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REVIEW

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The potential of resilient carbon dynamics for stabilizing crop reproductive development and productivity during heat stress

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Abstract

Impaired carbon metabolism and reproductive development constrain crop productivity during heat stress. Reproductive development is energy intensive, and its requirement for respiratory substrates rises as associated metabolism increases with temperature. Understanding how these processes are integrated and the extent to which they contribute to the maintenance of yield during and following periods of elevated temperatures is important for developing climate-resilient crops. Recent studies are beginning to demonstrate links between processes underlying carbon dynamics and reproduction during heat stress, consequently a summation of research that has been reported thus far and an evaluation of purported associations are needed to guide and stimulate future research. To this end, we review recent studies relating to source–sink dynamics, non-foliar photosynthesis and net carbon gain as pivotal in understanding how to improve reproductive development and crop productivity during heat stress. Rapid and precise phenotyping during narrow phenological windows will be important for understanding mechanisms underlying these processes, thus we discuss the development of relevant high-throughput phenotyping approaches that will allow for more informed decision-making regarding future crop improvement.

KEYWORDS
carbon metabolism, photosynthesis, reproduction | respiration

1 | INTRODUCTION

The majority of processes facilitating plant growth and productivity are temperature-sensitive (Dusenge, Duarte, & Way, 2019; Jagadish, 2020; Zhang & Sharkey, 2009). Concurrently, elevated temperatures are regularly attributed to yield reductions of economically important crops (Liu, Asseng, Müller, et al., 2016; Peng et al., 2004; Tigchelaar, Battisti, Naylor, & Ray, 2018). Terrestrial surface temperatures are estimated to increase by 1–6°C by 2050, with arable areas projected to see the greatest increases (Rowlands et al., 2012). Independent estimates of temperature-derived yield reductions demonstrate that with each degree Celsius increase in temperature yields of maize, rice and wheat will, on average, be reduced by 6.0, 3.2 and 7.4%, respectively (Zhao et al., 2017).

Processes underlying photosynthesis, for example, electron transport (Ferguson et al., 2020) and Rubisco activation (Perdomo, Capó-Bauçà, Carmo-Silva, & Galmés, 2017), and reproductive development, for example, anther dehiscence (Jiang et al., 2019) and pollen tube growth (Shi et al., 2018), are sensitive to moderate-to-high temperature increases. Consequently, disruptions to these key growth and productivity determining processes underlie a substantial proportion of yield decreases during heat stress (Chaturvedi, Bahuguna, Di, Pal, & Jagadish, 2017; Prasad, Boote, Allen, Sheehy, & Thomas, 2006; Thomey, Slattery, Köhler, Bernacchi, & Ort, 2019). Numerous recent

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reviews have comprehensively assimilated current understanding of the responses of carbon dynamics (e.g. Jagadish, Kavi Kishor, Bahuguna, Von Wirén, & Sreenivasulu, 2015; Slattery & Ort, 2019; Teskey et al., 2015; Zandalinas, Mittler, Balfagón, Arbona, & Gómez-Cadenas, 2018) and reproduction (e.g. Jagadish, 2020; Ruiz-Vera, Siebers, Jaiswal, Ort, & Bernacchi, 2018; Santiago & Sharkey, 2019; Sehgal et al., 2018; Siebers et al., 2015) to heat stress in plants. However, there is a lack of summation of the link between the two. Hence, this review is aimed at summarizing demonstrated and potential links between the maintenance of carbon dynamics to stabilized reproductive development and productivity during heat stress.

Physiological responses to temperature vary according to the prevailing environment. Decreasing humidity, for example, will increase the vapour pressure deficit (VPD) of crop growing areas (Byrne & O'Gorman, 2018). By reducing stomatal conductance, altering plant water potential and thereby impairing photosynthesis, rising VPD will have interactive effects on the tolerance of high temperatures (Grossiord et al., 2020). For this review, however, we focus on heat stress in isolation to establish clarity for the physiological interactions discussed. Heat stress is broadly defined as occurring when temperatures increase beyond optimums for processes that define growth and yield (Liu, Asseng, Liu, et al., 2016; Zhang, Li, Lin, & Chong, 2019), where optimums, and therefore heat stress severity, vary according to environmental and developmental factors. For the purpose of this review, we adhere as strictly as possible to this definition of heat stress.

2 | CARBON AVAILABILITY AND REPRODUCTIVE DEVELOPMENT

Photosynthetic fixation of CO_2 and sugar transport to reproductive organs are key processes determining the success of reproductive development and therefore yield (Li, Lawas, et al., 2015). While photosynthesis does occur within floral organs, reproductive development relies heavily on foliar photosynthesis as a source of carbon (Kirichenko, Krendeleva, Kukarshikh, & Nizovskaya, 1993). Carbohydrates are produced in photosynthetic tissues and transported into the phloem and towards sinks via sugar transporters (Figure 1), for example, *SUGARS WILL EVENTUALLY BE EXPORTED TRANSPORTER* (*SWEET*) and *SUCROSE UPTAKE CARRIER/TRANSPORTER* (*SUC/SUT*) proteins. There is a strong flow of photoassimilates towards developing floral organs, as flowers facilitate the formation of an associated gradient, becoming a strong sink (Borghi & Fernie, 2017). Peaks in sink strength occur during the young pollen microspore stage and during anthesis (Cheng et al., 2015; Ji et al., 2010; Zhang et al., 2010). These reproductive stages exhibit high energy requirements, which are reflected by respiration rates that have been observed to be 10 times higher than vegetative tissues (Tadege & Kuhlemeier, 1997). An increase in ethanolic fermentation pathways is observed at all stages of pollen development to assist in meeting these demands. Tadege and Kuhlemeier (1997) demonstrated that this flux is primarily controlled by sugar supply. During early reproductive stages, the anther and pollen have the highest energy demands and are therefore the biggest sinks for sugar transport (Clément, Burrus, & Audran, 1996). For male development, these trans-located soluble sugars and starch are stored within the tapetum, which serves to regulate the sugar availability to the whole anther (Castro & Clément, 2007). The tapetum is highly metabolically active, synthesizing pollen coat components, for example, lipids, flavonoids and proteins, which are then transferred to the locule for pollen growth. These processes require an abundant supply of energy (Chen, Wu, Lin, Jane & Suen 2019; Zhang, Liang, et al. 2008). While anthers are known to be photosynthetically active (Clément & Pacini, 2001), tapetal cells have never been demonstrated to contain chloroplasts, therefore they are dependent on the trans-location of photoassimilates fixed in other tissues to act as respiratory substrates. The importance of a substantial supply of energy to this end is reflected by dramatic increases in mitochondrial numbers (20–40-fold in some cases) in tapetum cells during pollen development, especially from pollen mother cell to meiosis stage and at tetrad to young microspore stage (Chen, Guo, et al., 2019; Lee & Warmke, 1979; Parish, Phan, Iacuone, & Li, 2012). Moreover, inability of tapetal cells to utilize photosynthates as respiratory substrates due to malfunctioning mitochondria is a mechanism commonly employed for the generation of cytoplasmic male sterility (CMS) for breeding purposes (Chase, 2007; Ducos, Touzet, & Boutry, 2001; Shaya et al., 2012; Xu et al., 2008).

As well as being metabolically active (Tadege & Kuhlemeier, 1997), and requiring a lot of energy [10 times greater rates of respiration compared to vegetative cells in lily (Dickinson, 1965) and tobacco (Taylor & Hepler, 1997)], there is also a rapid build-up in carbohydrates within the anther from pollen mitosis I stage, and at pollen maturation these starch molecules degrade into soluble sugars (glucose, fructose and sucrose) to reach a maximum at anthesis (De Storme & Geelen, 2014). After pollen maturation, anthesis is a further peak in sink strength within reproduction, being highly sugar dependent as it raises the osmotic potential within the endothecium to allow bursting and pollen grain release (Wilson, Song, Taylor, & Yang, 2011). Starch accumulation continues at this point, and the build-up of starch in the pollen during the final stages of development represents an essential energy source for pollen germination and tube growth (Clément, Chavant, Burrus, & Audran, 1994; Franchi, Bellani, Nepi, & Pacini, 1996).

Pollination is also a highly energy dependent process, requiring not only energy reserves from the pollen, but also from the stigma, for successful pollen germination and tube growth towards the ovaries (Borghi & Fernie, 2017). The sink strength of the ovary has been shown to peak after fertilization and during grain-filling to allow the embryos and seeds to form successfully (Zinselmeier, Westgate, Schussler, & Jones, 1995).

All these reproductive processes have high energy requirements; thus, they are heavily dependent on the energy provided through photosynthesis. In a number of different species, it has been shown that there is a linear increase in respiration and photosynthesis to meet these higher demands for energy during reproduction, these rates either peak during anthesis or grain-filling stages, before declining as plants mature (Albrizio & Steduto, 2003; Mohammed & Tarpley, 2009). Photosynthetic capacity, and activity, has been demonstrated to be correlated with grain yield in numerous studies dating back over 50 years (Carmo-Silva

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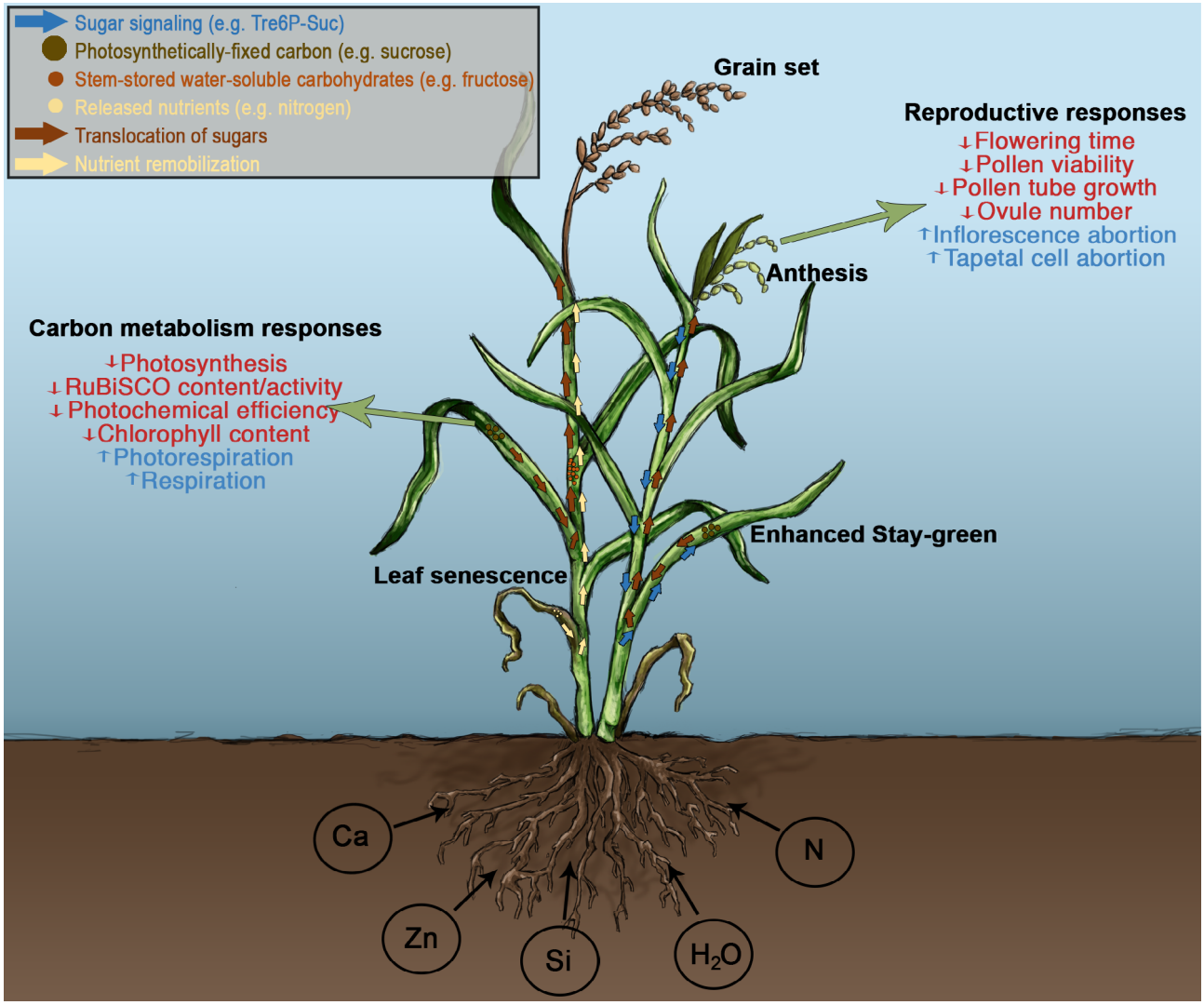

FIGURE 1 Schematic diagram highlighting the fundamental processes relating to carbon metabolism and reproductive development that are impaired by heat stress. We highlight important interactions between carbon metabolism and reproductive development that are key to affording stabilized yields during heat stress

et al., 2017; Shimshi & Ephrat, 1975; Simpson, 1968; Zhang et al., 2013). A number of studies have suggested that the availability of sugars during flowering is key to final yield (Demotes-Mainard & Jeuffroy, 2004), and inadequate availability of assimilates leads to pollen/floret death and low seed set highlighting the importance of this process (Ji et al., 2010; Kirby, 1988; Zinselmeier et al., 1995). This is further reflected by the relationship between yield and elevated atmospheric CO_2 as demonstrated by free air CO_2 enrichment experiments (Ainsworth & Long, 2005, 2020).

3 | REPRODUCTIVE SENSITIVITY TO HEAT STRESS

Particularly heat-sensitive stages of reproductive development are associated with fertility (Figure 1; Lohani, Singh, & Bhalla, 2020; Ozga, Kaur, Savada, & Reinecke, 2017; Prasad, Bheemanahalli, & Jagadish, 2017; Sage et al., 2015; Santiago & Sharkey, 2019). The meta-analysis of Prasad et al. (2017) observed that the level of damage is determined by crop sensitivity, timing of the heat stress as well as duration and intensity, where significantly higher yield losses occur during gametogenesis and flowering compared to stress exposure after flowering till maturity (Bac-Molenaar, Granier, Keurentjes, & Vreugdenhil, 2016; Espe et al., 2017; Pokharel et al., 2020).

Male reproduction has been identified as a predominant factor determining heat stress related yield losses (Jing, Wang, Zhu, & Chen, 2016; Prasad et al., 2017). Heat stress has been shown to accelerate flowering, disrupt meiosis (Endo et al., 2009) and negatively affect tapetal cell function (Ku, Yoon, Suh, & Chung, 2003; Suzuki, Takeda, Tsukaguchi, & Egawa, 2001), which cause abnormalities in the pollen exine wall (Djanaguiraman, Vara Prasad, Murugan, Perumal, & Reddy, 2014). It also leads to premature pollen development (Parish et al., 2012), reduced pollen viability and pollen germination (Djanaguiraman, Prasad, Boyle, & Schapaugh, 2013; Kaushal

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et al., 2013; Mohammed, Cothren, & Tarpley, 2013), and causes anther indehiscence (Arshad et al., 2017; Jiang et al., 2019).

Endo et al. (2009) have shown that, as well as heat responsive genes being regulated during heat stress (e.g. heat shock proteins), heat stress has also been shown to down-regulate genes associated with reproduction, such as those involved tapetum function, pollen wall development, pollen adhesion and germination during microsporogenesis. We re-analysed public transcriptomic data to query the response of genes known to regulate reproductive development and photosynthesis to heat stress in reproductive tissues (Figure 2). We observed that a number of genes involved in the tapetum and pollen development are differentially expressed during heat stress, as discussed below.

In *Arabidopsis thaliana* heat-stressed pollen (Figure 2a), we observed the up-regulation of *GAPCp1* and *CPD*, which are important for viable pollen development. The plastidial glycolytic glyceraldehyde-3-phosphate dehydrogenase (*GAPCp*) is important in the metabolic pathway to generate ATP, and mutants with this gene impaired demonstrate shrunken/collapsed pollen (Muñoz-Bertomeu et al., 2010), therefore up-regulation of this gene may reflect a response to energy requirements during heat stress. *CPD* is involved in brassinosteroid (BR) signalling, which has been shown to be important for pollen tube elongation (Szekeres et al., 1996), similarly the up-regulation of this gene may be part of a hormonal response to heat stress. BRs have been shown to be important in normal pollen development, and BR mutants have little or no male fertility, and have abnormal tapetal development and pollen exine patterns (Ye et al., 2010). The down-regulated gene *ANAPHASE-PROMOTING COMPLEX SUBUNIT 8* (*APC8*) (Figure 2a) is required for correct mitotic progression in the cell cycle. *APC8* mutants have no or just single sperm-like cells reducing both pollen viability and the ability to produce a pollen tube (Xu et al., 2019; Zheng, Chen, & McCormick, 2011). Genes involved in tapetum development are also affected as reflected by our querying of differential expression in rice panicles during heat stress (Figure 2b). Mutants in transcription factor genes *DYSFUNCTIONAL TAPETUM1 (DYT1)* and *ABORTED*

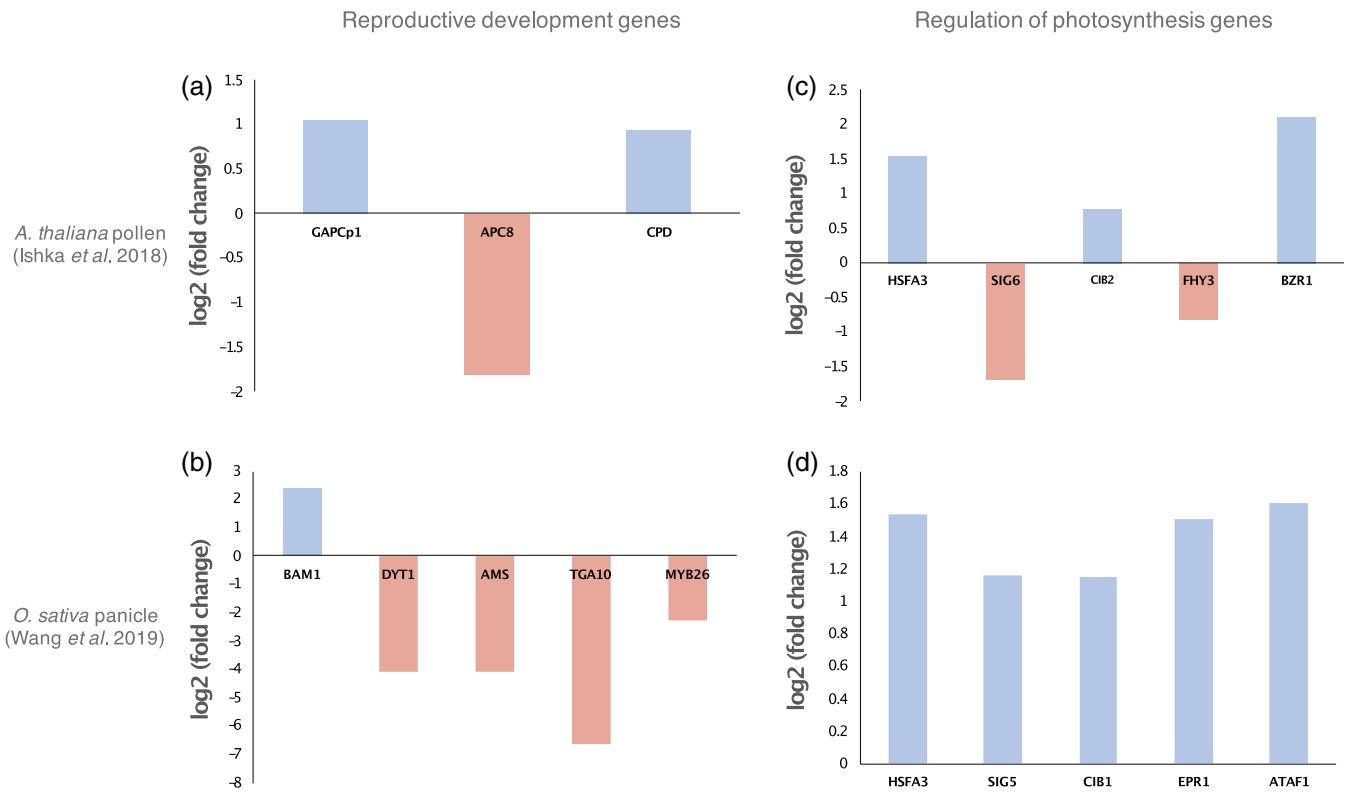

FIGURE 2 Differentially expressed genes involved in reproductive development and photosynthetic regulation in response to heat stress in reproductive tissues. Left barplots (a,b) show differential expression during heat stress of genes involved in reproductive development in *A. thaliana* pollen (Data obtained from Rahmati Ishka et al., 2018) and rice panicles respectively (Data obtained from Wang, Zhang, et al., 2019). Right barplots (c,d) show differential expression during heat stress of genes involved in photosynthesis (Wang, Hendron, & Kelly, 2017) in *A. thaliana* pollen and rice panicles from the same datasets. Full gene names: GLYCERALDEHYDE-3-PHOSPHATE DEHYDROGENASE OF PLASTID 1 (*GAPCp1*), ANAPHASE-PROMOTING COMPLEX SUBUNIT 8 (*APC8*), CONSTITUTIVE PHOTOMORPHOGENIC DWARF (*CPD*), HEAT SHOCK TRANSCRIPTION FACTOR A3 (*HSFA3*), SIGMA FACTOR 6 (*SIG6*), CRY2-INTERACTING BHLH 2 (*CIB2*), FAR-RED ELONGATED HYPOCOTYLS 3 (*FHY3*), BRASSINAZOLE-RESISTANT 1 (*BZR1*), BETA-AMYLASE 1 (*BAM1*), DYSFUNCTIONAL TAPETUM 1 (*DYT1*), ABORTED MICROSPORES (*AMS*), TGA MOTIF-BINDING PROTEIN 10 (*TGA10*), MYB PROTEIN 26 (*MYB26*), SIGMA FACTOR 5 (*SIG5*), CRY2-INTERACTING BHLH 1 (*CIB1*), EARLY-PHYTOCHROME-RESPONSIVE 1 (*EPR1*), ARABIDOPSIS NAC DOMAIN CONTAINING PROTEIN 2 (*ATAF1*) [Colour figure can be viewed at wileyonlinelibrary.com]

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MICROSPORES (AMS) are both involved in tapetal function and pollen development, with effects starting around meiosis *(DYT1/AMS*), to single microspore (*AMS*) and leading to microspore degradation (Sorensen et al., 2003; Zhang et al., 2006). In mutants of the *TGA9* and *TGA10* transcription factors, anther lobe development is affected, producing in-viable pollen grains and preventing anther dehiscence through disruptions to lignification and septum/stomium function (Murmu et al., 2010). The *MYB26/MALE STERILE35* (*MYB35*) gene is also involved in anther dehiscence and associated mutants have disrupted endothecium lignification that causes indehiscence (Yang et al., 2007). *BARELY ANY MERISTEM* (*BAM1*), however, was shown to be up-regulated and it is involved in very early anther development and promoting somatic cell fates and therefore the formation of anther layers and microspores (Hord, Chen, DeYoung, Clark, & Ma, 2006). This up-regulation may reflect the frequently observed changes in flowering time with heat-stressed plants showing accelerated flowering processes.

4 | PHOTOSYNTHETIC SENSITIVITY TO HEAT STRESS

Photosynthesis is also sensitive to high temperatures (as reviewed by: Hu, Ding, & Zhu, 2020). Photosynthesis is reduced via impairments to photosystem II (PSII), electron transport rate and Rubisco activase (Figure 1; Djanaguiraman et al., 2014; Guo, Zhou, & Zhang, 2006; Kaushal et al., 2013; Prasad & Djanaguiraman, 2011; Snider et al., 2009), as well as via direct damage to thylakoid membranes (Pokharel et al., 2020; Prasad, Pisipati, Ristic, Bukovnik, & Fritz, 2008). PSII is the most heat-sensitive component of photosynthetic biochemistry (Hu et al., 2020), as such reduced PSII activity is often the most common determiner of reduced photosynthesis (Tang et al., 2007). For this reason, chlorophyll fluorescence techniques are often employed to benchmark heat tolerance (Ferguson et al., 2020; Sharma, Andersen, Ottosen, & Rosenqvist, 2015; Sharma, Torp, Rosenqvist, Ottosen, & Andersen, 2017). High temperatures have also been shown to negatively affect the balance between photosynthesis and photorespiration, which in turn reduces the overall carbohydrate pool and ultimately yield (Prasad et al., 2017). The importance of photorespiration to this end has been relatively understudied, as such we highlight it below as a unique constraint and target for improving heat tolerance.

Photorespiration detoxifies glycolate and recycles the majority of the constituent carbon back into the photosynthetic cycle – the remaining carbon (~25%) is lost as CO_2 (Foyer, Bloom, Queval, & Noctor, 2009; Walker, Vanloocke, Bernacchi, & Ort, 2016). With respect to heat stress, there are two important considerations to make here. As temperatures increases, CO_2 solubility decreases more rapidly than O_2 solubility (Ku & Edwards, 1977) and Rubisco specificity for CO_2 compared to O_2 declines (Jordan & Ogren, 1984). Consequently, photorespiration increases under heat stress, because Rubisco oxygenation is less restricted and O_2 is more readily available (Walker et al., 2016). This limits the production of carbohydrates, which are in high demand due to increasing rates of mitochondrial respiration, especially during reproductive development. Consequently, bypassing photorespiration or increasing its recycling efficiency may help improve carbon supply under heat stress, thereby mitigating the detrimental impact of elevated respiration and assist in the stabilization of crop growth and productivity (Betti et al., 2016; Walker et al., 2016). This is demonstrated by the study of Wang et al. (2015), who showed that protecting against Rubisco degradation during heat stress in tomato improved biomass accumulation, thereby hinting at an important role for reducing photorespiration during heat stress to improve productivity. Further studies that determine the performance of varieties that bypass photorespiration, or perform it more efficiently under a range of combined and isolated environmental constraints, are required to determine its capacity to balance carbon supply with increasing respiratory demand during heat stress (Xin, Tholen, Devloo, & Zhu, 2015). This will be important because evidence suggests enhanced photorespiration may facilitate important photo-physiological re-programming during other environmental stresses that can co-occur with heat stress, such as drought (Eisenhut et al., 2017; Guan, Zhao, Li, & Shu, 2004; Wingler et al., 1999).

Photosynthetic gene expression changes during heat stress, for example, Zhang et al. (2013) showed that in rice flag leaves there is a repression of genes involved in PSII, which is associated with lower photosynthesis and light reaction rates. Interestingly, photosynthetic genes are not only down-regulated in leaves but also in floral tissues, such as anthers (Oshino et al., 2007), and even pollen (da Costa-Nunes & Grossniklaus, 2003). Our analysis of public transcriptomic data to query the response of photosynthetic genes (as outlined by Wang et al., 2017) to heat stress in reproductive tissues highlighted expression changes for many of these genes (Figure 2c,d), suggesting stabilizing carbon metabolism in reproductive structures may be important for maintaining associated development. This idea feeds into our subsequent discussions on the importance of non-foliar photosynthesis and maintaining net carbon balance in pollen. Heat shock family (*HSF*) transcription factors are essential for regulating photosynthesis under sub- and supra-optimal light conditions (Bechtold et al., 2013; Jung et al., 2013). Up-regulation of *HSFA3* in response to heat stress in both *A. thaliana* pollen and rice panicles (Figure 2c,d) hints towards the importance of maintaining carbon metabolism in these structures, moreover overexpressing *HSFA3* has been demonstrated to reduce chlorophyll degradation during heat stress by increasing galactinol biosynthesis, thereby maintaining photosynthesis (Song, Chung, & Lim, 2016). Similarly, the *SIGMA FACTOR* (*SIG*) and *CRYPTOCHROME-INTERACTING BASIC-HELIX–LOOP HELIX* (*CIB*) proteins are critical for chlorophyll biogenesis (Kanamaru et al., 1999) and degradation (Meng, Li, Wang, Liu, & Lin, 2013), respectively, such that differential expression of associated genes (Figure 2c,d) may reflect attempts to balance net carbon gain during heat stress (Hörtensteiner, 2009; Oh, Strand, Kramer, Chen, & Montgomery, 2018). Additionally, differential expression of genes central to phytochrome signalling, that is, *FAR-RED ELONGATED HYPOCOTYL3* (*FHY3*; Liu et al., 2019) and *EARLY-PHYTOCHROME-RESPONSIVE1* (EPR1; Kuno et al., 2003; Figure 2c,d), typically

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stimulates increasing concentrations of carotenoids and flavonoids (Kreslavski et al., 2018), which may represent an approach to scavenge photosynthetically generated ROS in chloroplasts during heat stress (Brunetti, Di Ferdinando, Fini, Pollastri, & Tattini, 2013; Hu et al., 2020).

5 | THE ROLE OF SOURCE–SINK DYNAMICS AND CARBOHYDRATE RESERVES IN HEAT STRESS RESPONSES

Photosynthesis in foliar and non-foliar organs supports the construction of the vegetative canopy to maximize light capture and reproductive development. The partitioning of carbon towards the latter is of high importance at multiple stages in the formation of high yields in cereals and requires the existence of a high sink strength to match high photosynthetic activity. In determining the relative importance of the strengths of sources and sinks in yield formation, there are several processes involved including the rate of leaf and canopy photosynthesis, the size and activity of the reproductive sink and the size and activity of the *intermediate sinks*. Source strength is determined by the capacity to generate and export photosynthates while sink strength relates to size, metabolic capacity and distance from the source (Smith, Rao, & Merchant, 2018).

To best understand limitations to yields, it is crucial that comprehensive assessments of whole-plant resource allocation and plant development are considered (Abdelrahman, Burritt, Gupta, Tsujimoto, & Tran, 2020; Smith et al., 2018). Source limitations occur primarily at energy-intensive early vegetative stages and again at reproductive stages through to anthesis, where these limitations define the success of reproductive development and biomass accumulation, therefore sink capacity as well (Abdelrahman et al., 2020). Conversely, sink limitations are most prominent post-anthesis during grain-filling (Reynolds, Pellegrineneschi, & Skovmand, 2005), where capacity to derive carbohydrates and trans-locate these to sinks is critical. During heat stress, harvest index may be dictated by the balance of source strength and the efficiency of the use of fixed carbon with respect to facilitating apposite reproductive development and then grain-filling (sink strength) (Abdelrahman et al., 2020). Virtually all of the processes that dictate this balance, that is, the production, transport, remobilization, storage and use of photoassimilates, are in some way impacted by heat stress (Figure 1; Asseng, Kassie, Labra, Amador, & Calderini, 2017; Kumar et al., 2017) and therefore disruption to this balance causes yield losses (Abdelrahman et al., 2020; Alonso et al., 2018; Kumar et al., 2017; Schapendonk, Xu, Van Der Putten, & Spiertz, 2007). Developing an understanding of the molecular underpinnings of the signalling systems that control source–sink dynamics will facilitate the development of improved heat tolerance. For example, it is well understood that the metabolism of sucrose and trehalose is linked via a signalling hub that dictates resource allocations, where the trehalose-6-phosphate (Tre6P) enzyme is critical to this end since it acts as a signalling molecule for sucrose availability (Figure 1; Vandesteene et al., 2012). At sources, Tre6P can regulate biosynthetic enzymes and pathways related to sucrose synthesis and partitioning, and at sinks it can stimulate the mobilization and consumption of sucrose reserves (Griffiths et al., 2016; Martínez-Barajas et al., 2011). Concurrently, manipulating Tre6P levels in organ-specific and phenological-specific manners may represent a novel approach for engineering thermotolerance. This has been demonstrated for heat stress at the seed germination stage in tomato (Lyu et al., 2018), but not yet at adult phenological stages. However, the work of Nuccio et al. (2015) demonstrated that reducing the concentration of Tre6P in developing maize ears in a tissue-specific manner improves sucrose availability to male reproductive tissues allowing for improved pollination success and yield during drought stress. Since heat stress, like drought stress (Rodrigues, Inzé, Nelissen, & Saibo, 2019), limits source capacity (Abdelrahman et al., 2020), this approach may also be effective for developing heat tolerance.

In the case of the *intermediate sinks*, in rice and wheat, these are important for the maintenance of yield during suboptimal and stressful periods and are dominated by the storage of significant quantities of carbohydrates [either starch in the case of rice or water-soluble carbohydrates (WSCs) in the case of wheat; Figure 1] in the stem and associated tissue (McIntyre et al., 2012; Ruuska et al., 2006; Watanabe, Nakamura, & Ishii, 1997). For example, in wheat, dry matter at pre-anthesis is divided between the leaf lamina, leaf sheath, stem and the spike. Substantial amounts of WSCs (commonly fructans) are stored within the stems pre-anthesis and remobilized post-anthesis to provide fixed carbon for grain-filling. The stem tissue, therefore, provides a substantial available sink prior to the formation of the spike (Rebetzke et al., 2008). The amount of the final grain weight that is made up from stem WSCs is genotype and environment dependent. A striking example can be seen by shading leaves at pre-anthesis, which reduces WSCs and subsequently final grain yield in wheat (Beed, Paveley, & Sylvester-Bradley, 2007). As well as being influenced by architectural traits such as branching and panicle size (Fu et al., 2013; Yang, Yunying, Zhang, Liu, & Zhang, 2008; Zhao et al., 2020), sink size in rice is determined by the number of endosperm cells formed pre-anthesis, which correlates with the availability of WSCs (Fu, Huang, Wang, Yang, & Zhang, 2011) and can be affected by heat stress at this stage (Zhen et al., 2020). It follows from the above that any factor that reduces the capacity for foliar photosynthesis pre-anthesis (such as heat stress) jeopardizes both the development of a viable and strong reproductive sink and a reserve of carbon that later contributes to grain-filling and can buffer yield against further environmental perturbation. Numerous studies have shown that the presence of stem reserves is important for yield performance of cereal crops post-anthesis. Factors that reduce photosynthesis such as heat stress and drought during the grain-filling phase increase reliance of reproductive development on stored carbohydrate (Blum, 2011; Morita & Nakano, 2011). The capacity of the stem to accumulate WSCs has been associated with yield in wheat and quantitative trait loci (QTL) (Snape et al., 2007; Zhang, Huang, et al. 2008). A recent study was unable to pinpoint specific genes that regulate WSC capacity in wheat (Li, Liu, et al., 2020); however, recent genome-wide association studies have identified molecular markers (Fu et al., 2020).

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6 | THE CAPACITY OF NON-FOLIAR PHOTOSYNTHESIS TO CONTRIBUTE TO YIELD AND REPRODUCTIVE DEVELOPMENT DURING HEAT STRESS

6.1 | Quantifying non-foliar photosynthesis during heat stress

To date, photosynthetic research has focused predominantly at the leaf level. The importance of leaf-level photosynthesis is highlighted by successful approaches to fine tune associated mechanisms that in turn increase yield (Głowacka et al., 2018; Gu, Qiu, & Yang, 2013; Kromdijk et al., 2016; López-Calcagno et al., 2019). Long-standing evidence exists demonstrating that photosynthesis also occurs in non-foliar organs, including reproductive structures (Bazzaz, Carlson, & Harper, 1979; Biscoe, Gallagher, Littleton, Monteith, & Scott, 1975). Gnan, Marsh, and Kover (2017) highlighted the importance of non-foliar photosynthesis in *A. thaliana* by demonstrating negligible fitness costs following the removal of rosette leaves at floral transitioning. This highlights the importance of photoassimilates provided by the fruits and inflorescence for facilitating reproductive development and seed set. However, we lack an understanding of the factors that limit and regulate photosynthesis in non-foliar tissues.

The capacity for photosynthesis in reproductive tissues to facilitate reproductive development and yield has seen a resurgence in interest in the past decade (Chang et al., 2020; Hiratsuka, Suzuki, Nishimura, & Nada, 2015; Hu et al., 2012; Molero & Reynolds, 2020; Sanchez-Bragado, Molero, Reynolds, & Araus, 2014, 2016; Sui et al., 2017). Molero and Reynolds (2020) measured ear and flag leaf photosynthesis in a panel of ~200 spring wheat accessions across multiple field trials. Their observation that ear photosynthesis was more closely associated to yield and showed enhanced variation and greater heritability than that of flag leaf photosynthesis represents a turning point in the understanding of the photosynthetic determination of yield. The same group has previously demonstrated the importance of heat stress on flag leaf gas exchange in wheat (Pinto, Molero, & Reynolds, 2017). However, in their more recent study, they were unable to measure ear photosynthesis under heat stress due to technical difficulties with respect to stabilizing high temperatures within their custom gas analyser (Molero & Reynolds, 2020). Herein lies a fundamental issue with understanding and harnessing spike/ear photosynthesis: it is inherently difficult to measure (as reviewed by: Simkin, Faralli, Ramamoorthy, & Lawson, 2020), especially under heat stress (Molero & Reynolds, 2020).

6.2 | Solutions to the challenge of phenotyping non-foliar photosynthesis during heat stress

Chlorophyll fluorescence is a somewhat underutilized approach for understanding photosynthesis in non-foliar structures. Key exceptions here are the studies of Šebela, Bergkamp, Somayanda, Fritz, and Jagadish (2020) and Šebela, Quiñones, Olejníčková, and Jagadish (2015), where a chlorophyll fluorescence methodology was developed and utilized to determine temperature-derived alterations to the optical properties of rice panicles and wheat spikes, respectively. Via this methodology, the authors were able to pinpoint the initiation of heat-induced panicle senescence. This is crucial since if senescence of reproductive support organs is accelerated too close to the timing of anthesis, energy for reproductive processes will be limited (Doku et al., 2019). For this reason, the maintenance of the effective quantum yield of PSII (ΦPSII) during heat stress in the developing panicles of the N22 rice variety (Šebela et al., 2015) is likely critical for supplying energy to support the improved pollen viability and spikelet fertility of N22 under heat stress (Poli et al., 2013; Wada et al., 2020). PSII is one of the most thermolabile components of photosynthetic biochemistry (Figure 1). A sustained decline in PSII efficiency can be quickly assayed via dark-adapted chlorophyll fluorescence (Murchie & Lawson, 2013), consequently assessing the maximum efficiency of PSII (F_v/F_m) under heat stress in reproductive structures has potential as a high-throughput platform from which to gauge heat tolerance that will contribute to sustained reproductive development. To this end and as a proof of concept for this review, we employed our recently published approach of gauging F_v/F_m responses to incrementally increasing temperatures in rice leaves (Ferguson et al., 2020) to wheat ears undergoing grain-filling of two distinct accessions (Figure 3). Here, we observed a significant difference in the maintenance of F_v/F_m under heat stress between the two accessions, which is likely to be driven by the previously described PSII responses to temperature that impairs electron transport. This observation highlights this methodology as a tool to identify key genetic variation in heat tolerance that could be employed for use with diverse tissue types.

A further promising methodology that warrants attention as a tool to benchmark the importance of photosynthesis in reproductive organs is via the abundance of stable isotopes (Sanchez-Bragado et al., 2014). By comparing the carbon isotope composition ($\delta^{13}C$) of reproductive structures and mature grains, Sanchez-Bragado et al. (2014) demonstrated that a significant proportion of fixed carbon was trans-located from reproductive support structures to grains in wheat. We suggest that this approach may be a highly efficient means to benchmark the importance of non-foliar photosynthesis for stabilizing reproductive output during heat stress, especially since it provides a time-integrated measure of photosynthesis compared to the *snapshot* style measurements achieved via gas exchange. However, recent work has demonstrated that in situations where photosynthesis is low and respiration is high, such as during heat stress, traditional models of $\delta^{13}C$ need to be approached with caution, since they do not accurately reflect photosynthetic biochemistry (Busch, Holloway-Phillips, Stuart-Williams, & Farquhar, 2020). This may prove to be less important for non-foliar photosynthesis than for foliar photosynthesis, since much of the fixed carbon in these tissues is understood to be recycled from CO_2 released via mitochondrial respiration, rather than being fixed from atmospheric CO_2 (Aschan & Pfanz, 2003; Ávila, Herrera, & Tezara, 2014; Millar, Whelan, Soole, & Day, 2011).

Non-foliar photosynthesis plays a role in stabilizing both reproductive development and output during heat stress (Maydup

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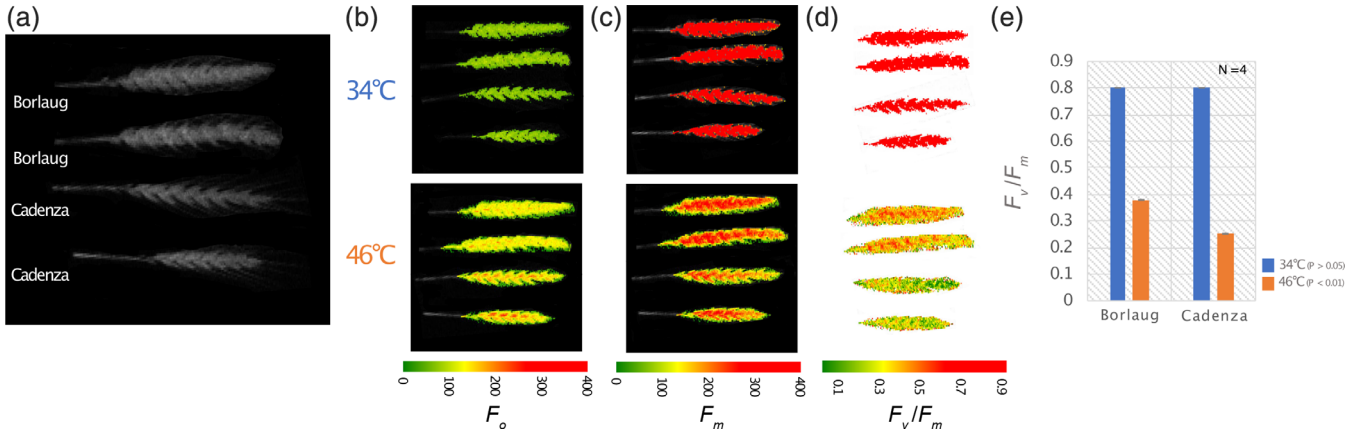

FIGURE 3 Wheat ear photosynthetic responses to heat stress. Ears from two wheat genotypes (Borlaug and Cadenza) were subjected to rapid incremental increases in temperature with concurrent measurements of chlorophyll fluorescence following the protocol of Ferguson et al. (2020). Data at two temperature points [34°C (top) and 46°C (bottom)] are shown. (a) Grey-scale image showing position of two representative ears of each genotype. (b) Minimum fluorescence (F_o) at both temperatures. (c) Maximum fluorescence (F_m) at both temperatures (F_m). (d) Maximum efficiency of photosystem II (F_v/F_m) at both temperatures. (e) Whole-ear average F_v/F_m at both temperatures for both genotypes. F_v/F_m was significantly reduced at 46°C in Cadenza compared to Borlaug ($p > .01$) according to a one-way ANOVA [Colour figure can be viewed at wileyonlinelibrary.com]

et al., 2010; Santiago & Sharkey, 2019; Šebela et al., 2015). It is important that the significance of this role is affirmed through further testing that incorporates more species and intra-specific variation. This will require the development of rigorously tested phenotyping methodologies as described above (Figure 3; Molero & Reynolds, 2020; Šebela et al., 2015). Moreover, combining these methodologies with high-throughput approaches for benchmarking traits related to pollen and floret fertility and seed physiological maturity (Dreccer, Molero, Rivera-Amado, John-Bejai, & Wilson, 2019) will enable large-scale testing of associations between carbon dynamics and reproductive development. Key examples to this end include the use of impedance flow cytometry for high-throughput screening for pollen viability (Heidmann, Schade-Kampmann, Lambalk, Ottiger, & Di Berardino, 2016) and automated image-based assessments of panicle and spikelet phenotypic traits for rapid assessment of spikelet fertility (Yang et al., 2014).

Despite the difficulties of phenotyping non-foliar photosynthesis under heat stress, the evidence describing the significance of non-foliar photosynthesis under favourable agronomical or ecological conditions allows us to consider its importance under heat stress. We discuss a number of considerations to this end below.

6.3 | Disruptions to reproductive development and productivity due to non-foliar photosynthesis during heat stress

Photosynthesis is characterized by multiple redox reactions, since reactive oxygen species (ROS) are readily generated by photosynthesis (Foyer, 2018). Heat inactivation of PSII electron acceptors and donors increases the generation of ROS (Figure 1; Pospíšil, 2016). Consequently, heat stress will enhance ROS production in photosynthetically active non-foliar tissues. This is an important consideration for two reasons. Firstly, ROS can cause DNA damage (Kumar, Oldenburg, & Bendich, 2014), which can have cross-generational impacts if mutations occur in the gametal precursor cells. While ROS-induced DNA mutations in male and/or female gametes may not represent a hugely important consideration for agricultural productivity, it may have implications for research and breeding and will have eco-evo consequences for natural systems (Raven & Griffiths, 2015). The second important consideration regarding increased photosynthetic ROS production in reproductive structures during heat stress is with respect to the importance of ROS accumulation for various aspects of pollination (Figure 1). For example, ROS accumulation is critical for tapetum-delayed programmed cell death (PCD), establishing pollen tube growth (Foreman et al., 2003; Speranza, Crinelli, Scoccianti, & Geitmann, 2012), embryo sac development (Victoria Martin, Fernando, Sundaresan, Julián, & Pagnussat, 2013) and fertilization (McInnis, Desikan, Hancock, & Hiscock, 2006; Sharma & Bhatla, 2013). Consequently, increased levels of ROS associated with heat-impaired photosynthesis could potentially disrupt pollen development and pollination. This possibility is highlighted by evidence that suggests germinating pollen grains produce nitric oxide (NO; Hiscock, Bright, McInnis, Desikan, & Hancock, 2007; Zafra, Rejón, Hiscock, & de Dios Alché, 2016), to act as an antioxidant for ROS scavenging (Romero-Puertas & Sandalio, 2016). The capacity for pollen grains to balance ROS levels during elevated temperatures represents an interesting future avenue for research to prime crops for heat stress during reproductive growth. Employing established high-throughput biochemical assays (Fimognari et al., 2020) or hyper-spectral reflectance sensing-based approaches (Yendrek et al., 2017) that can rapidly quantify ROS production would facilitate forward genetics approaches to identify novel genetic regulators to this end.

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Heat stress may also initiate important crosstalk for maintaining photosynthesis and reproductive development with respect to the activity of sugar transporter genes. Sugar transporters are essential for partitioning carbohydrates fixed via photosynthesis (Ainsworth & Lemonnier, 2018; Julius, Leach, Tran, Mertz, & Braun, 2017). They are differentially expressed in response to heat stress, where some evidence suggests up-regulation (Jian et al., 2016) and others down-regulation (Qin et al., 2008).

It is plausible that this regulation is linked with the maintenance of sugar content in photosynthesising tissue pre- and post-anthesis, which in turn decelerates the decline in net carbon balance to achieve heat tolerance (Julius et al., 2017; Zhou et al., 2017). Concurrently, SWEET, for example, *RPG1* (Milner et al., 2020), and SUC/SUT, for example, *SUC1* (Sivitz, Reinders, & Ward, 2008; Xu, Chen, Yunjuan, Chen, & Liesche, 2018), sugar transporters have been implicated in pollen development, most significantly by facilitating water transport out of endothecium cell walls to increase tension and enable pollen dehiscence (Keijzer, 1987; Wilson et al., 2011). Consequently, photosynthetic activity in reproductive structures, especially anthers (Clément & Pacini, 2001), may result in fine-tuning of sugar transporter activity given elevated temperatures in order to maintain cellular sugar status. At the same time, this may limit sugar-efflux activity necessary for anther dehiscence and pollen viability (Santiago & Sharkey, 2019). Understanding the balance herein will allow for an improved understanding of the capacity to maintain reproductive development given elevated temperatures: near-infrared spectroscopy represents a key phenotyping technology for use here, since it can be used to predict carbohydrate content in different tissue types (Ramirez et al., 2015).

6.4 | Benefits achieved through non-foliar photosynthesis during heat stress

A fundamental benefit of non-foliar photosynthesis is that it reduces the carbon demand from foliar tissues (Raven & Griffiths, 2015). This benefit more directly relates to perennial crops, such as certain bioenergy grasses (Whitaker et al., 2018) and tree crops (Mercado-Blanco et al., 2018); however, it may also afford some benefit to annual crops during heat stress too. In this sense, the constraining of carbon fixation and sugar transport (see above) from foliar sources during heat stress can be offset by photosynthesis in the stems and reproductive structures. This is more critical for perennial species, because it will allow essential non-foliar structures to avoid senescence while not limiting reproductive development and productivity. Additionally, in bioenergy grasses, the accumulation of stem sugars is essential for productivity (Feltus & Vandenbrink, 2012), such that enhancing export to stems has been proposed as a target trait for improvement in these crops (McGaughey et al., 2016). As we have previously discussed, however, sugar transport activity is impaired by heat stress, thereby highlighting the importance of stem and ear photosynthesis in such situations. In general, photosynthesis in stems is achieved either through assimilating atmospheric CO_2, by recycling respired CO_2, or through decarboxylating organic acids within the xylem and phloem (Ávila et al., 2014; Hibberd & Quick, 2002), although this varies depending on species. Wheat, for example, appears to have culm stomata that are similarly sized to those found on the flag leaf (Simkin et al., 2020), suggesting that stem photosynthesis in wheat may to large extent rely on the assimilation of atmospheric CO_2, however functionality in terms of CO_2 diffusion or cooling capacity remains to be tested. Conversely, ecological studies have demonstrated that deciduous species from warm and dry environments have much smaller stomata to facilitate more precise control of transpiration, which minimizes the potential to fix atmospheric CO_2, but enhances drought tolerance (Smith & Osmond, 1987). Concurrently, the amount of fixed carbon recycled from respiration can be as much as 10 times greater than the amount fixed from atmospheric CO_2 in such species, which equates to enhanced overall water-use efficiency (Smith & Osmond, 1987). While this would initially appear to limit heat tolerance capacity, the recent study of Ávila-Lovera, Zerpa, and Santiago (2017) demonstrated that in multiple desert species functional stem photosynthesis allows plants to better coordinate stem hydraulics, measured as evaporative flux, thereby more efficiently facilitating heat tolerance via cooling.

Further studies incorporating key crops and different tissues are required to understand the extent to which photosynthesis occurring in non-foliar structures is characterized by recycled CO_2 and/or CO_2 assimilated from the atmosphere. This is critical because this balance will have important implications for heat tolerance, since fixing atmospheric CO_2 necessitates the presence of functional stomata, which can in turn facilitate heat tolerance via transpiration (cooling; e.g. Li, Zhang, et al., 2020), and because of the previously discussed responses of photosynthesis and respiration to heat stress. However, it is worth noting that temperature-derived increases in evaporative cooling (stomatal conductance) can in some instances be decoupled from photosynthesis and respiration responses (Urban, Ingwers, McGuire, & Teskey, 2017). Since respiration increases with temperature (Teskey et al., 2015), high temperatures will increase non-photorespiratory release of CO_2 available for recycling. Concurrently, as temperatures rise, there may be a temperature range where enhanced respiration is increasing the availability of CO_2 for recycling before photosynthesis is impaired. This means high temperatures that would not necessarily equate to heat stress per se may increase carbon fixation in non-foliar structures that predominantly recycle respiration compared to leaves, such that the photosynthesis response to temperature will be greater before impairment (Bloemen, McGuire, Aubrey, Teskey, & Steppe, 2013). For reference, this theoretical range for a C_3 species is highlighted in yellow around the respiration response in Figure 4. This range will be higher for C_4 species, due to the inhibition of Rubisco oxygenase activity (Crafts-Brandner & Salvucci, 2002); however, the increase in CO_2 availability with increasing temperatures may reduce photorespiration (Ehlers et al., 2015) and increase heat tolerance in non-foliar tissues of C_3 species also. Studies on temperature response of respiration (photo- and non-photo) and photosynthesis of non-foliar structures are much needed to provide insights to this end.

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Functional stomata on non-foliar epidermal surfaces that support gas exchange also have the potential to afford important benefits for improving heat tolerance. Firstly, if reproductive structures are actively exchanging CO_2 and water vapour with the atmosphere, this will enhance the overall transpiration stream towards non-foliar tissue (Qaderi, Martel, & Dixon, 2019). Concurrently, this will increase the supply of immobile nutrients that are critical for reproductive development (Sofield, Wardlaw, Evans, & Zee, 1977; Yamaji, Chiba, Mitani-Ueno, & Ma, 2012; Yamaji & Jian Feng, 2009). Such nutrients include silicon and calcium, in which both have long understood roles in reproductive development (Figure 1; Brewbaker & Kwack, 1963; Raven, 1983) and yield outputs (Epstein, 1994; Schultz & French, 1976). Perhaps, the more clear benefit afforded by active gas exchange in reproductive structures during heat stress is evaporative cooling via transpiration. Plants that develop in, or are adapted to, high temperatures demonstrate enhanced water use via this mechanism to maintain growth and fitness (Crawford, McLachlan, Hetherington, & Franklin, 2012). This suggests that enhancing the stomatal conductance of reproductive structures may limit heat-induced impairment of reproductive processes. Moreover, this may enhance carbon fixation in these structures to provide carbohydrates for energy-intensive reproductive processes and yield (Figure 1). To this end, enhanced carbon fixation in ears has been linked to increased wheat yield via transgenic manipulation (Driever et al., 2017; Simkin et al., 2020) and by observing natural variation (Molero & Reynolds, 2020). In general, stomatal physiology and behaviour in reproductive structures appear to be uncoupled from that of leaves (Aschan & Pfanz, 2003; Lu et al., 2017; Simkin et al., 2020). In *Brassica napus*, for example, stomata are far larger and less frequent on siliques (fruits) than on leaves, however stomatal conductance is much lower in siliques (Lu et al., 2017). This suggests there may be opportunities to select for altered stomatal physiology to promote enhanced gas exchange in reproductive tissues that may boost carbon fixation and enhance heat tolerance. A critical caveat here relates to the co-occurrence of high temperatures with reduced precipitation. Enhanced stomatal conductance may promote more rapid dehydration of non-foliar tissues as demonstrated at the whole-plant level in recent transgenic studies incorporating lines with reduced stomatal densities (Caine et al., 2019; Hughes et al., 2017); however, drought susceptibility in these studies was predominantly attributed to leaf-level transpiration. Consequently, this may only really represent a viable non-foliar heat tolerance target trait for environments where drought and heat stress do not frequently co-occur, or where supplemental irrigation is available.

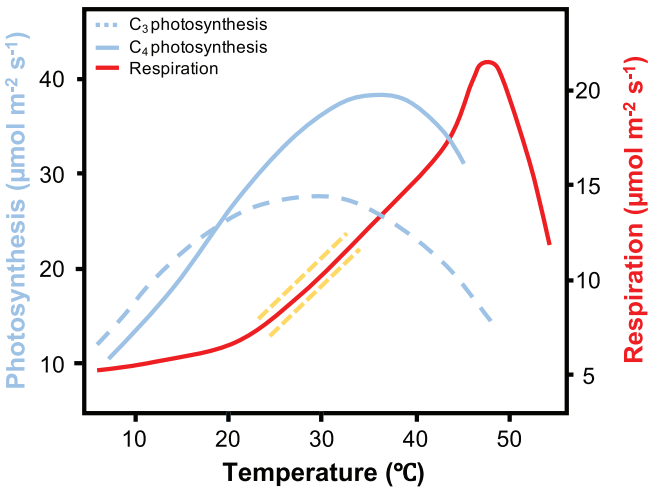

FIGURE 4 An idealized diagram of the temperature response of CO_2 fixation (C_3 and C_4 photosynthesis; Adapted from: Yamori, Hikosaka, & Way, 2014) and CO_2 release (respiration; Adapted from: Teskey et al., 2015) in leaves assuming current atmospheric CO_2. Mechanisms underlying these responses are described in the text. Insufficient evidence exists to understand how these responses will manifest in non-foliar tissues, for example, stems, where confounding factors such as the recycling of respiratory CO_2 could impact photosynthesis. Recycling CO_2, for example, may enhance the carbon assimilation response in non-foliar tissues, compared to leaves, in the temperature range where respiration is increasing before photosynthesis is impaired (as highlighted in yellow around the respiration response for a C_3 species in this example, where the range would be extended for C_4 species) [Colour figure can be viewed at wileyonlinelibrary.com]

7 | NET CARBON GAIN AS A LIMITING FACTOR FOR REPRODUCTIVE DEVELOPMENT AND OUTPUT DURING HEAT STRESS

7.1 | The cost of respiration

Respiratory metabolism is essential for sustaining plant growth and productivity. Most crucially, respiration oxidizes triose-phosphate produced by photosynthetic CO_2 fixation in order to generate ATP essential for metabolism (Dusenge et al., 2019; O'Leary, Asao, Millar, & Atkin, 2019). The importance of respiration for growth and productivity is highlighted by its association with agricultural productivity (Ainsworth & Long, 2005). More specifically and as we have already discussed, processes underlying reproductive development are often highly energy intensive (Rounds, Winship, & Hepler, 2011).

Crops lose as much as 60% of the total carbon fixed via photosynthesis to respiration (Cannell & Thornley, 2000; Gifford, Thorne, Hitz, & Giaquinta, 1984). To understand the importance of respiration for defining yield, it is important to consider that the total amount of fixed carbon harvested as yield is at most 25% (Gifford et al., 1984), thereby highlighting the potential of crop respiration to be *wasteful*. For conceptualisation purposes, it is further important to consider the McCree (1970) paradigm of plant respiration that divides respiration into that necessary for *growth* and that contributing to *maintenance*. Growth respiration provides ATP and carbon skeletons/precursors for growth, thus contributing to biomass accumulation, reproductive development and yield. Conversely, maintenance respiration relates to cyclic processes not directly related to productivity (Plaxton & Podestá, 2006). Comparisons of respiration to growth have

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demonstrated that the split in carbon consumption between these two components is roughly equal (Amthor, 1989). So, while it is clear that respiration is critical for sustaining many growth and yield-determining processes, including reproduction, it is also evident that substantial improvements may be possible to this end that may divert photoassimilates towards improving yield or sustaining reproductive development (Amthor et al., 2019). Furthermore, and as we introduce below, rates of respiration increase with heat stress, such that it is a key target for crop productivity in a warming world.

7.2 | Respiration sensitivity to increasing temperatures

Plants acclimate respiration according to the demand for respiratory substrates as determined by the prevailing temperature (Coast et al., 2020; Dusenge et al., 2019; O'Leary et al., 2017). Genotypes from warm environments demonstrate reduced respiration than those from colder environments when grown at commonly high temperatures (Atkin & Tjoelker, 2003). This is a key point and hints at the potential for confounding genotype × environment (GxE) interactions for respiration that should be considered when large diversity sets are evaluated in common environments (Ferguson, 2019). The study of De Vries, Witlage, and Kremer (1979) demonstrated that in C_3 and C_4 crops whole-plant respiration increases exponentially with temperature. Rising temperatures stimulate growth, which necessitates increased respiratory metabolism. Consequently, De Vries et al. (1979) observed that the increase and eventual decrease in the rate of leaf elongation in response to temperature is coupled to the respiration response. This response of respiration to temperature has been validated in other species (Katja et al., 2012; O'Sullivan et al., 2013). Respiration has a higher temperature optimum than photosynthesis (Figure 4; Atkin & Tjoelker, 2003; Crous et al., 2012; Teskey et al., 2015). Temperatures are unlikely to reach these optimums, meaning maximum respiration is an improbable scenario in natural environments. However, controlled experimental work allows us to understand that if temperatures exceed this point, respiration rapidly declines due to severe mitochondrial and cellular damage (Kolb & Robberecht, 1996; O'Sullivan et al., 2013; Posch et al., 2019; Teskey et al., 2015).

The response of respiration to temperature is largely driven by the demand for respiratory products to sustain increased growth and development. Indeed, source–sink modelling links the temperature dependence of respiration to local and remote demand for respiratory products, where high temperatures increase carbohydrate transport and utilization above- and below-ground, while limiting carbohydrate accumulation within the leaf (Farrar & Williams, 1991; Posch et al., 2019). Short-term photosynthetic responses to temperature are less than those of respiration (Figure 4; Dusenge et al., 2019; Posch et al., 2019). Concurrently, plants can demonstrate respiratory homeostasis by acclimating rates of respiration in order to stabilize overall carbon balance and limit the demand for ATP if elevated temperatures persist (Eustis, Murphy, & Barrios-Masias, 2020; Kurimoto, Day, Lambers, & Noguchi, 2004). Therefore, improving the respiratory response to short-term heat waves may not harmonize with important thermotolerance traits associated with longer-term stress. The same is also true for photosynthesis, where acclimation allows for the maintenance of maximum photosynthesis under a variety of temperature regimes as demonstrated via mechanistic modelling incorporating data from >100 species (Vico, Way, Hurry, & Manzoni, 2019). Selection in warmer environments will result in genotypes with reduced respiration under high temperatures. Despite the potential for adaption and acclimation, instances of heat waves in these warm and colder environments will impact yield and yield quality. Moreover, it is clear that stimulated respiration plays a key role to this end (Fitzgerald et al., 2016; Köhler, Huber, Bernacchi, & Baxter, 2019; Nuttall, Barlow, Delahunty, Christy, & O'leary, 2018; Thomey et al., 2019).

7.3 | Limitations to productivity imposed by respiration during heat stress

The rate of change in photosynthesis to temperatures is less than that of respiration (Figure 4). This is reflected in our demonstration of increased plasticity to heat stress for respiration compared to photosynthesis calculated from available data in rice and wheat (Figure 5a, b). Data from quinoa suggest a relative lack of plasticity in response to heat stress (Figure 5c; Eustis et al. (2020), where night-time respiration is actually reduced in plants grown under a high temperature regime. This is likely because, in this study, heat-stressed plants were constantly grown under high temperatures, as opposed to the associated rice study (Ferguson et al., 2020), for example, where a heat wave was simulated by a sudden increase in temperature. If plants develop under high temperatures in the long term, they can demonstrate thermal acclimation of carbon metabolism (Atkin & Tjoelker, 2003). This is likely the basis of the reduced plasticity to heat stress in the quinoa study as opposed to being due to rapid depletion of respiratory substrates, especially since productivity was only marginally impacted (Eustis et al., 2020). In situations, where suitable acclimation is not possible, for example, strong heat waves, an energy imbalance results, since the demand for photoassimilates for respiration outpaces active supply from photosynthetic CO_2 fixation (Figures 1 and 4). This imbalance increases as temperatures rise because photosynthetic rates begin to decline earlier than respiration. In C_4 plants, CO_2 fixation is predominantly limited by the capacity of the Phosphoenolpyruvate carboxylase (PEPCase) enzyme (Crafts-Brandner & Salvucci, 2002), whereas C_3 plants are limited by Rubisco (Salvucci, Osteryoung, Crafts-Brandner, & Vierling, 2001). PEPcase capacity is relatively independent of moderate-to-high temperatures, whereas the activation of Rubisco by Rubisco activase is thermosensitive (Perdomo et al., 2017). Consequently, the extent to which elevated temperatures mismatch carbon demand with active carbon supply is typically more important for C_3 species. This can be further confounded by increasing photorespiration, where Rubisco preferentially oxygenates rather than carboxylates RuBP, as temperatures increase (Figure 1; Peterhanse & Maurino, 2011). It is for this

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reason, among others, that introducing the C_4 photosynthetic pathway into rice is targeted as an approach to better adapt rice to warmer environments (Karki, Rizal, & Quick, 2013). As photosynthesis declines and respiration increases, net carbon supply, which is typically determined as photosynthesis minus respiration (Amthor et al., 2019), is restricted. This situation necessitates that already assimilated non-structural carbohydrates be diverted towards respiratory metabolism (Sita et al., 2017). Since a substantial proportion of this metabolism does not equate to growth or productivity, this repartitioning of carbon resources can limit carbon available to support reproductive development and ultimately reduce that which is available for seed or grain-filling (Plaut, Butow, Blumenthal, & Wrigley, 2004; Suwa et al., 2010; Zhou et al., 2017). For example, Mohammed and Tarpley (2009) report a 27% greater loss in carbon due to respiration in rice plants when grown at high night-time temperatures compared to plants grown at ambient temperatures, which contributed to a substantial reduction in grain weight per plant. Similarly, Thomey et al. (2019) observed a substantial reduction in total non-structural carbohydrates, likely due to increased respiration, in leaves of field grown soybean exposed to heat waves, which in turn contributed to discernible total biomass and yield reductions.

The timing of elevated temperature events relative to phenological stages shapes the extent to which temperature-induced respiration may impact reproductive output. If increasing temperatures impair net carbon supply pre-anthesis, this may have a minimal impact on reproductive output. Similarly, minimal impact may occur if temperatures fall before and during the initiation of flowering or if respiration and photosynthesis acclimate to stabilize carbon supply and demand. If pre-anthesis heat stress increases respiration enough to cause severe ROS accumulation, this will lead to non-reversible degradation of cellular components, for example, chlorophyll, and senescence, thereby reducing photosynthetically active leaf area and limiting future carbon fixation and supply during reproductive development. Equally, if pre-anthesis heat stress diverts WSCs towards respiratory metabolism, this may severely limit sugar availability for reproductive development, which can be essential for some crops especially for buffering against conditions unfavourable for carbon fixation during reproductive development and grain-filling (Li, Zhang, Li, Chang, & Jing, 2015; Ovenden et al., 2017). In general, if heat stress coincides with anthesis and/or seed filing, diversion of actively assimilated and pre-assimilated carbon towards maintenance respiration will constrain reproductive output (Jagadish, 2020; Jagadish et al., 2015).

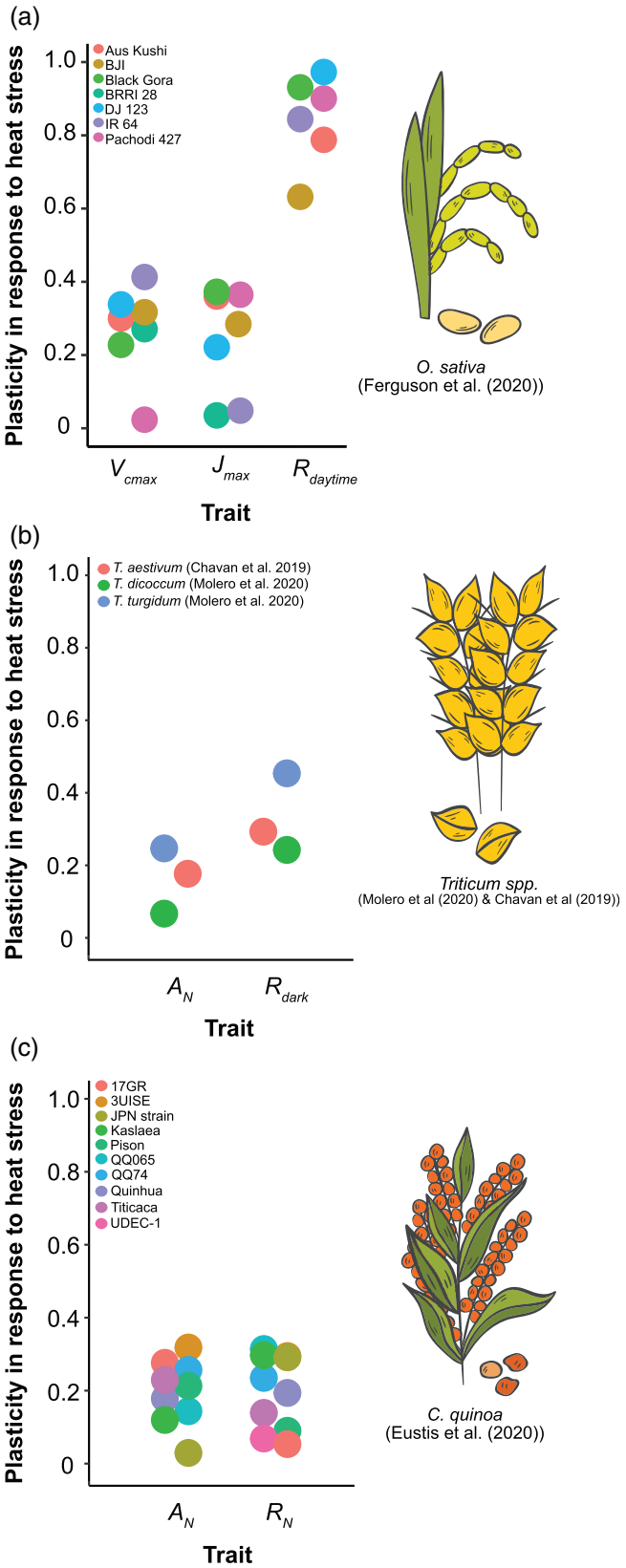

FIGURE 5 Phenotypic plasticity (calculated as the Phenotypic Plasticity Index; Valladares, Sanchez-Gomez, & Zavala, 2006) of photosynthesis and respiration to heat stress. (a) Plasticity of the maximum rate of Rubisco carboxylation (V_{cmax}), maximum rate of electron transport (J_{max}) and daytime respiration (R_{day}) in seven rice genotypes. Data reproduced from Ferguson et al. (2020). (b) Plasticity of net photosynthesis (A_N) and dark respiration (R_{dark}) in wheat species. Data reproduced from Chavan, Duursma, Tausz, and Ghannoum (2019) and Molero & Reynolds (2020). (c) Plasticity of A_N and night-time respiration (R_N) in 10 quinoa genotypes. Data reproduced from Eustis et al. (2020) [Colour figure can be viewed at wileyonlinelibrary.com]

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Since the developmental timing of elevated respiration events is central to defining their impact, it is vital that non-destructive staging of reproductive development is established across key crops (Fernández-Gómez, Talle, Tidy, & Wilson, 2020). These methodologies will allow high-throughput phenotyping of carbon metabolism that is timed to co-occur with heat-sensitive reproduction events.

Substantial evidence points towards crop productivity being at least co-limited by net carbon gain, that is, source co-limited (Ainsworth & Long, 2005; Ort et al., 2015; Sonnewald & Fernie, 2018). This is reflected by observations of elevated respiration due to heat stress impairing net carbon gain and limiting productivity in rice and soybean (Gray et al., 2016; Mohammed & Tarpley, 2009; Thomey et al., 2019). It is further corroborated by wheat field trials that have shown maximum daily temperature as a key limiting factor for grain yield (Reynolds, Balota, Delgado, Amani, & Fischer, 1994). Moreover, negative correlations between respiration and yield across multiple species are especially strong during heat stress (Evans & Rawson, 1970; Jacoby, Millar, & Taylor, 2016; Molero & Reynolds, 2020; Pinto et al., 2017; Wilson & Jones, 1982), further highlighting that reducing the response of respiration to heat stress is a key target trait for balancing net carbon gain and stabilizing productivity in a warming world.

7.4 | Stay green as physical marker for benchmarking net carbon gain during heat stress

Stay green is a general term given to a genetic variant that demonstrates delayed senescence (Thomas & Howarth, 2000; Thomas & Ougham, 2014). It is closely coupled to the loss of chlorophyll and as an optically apparent phenotype is typically assessed via visual metrics (Ferguson et al., 2020; Rebetzke, Jimenez-Berni, Bovill, Deery, & James, 2016; Xu, Rosenow, & Nguyen, 2000), therefore it is a useful marker for plant breeding (Figure 1; Vadez, Deshpande, Kholova, Ramu, & Hash, 2013). Functional stay green increases photosynthetic activity and leaf longevity (Suárez, 2010), which can be critically important for sustaining active supply of photoassimilates for growth, thereby facilitating heat tolerance. Consequently, it is typically considered an important trait pre-anthesis and during fertilization where it can support the huge energy demand of processes associated with reproductive development (Figure 1; Jagadish et al., 2015; McLaughlin & Boyer, 2004; Zinselmeier et al., 1995). Conversely, stay green can be disadvantageous during grain-filling, where accelerating foliar senescence has been demonstrated to increase grain weight and yield by allowing for more effective remobilization of carbon and nitrogen (Figure 1; Li et al., 2012; Wingler et al., 2012; Yang & Zhang, 2006; Zarrouk et al., 2016), moreover senescence in older leaves of herbaceous crops has been demonstrated to allow younger leaves to survive environmentally challenging conditions in the summer (Munné-Bosch, Jubany-Marí, & Alegre, 2001).

Satler and Thimann (1983) first demonstrated that respiration and senescence, that is, reduced stay green, co-occur. Currently, it is not abundantly clear whether respiration leads to senescence or vice versa (Brouwer, Gardeström, & Keech, 2014; Ferguson et al., 2020; Launay et al., 2019; Law et al., 2018), indeed it is likely that both processes interact with each other. ROS are key to regulating senescence (Giraud et al., 2008; Panchuk, Zentgraf, & Volkov, 2005). Premature senescence in flag leaves of a mutant rice line has been determined to be a result of ROS over-accumulation due to ascorbate peroxidase inactivity (Wang et al., 2016). It is plausible to assume that increased ROS accumulation resultant from increased rates of respiration during heat stress will impair the capacity for effective ROS scavenging for regulating senescence. However, this hypothesis remains to be tested. Senescence is a precisely arranged series of dynamic processes designed to allow plants to remobilize resources (Bresson, Bieker, Riester, Doll, & Zentgraf, 2018; Jagadish et al., 2015). Detoxification through anthocyanin accumulation and activity remains persistent throughout this process, since it stabilizes mitochondrial activity (He & Monica Giusti, 2010; Zimmermann, Heinlein, Orendi, & Zentgraf, 2006). This is important because senescence relies on the existence of viable mitochondria (Bresson et al., 2018; Keech et al., 2007; Ruberti et al., 2014), as such it is conceivable that senescence drives increased respiration. Regardless of the precise dynamics between senescence and respiration, it can be concluded that increasing the capacity of a plant to stay green during heat stress will balance net carbon gain (Figure 1). This can be important because it can spare non-structural carbohydrates from diversion towards supporting unnecessary maintenance metabolism; however, the phenological timing here is key to determining the yield benefit or lack thereof. Engineering phenological timing of stay green is pivotal for developing crops with increased heat tolerance (Jagadish et al., 2015) and has stimulated much discussion on the notion of whether 'living to die' or 'dying to live' is more important during heat stress (Munné-Bosch & Alegre, 2004; Schippers, Schmidt, Wagstaff, & Jing, 2015).

7.5 | The impact of enhanced respiration on reproductive development

As discussed earlier, pollen development, anthesis, pollen germination and growth of the resultant pollen tube are particularly sensitive to heat stress. The vast majority of the energy needed to facilitate and sustain pollen development, germination and pollen tube growth is from respiration sustained by carbohydrates accumulated in the vegetative pollen cell during anther development. As such, it is conceivable that enhanced respiration caused by increasing temperatures may rapidly deplete respiratory substrates at multiple stages, such as when the tapetum is trans-locating carbohydrates to the developing pollen or during pollen maturation and anther dehiscence. At any stage this will limit the capacity for pollen and pollen tubes to generate ATP, which will in turn reduce successful fertilization events and yield. There is increasing empirical evidence supporting this notion. If wheat anthers lack or have very low levels of glucose, the subsequently released pollen will demonstrate very low levels of viability, as such profiling anther biochemical composition can serve to forecast pollen viability (Impe et al., 2020). Similarly, if heat stress co-occurs with the

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later stages of anther development in tomato, starch accumulation is limited just prior to anthesis, which substantially decreases sugar concentrations within the mature pollen grains leading to reduced germination ability and decreased yields (Pressman, Peet, & Pharr, 2002). Comparable observations have been made in chickpea (Kaushal et al., 2013) and wheat (Dhanda & Munjal, 2009), where heat stress has been observed to reduce sucrose availability for anthers and pollen. With respect to later stages of development, the study of Bahuguna, Solis, Shi, and Jagadish (2017) tested the impact of high night-time temperature post-anthesis in rice and observed that elevated rates of respiration in heat susceptible varieties coincided with reduced panicle starch, which concurrently reduced grain weight and quality. Similar results have been observed in wheat, where increased respiration did not totally impair fertilization but did result in immature grains (Johkan, Oda, Maruo, & Shinohar, 2011), and tomato, where the maintenance of carbohydrate content in pollen grains through reduced respiration was observed to be critical in allowing stabilized fruit production (Firon et al., 2006). Equally, it should be noted that reduced rates of respiration in associated tissues and cell types do represent a *silver bullet* for stabilizing the reproductive development of crops in warmer environments. This is demonstrated by the well-cited study of Sato, Peet, and Thomas (2000) that showed that mild heat stress impaired fruit set in tomato and that this was a factor of pollen release and germination; however, cultivar differences in the respiration response to temperature could not explain these casual factors. This highlights the need to evaluate the proposed and developed thermotolerance mechanisms at a variety of growing temperatures.

It is apparent that reducing the rate of response of respiration of developing anthers and pollen, mature germinating pollen, and pollen tubes to increasing temperatures is a critical target for improving the efficiency of reproductive development in crops. One possible avenue to this end is enabling or improving photosynthetic activity of anthers and pollen. There is substantial evidence pointing towards the photosynthetic potential of anthers in angiosperms (as reviewed by Clément & Pacini, 2001), however there has been little examination of this potential in planta (Murphy, Egger, & Walbot, 2015). Additionally and despite reports regarding the lack of photosynthetic activity of pollen grains, it is demonstrated that a significant proportion of angiosperms contains chloroplasts in pollen generative cells (Birky, 1995; Hu, Zhang, Rao, & Sodmergen, 2008; Sobanski et al., 2019). Moreover, important work to chart cytoplasmic dynamics during generative cell formation in *A. thaliana* by Kuang and Musgrave (1996) shows that released microspores actively accumulate starch. Concurrently, it is apparent that there is potential for active CO_2 fixation during and after pollen development, which is reflected by the differential expression during heat stress of genes known to regulate photosynthesis in pollen grains (Figure 2c; Rahmati Ishka et al., 2018). Improvements to this end could boost respiratory substrate reserves of mature pollen grains to cope with increasing demand during heat stress. As we have already discussed, excessive respiration during elevated temperatures also results in over-accumulation of ROS, which can impair pollen germination and pollen tube growth as demonstrated in multiple species (Kaya et al., 2015; Maksimov, Evmenyeva, Breygina, & Yermakov, 2018; Speranza et al., 2012). This has in turn been linked to reduced seed set in sorghum by more than 60% due in part to reduced pistil viability (Djanaguiraman et al., 2018). Consequently, improving ROS homeostasis, potentially via the action of flavanols (Muhlemann, Younts, & Muday, 2018) or ABA (Li, Zhang, et al., 2020), maybe a key avenue to improve the thermotolerance of reproductive development. Finally, it may be possible to counter the demand from increasing respiration during development, germination and pollen tube growth under heat stress via more efficiently utilizing alternative respiratory substrates via autophagy, which is an important action for aiding cells in coping with harsh environments and achieving pollen germination (Zhang et al., 2011). The potential of autophagy to this end is discussed in the subsequent section.

7.6 | Negating respiratory carbon loss via autophagy during reproductive development

The maintenance of cellular homeostasis through intracellular recycling represents a novel adaptive approach through which plants may limit the detrimental impact increased respiration has on reproductive development (Chen, Shinozaki, et al., 2019). The imbalance in carbon supply and demand shaped by declining photosynthesis and increasing respiration during heat stress perturbs energy homeostasis (Avin-Wittenberg et al., 2015; Su et al., 2020). Autophagy, that is, the intracellular recycling of cytoplasmic components, can contribute to energy supply under conditions of carbon starvation by providing alternative respiratory substrates, for example, free amino acids (Izumi, Hidema, Makino, & Ishida, 2013; Plaxton & Podestá, 2006). This is well demonstrated by the study of Avin-Wittenberg et al. (2015), where the authors measured the response to carbon starvation of mutant *A. thaliana* seedlings incapable of initiating autophagy. Autophagy mutant lines demonstrated both decreased flux to net protein synthesis and increased respiration compared to non-mutants, thereby highlighting the importance of autophagy during carbon starvation for supplying energy (Avin-Wittenberg et al., 2015). A more recent study focusing again on *A. thaliana* observed that autophagy deficient mutants demonstrated almost complete male sterility under high temperatures where wild-type lines did not (Dündar et al., 2019), thus demonstrating the importance of autophagy to address the increasing respiratory demand of reproductive structures and microspores during heat stress. It is further interesting to note that in our querying of the response of genes involved in photosynthetic regulation (Wang et al., 2017) to heat stress in *A. thaliana* pollen, *BRASSINAZOLE-RESISTANT1* (*BZR1*) is significantly up-regulated in response to heat stress (Figure 2c). This is interesting because *BZR1* has recently been implicated in mediating brassinosteroid-induced autophagy in tomato (Wang, Cao, et al., 2019). Tomato is particularly sensitive to high temperatures during flowering (Gonzalo et al., 2020), consequently exploring the importance of *BZR1* in this context may represent an interesting approach for mitigating heat stress. A gene involved in photosynthetic

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regulation, *ARABIDOSPSIS TRANSCRIPTION ACTIVATION FACTOR 1* (*ATAF1*), was observed to be significantly up-regulated in our querying of differentially expressed genes in rice panicles in response to heat stress (Figure 2d; Wang, Zhang, et al., 2019). *ATAF1* has been identified as a master-regulator of multiple genes that elicit autophagy in response to carbon starvation by facilitating amino acid catabolism, thereby allowing the use of free amino acids as alternative respiratory substrates (Garapati et al., 2015).

8 | CONCLUDING REMARKS

Fertilization and grain-filling are dependent on the availability and trans-location of photosynthetically fixed carbon (Ainsworth & Long, 2020; Li, Lawas, et al., 2015). Rising temperatures modify carbon metabolism and impair reproductive development (Figure 1). These processes are linked via source–sink relationships (Smith et al., 2018); however, the mechanisms that stabilize this dynamic during heat stress are phenology-dependent (Wingler, Purdy, Edwards, Chardon, & Masclaux-Daubresse, 2010). This developmental specificity defines the importance of heat tolerance mechanisms and is reflected by the importance of fine-tuning net carbon gain and carbon allocation with flowering (Lyu et al., 2018; Nuccio et al., 2015). Upon floral transitioning, harnessing of intermediate sources of photoassimilates and fixing carbon directly within sinks via non-foliar photosynthesis holds great promise for the supply of respiratory substrates for reproduction, as energy demands increase with temperature. To this end, studies are now beginning to report links between resilient carbon dynamics and stabilized reproduction during heat stress (Molero & Reynolds, 2020; Sanchez-Bragado et al., 2016; Šebela et al., 2015). Moving forward, developing and combining rapid and non-invasive phenotyping approaches that facilitate the quantification of reproductive development and carbon metabolism at multiple scales will facilitate a rigorous testing of potential links. Determining the importance of these links across environments will be critical for informing crop development to account for cofounding environment interactions and ultimately for breeding for heat stress resilience.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

John N. Ferguson conceived and outlined the structure of the review. All authors contributed to the writing of the article. Alison C. Tidy performed the bioinformatic analyses associated with and produced Figure 2. John N. Ferguson produced and conceived all additional figures.

DATA AVAILABILITY STATEMENT

The data used to produce the figures in this manuscript are available upon request to the corresponding author.

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