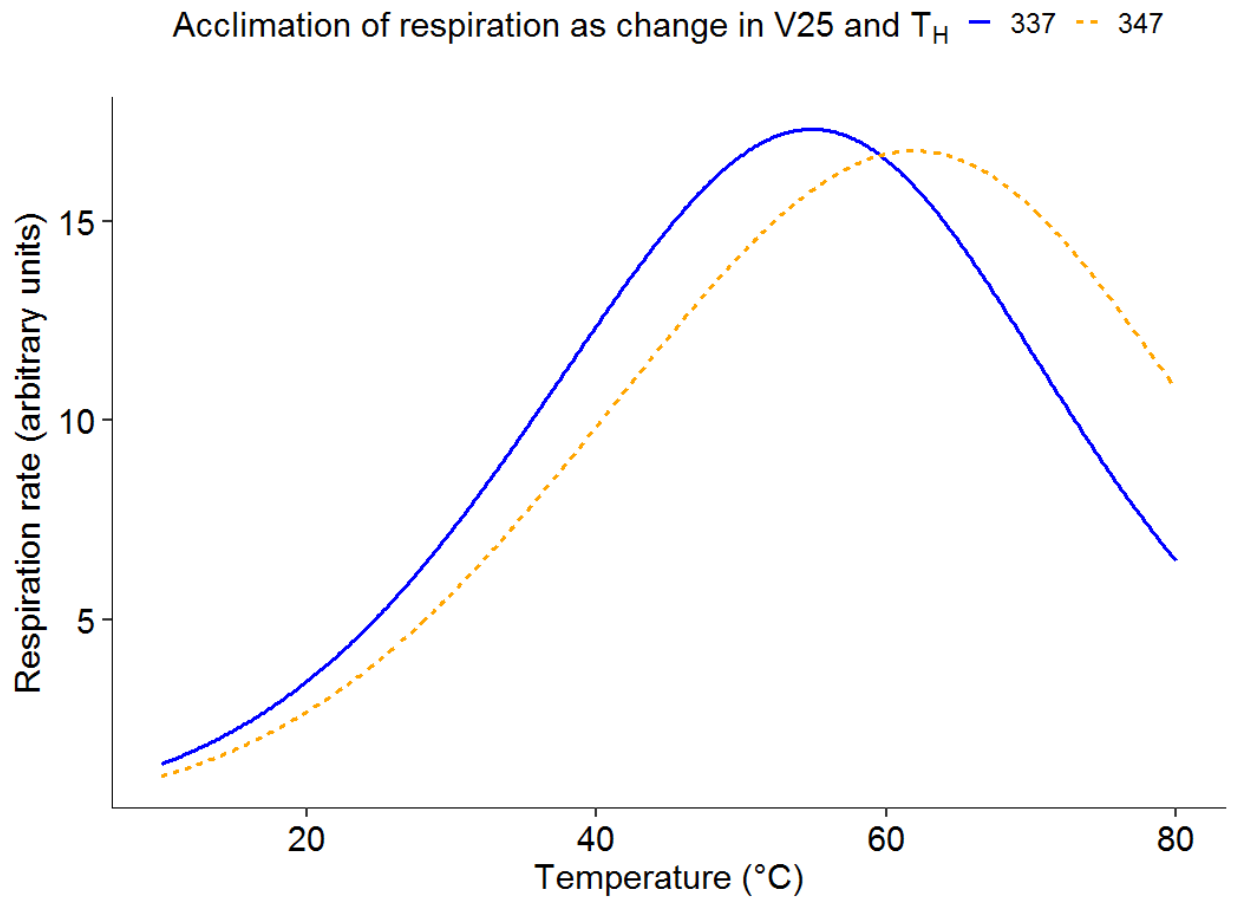


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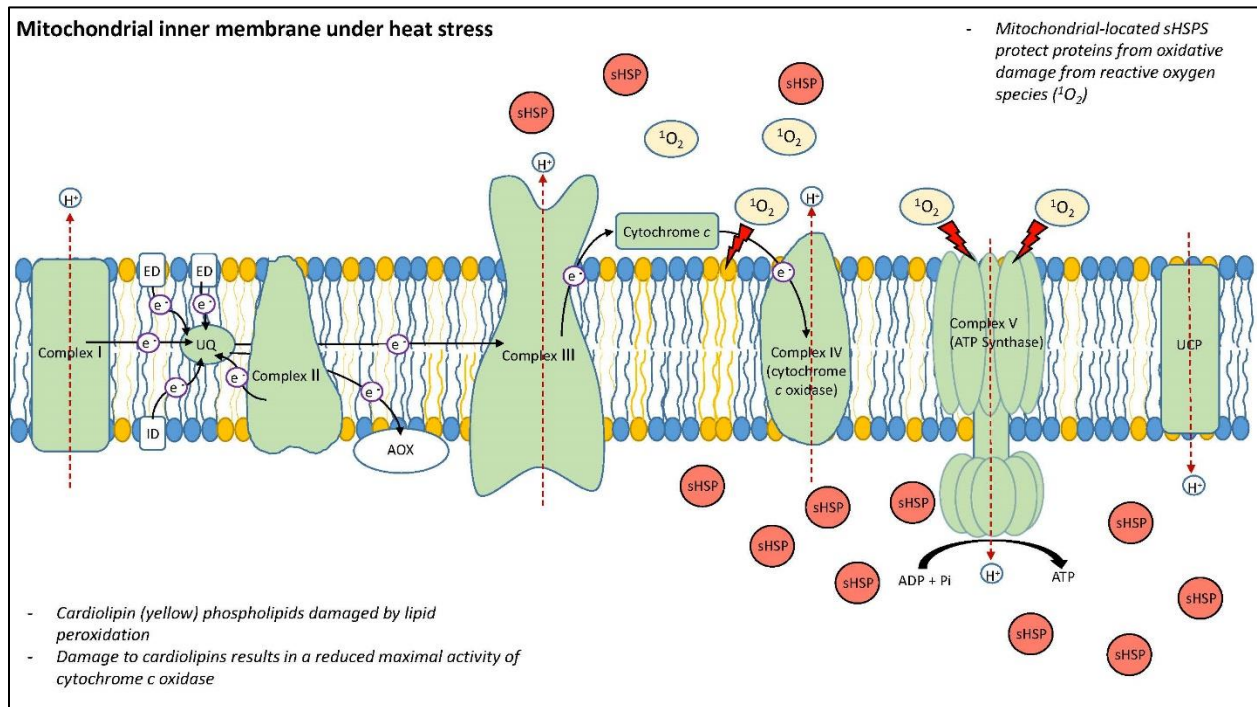
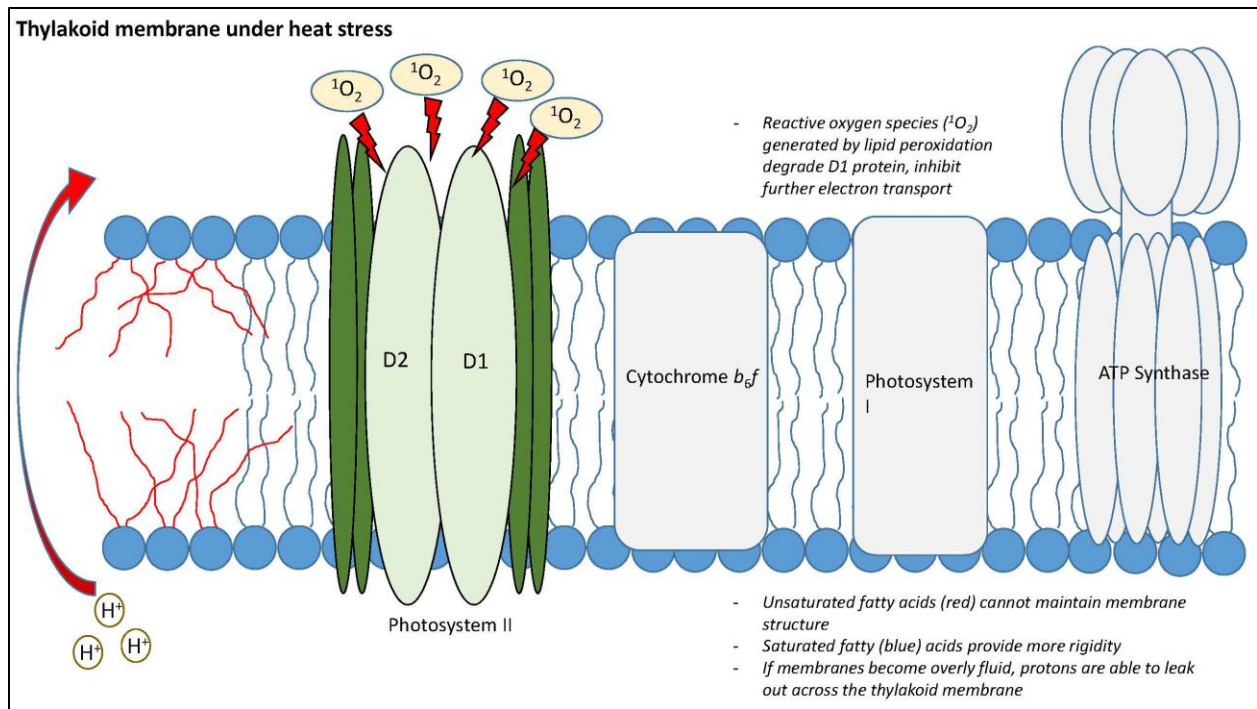


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