

REVIEW

Crop Economics, Production, & Management

Elevated temperature effects on functional yield drivers in cotton

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Abstract

Gossypium hirsutum L. (cotton) yields are limited by heat stress. Breeding for heat tolerance is an important goal, yet the most important functional contributors to heat-induced yield loss must first be defined. Although Monteith defined crop yield decades ago as the product of intercepted photosynthetically active radiation, radiation use efficiency (RUE), and harvest index (HI), a review of heat stress effects on these functional yield drivers or their underlying processes is still needed for cotton. Heat stress is known to affect canopy development, which could impact radiation interception. Specifically, leaf area declines when plants are exposed to maximum air temperatures greater than 35°C. However, direct evidence for a yield-limiting decline in intercepted radiation under high temperature is lacking. Though information is limited in peer reviewed literature, RUE (photosynthetic efficiency of the canopy) may be an important contributor to heat-induced yield loss, and this review explores the heat sensitivity of RUE and underlying photosynthetic processes. HI is the ratio of economic yield to biological yield, and current evidence indicates that reproductive processes are more heat sensitive than vegetative growth processes. Therefore, lower HI is discussed as a potentially significant contributor to heat-induced yield loss, and the relative heat sensitivity of reproductive processes and specific yield components is explored in detail. In the future, there is a need for (1) field studies addressing the temperature responses of canopy-scale yield drivers, (2) further exploration of nighttime temperature effects, and (3) targeted selection for increased heat tolerance of physiological yield drivers.

Plain Language Summary

Many studies have explored how heat stress affects cotton plants. This review addresses how heat influences three main drivers of yield: light interception by the crop canopy, how efficiently plants convert that light into biomass, and biomass into the harvestable portion of the crop (harvest index). Although there is limited information available, we know that leaf area declines at air temperatures of 35°C–40°C. This may reduce the amount of light the crop can receive if chronic heat stress is experienced before canopy closure, but there is little evidence that light interception

Abbreviations: HI, harvest index; IPAR, intercepted photosynthetically active radiation; LAI, leaf area index; RUE, radiation use efficiency.

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is an important driver of heat-induced yield loss. In controlled studies, the ability of cotton plants to use absorbed light for canopy level photosynthesis and biomass production declines under heat stress during reproduction. Harvest index might be an important contributor to yield losses under heat stress because reproductive growth (especially the number of cotton bolls produced) is more sensitive to heat than is vegetative growth. Moving forward, it is clear that more field studies on the effects of heat stress on these three functional yield drivers will be needed.

1 | INTRODUCTION

1.1 | The problem

Upland cotton (*Gossypium hirsutum*) is the most widely grown fiber crop in the world, and the United States ranks fourth in cotton production and second in cotton export globally (Lanclos et al., 2025). The downstream economic impacts of the US cotton industry make it the number one value-added crop in the country (Gaussoin et al., 2015), accounting for approximately \$100 billion in total economic activity annually (NCCA, 2019). The income generated from cotton production is also an integral part of food security on smallholder farms across the globe (Ferreira, 2019). In addition to its importance as a fiber crop for the textile industry, cottonseed is an important source of protein-rich feed for livestock and oil for cooking purposes (NCCA, 2019), making cotton one of the most diversely valuable crops ever domesticated. As a result, environmental stresses that have widespread negative effects on cotton production can be devastating for rural communities, the national economy, and the global economy.

Cotton flowering and boll development occur during summer months when exposure to heat stress is most likely (Snider et al., 2021). This is particularly concerning for the following reasons: (1) Excessively high air temperatures during these stages are already considered important drivers of extreme year-to-year yield variability for irrigated cotton in the southern United States (Oosterhuis, 2002). (2) Many cotton production regions of the globe routinely exceed the optimum temperature range for reproductive development and yield formation (Oosterhuis & Snider, 2011; Snider & Oosterhuis, 2012; Snider et al., 2013). (3) The frequency, duration, and intensity of extreme heat wave events are only expected to increase in the decades to come (Meehl & Tebaldi, 2004). Another major challenge to sustainable cotton production is the low genetic diversity among modern cotton cultivars. Selection for agronomically desirable traits during domestication and subsequent crosses between closely related genotypes has led to consistent improvements in yield for upland cotton (Campbell et al., 2011; Conaty & Constable, 2020). However, these selective breeding efforts have resulted in drastic reductions in allelic diversity when compared with wild rel-

atives (Brubaker et al., 1999; Lubbers & Chee, 2009; May et al., 1995; Wendel et al., 1992). The end result has been a shallow gene pool from which to select for other potentially valuable traits such as tolerance to abiotic stresses (Paterson et al., 2004). Although some investigators have screened for heat tolerance in existing cotton cultivars (Cottee et al., 2010; Jaconis et al., 2021), selective breeding for heat tolerance has been nonexistent (Saranga et al., 2009). Consequently, the cotton industry will be exceptionally vulnerable to extreme high temperature events if efforts are not made to accelerate targeted selection for heat tolerance. To accomplish this, it will be essential to first identify the most heat-sensitive functional contributors to yield.

1.2 | Functional yield drivers

Irrespective of crop, it has been known for decades that yield is a product of the total amount of photosynthetically active solar radiation intercepted by a crop canopy during a growing season, the efficiency with which that radiation is converted into biomass, and the fraction of total biomass distributed to the economically valuable portion of the crop (Earl & Davis, 2003; Monteith, 1977). Using the terminology defined extensively elsewhere (Conaty & Constable, 2020; Earl & Davis, 2003; Ermanis et al., 2021; Pokhrel et al., 2023; Virk, Snider, Chee, et al., 2023), we will refer to these yield drivers as intercepted photosynthetically active radiation (Σ IPAR), radiation use efficiency (RUE), and harvest index (HI). The underlying factors governing Σ IPAR include environmental factors that have little to do with the inherent physiology of the crop (daily insolation and growing season length) and plant-specific factors such as leaf area and the light extinction coefficient of the canopy (Conaty & Constable, 2020; Constable & Bange, 2015). RUE can be influenced by crop-specific differences in photosynthetic strategy (C3 versus C4 crops) (Choudhury, 2001; Long et al., 2006; Zhu et al., 2010), canopy architecture (Gonias et al., 2011; Reynolds et al., 2000), and the efficiency of photosynthate conversion to specific macromolecules (Rosenthal & Gerik, 1991; Sadras et al., 2016). For a crop like upland cotton, HI is influenced by the fraction of total aboveground growth allocated to fruit (bolls) and the intra-boll distribution of biomass to specific yield com-

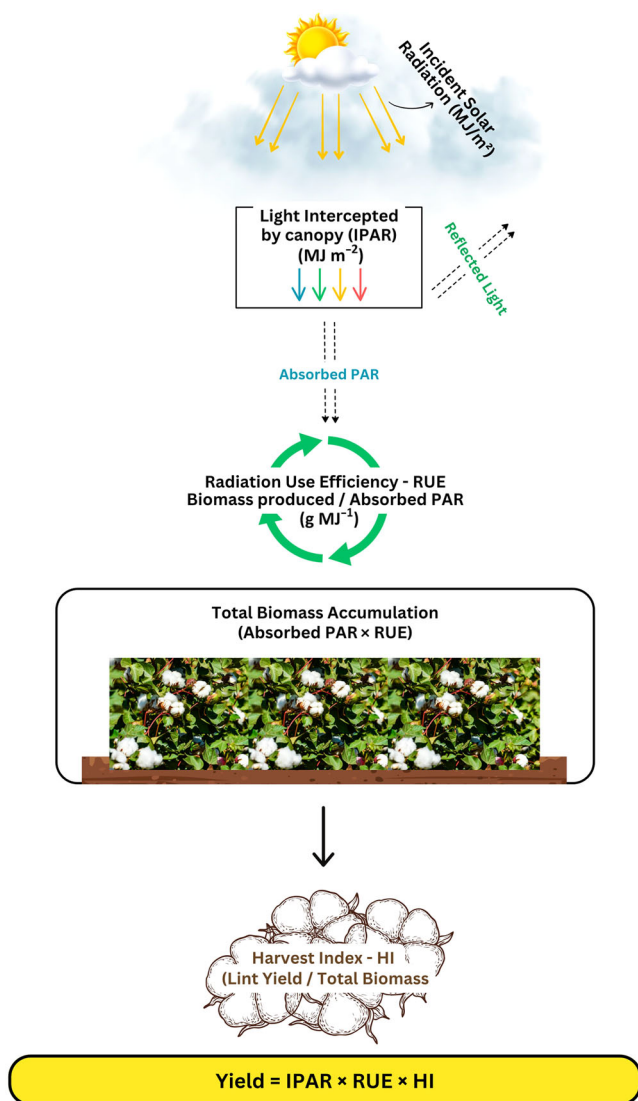


FIGURE 1 Physiological framework for cotton yield formation. While it is true that radiation use efficiency (RUE) would be most accurately estimated by using absorbed photosynthetically active radiation (PAR) in its calculation, in practice, intercepted PAR is most commonly utilized. Figure created with Canva (www.canva.com). HI, harvest index.

ponents (Conaty & Constable, 2020; Lee et al., 2023; Virk et al., 2024; Virk, Snider, & Bourland, 2023; Virk, Snider, Chee, et al., 2023; Wells & Meredith, 1984). An overview of the physiological framework for yield formation is provided in Figure 1. The importance of $\sum$ IPAR, RUE, and HI in governing yield variation has been addressed in the literature for upland cotton in response to genotype (Kaur et al., 2024; Virk, Snider, Chee, et al., 2023) and in response to management practices such as irrigation and nitrogen fertilization (Ermanis et al., 2021; Pokhrel et al., 2023). Our understanding of the extent to which each of the processes contributes to heat-induced yield loss is much more limited. Consequently, the purpose of this review is to (1) provide a synthesis of available literature on the heat sensitivity of functional yield drivers

Core Ideas

- Monteith (1977) defined crop yield as the product of intercepted photosynthetically active radiation, radiation use efficiency, and harvest index.
- A review of heat stress effects on these yield drivers or their underlying processes is still needed for cotton.
- Canopy growth is sensitive to high temperature, but there is no evidence for a yield-limiting decline in intercepted radiation.
- Radiation use efficiency and harvest index decline substantially and may co-limit yield under heat stress.
- Differential heat sensitivities of reproductive and vegetative processes contribute to reductions in harvest index.

in upland cotton and (2) identify significant knowledge gaps and opportunities for future research aimed at improving cotton tolerance to high-temperature extremes. At the outset, it is important to note, unless otherwise stated, the term “temperature” refers to the air temperature the plant is exposed to and not necessarily the plant temperature. This is an important distinction because transpiration is an important energy dissipation mechanism that cools canopy surfaces (Chastain, Snider, Collins, et al., 2016; Conaty et al., 2014, 2015). In fact, early observations indicated that cotton plants exhibited some level of limited homeothermy by keeping leaf temperature below 35°C, even under high air temperature extremes (40°C) (Upchurch & Mahan, 1988). The exact temperature differential between leaves and the surrounding air depends on water availability and vapor pressure deficit (Chastain et al., 2016). Under water deficit conditions, stomatal closure can lead to leaf temperatures that are equivalent to or in excess of air temperature (Chastain et al., 2016; Chastain et al., 2016; Snider, Chastain, et al., 2015). For well-watered plants, increases in vapor pressure deficit lead to greater leaf to air temperature differentials (Chastain et al., 2016), but cultivar differences in transpiration response to vapor pressure deficit have also been reported (Shekoofa et al., 2021; Wedegaertner et al., 2022). As a result, tissue temperatures could even differ among cultivars exposed to the same air temperatures.

2 | HEAT STRESS EFFECTS ON LIGHT CAPTURE BY COTTON CANOPIES

Despite the paucity of data on heat-stress effects on canopy light capture in cotton, inferences can be made from previous studies on shoot growth responses. This is because the leaf area index (LAI) is one of the primary factors governing

the fraction of light intercepted by the crop canopy (Conaty & Constable, 2020). In a field setting, planting date is well-known to affect early-season crop growth rates, primarily by altering the rate of leaf expansion and, by extension, LAI (Virk et al., 2019, 2020). Planting date-dependent variation in early season canopy growth is generally attributed to prevailing soil and air temperature conditions at planting and soon thereafter, with suboptimal temperatures being the dominant driver of slow growth (Virk et al., 2019). Most research addressing the effects of high-temperature extremes on early season plant growth has been done in controlled environment facilities (K. R. Reddy et al., 1992; Kaur, Snider, Parkash, et al., 2023; K. R. Reddy et al., 2017; V. R. Reddy, Reddy, & Baker, 1991; Virk et al., 2021). For example, one of the most extensive studies of high-temperature effects on early canopy development (K. R. Reddy et al., 1992) evaluated plant growth for cotton in sunlit chambers under five different temperature regimes from 0 to 56 days after emergence. Rates of mainstem node development were positively affected by increases in temperature up to daily maximums of 40°C. However, the authors noted that leaf area per plant by the end of the experimental period peaked at a daily maximum of 30°C and then declined substantially (~50% at 40°C) at successively higher temperatures. Total biomass trends were comparable to total leaf area trends. The mechanistic basis for these observations is that high-temperature-grown plants produced the most leaves due to rapid initial development; however, those leaves had much lower individual areas due to heat-induced reductions in individual leaf expansion. Recent studies have reported similar reductions in leaf area and concomitant increases in the number of mainstem nodes in the early stages of seedling growth (2–4 weeks) when maximum daytime temperatures reached 40°C (Adegbenro et al., 2025; Kaur, Snider, Parkash, et al., 2023; Virk et al., 2021). In contrast, where high air temperatures are experienced during reproductive phases of growth, poor seed set or heat-induced fruit loss can lead to excess vegetative growth, producing taller plants, self-shading, and a need for more aggressive growth control strategies (Hake & Silvertooth, 1990; Snider et al., 2021).

Collectively, these reports indicate that the impact of high temperature extremes on light capture by cotton canopies will be highly dependent on the growth stage at which heat stress is experienced. High temperatures between 35°C and 40°C will decrease leaf area and shoot biomass substantially if the stress is experienced for a sufficient period of time between planting and canopy closure. If heat stress is experienced after canopy closure, typically 2 weeks after the start of flowering (Ritchie et al., 2007), the expansion of new leaves may be negatively impacted, but limitations to whole-canopy light interception should be minimal. To our knowledge, there is only one study in which light interception by the cotton canopy and other yield drivers addressed in this review, were quanti-

TABLE 1 Optimum temperature ranges for canopy growth traits and photosynthetic activities in cotton (Kaur, Snider, Parkash, et al., 2023; Lokhande & Reddy, 2014; Parkash et al., 2024; K. R. Reddy, Hodges, & Reddy, 1992; Virk et al., 2021).

Processes	Optimum temperature (°C)	Critical temperature (°C)
Leaf area	30–35	>35
Mainstem nodes	30–40	>40
Plant height	30–35	>35–40
Dry biomass	30–35	>35
Net photosynthesis	30–35	>35–40

fied in response to yield-limiting heat stress (Álvarez et al., 2025). The authors utilized transparent enclosures, which led to increases in average daily maximum temperature during their experimental period ranging from 5.8°C to 5.9°C above ambient. Stress was imposed either prior to or during the flowering period. Despite yield losses ranging from 42% to 75% under heat stress, cumulative IPAR during the growing season was unaffected by any of the high-temperature treatments. Table 1 summarizes the optimum temperature ranges for canopy growth traits.

3 | HEAT STRESS EFFECTS ON RADIATION USE EFFICIENCY AND PHOTOSYNTHETIC RESPONSES

Similar to studies addressing light interception in cotton, those addressing the impacts of high temperature on whole canopy RUE are limited. Before delving further into high-temperature effects on RUE by the canopy, it is important to first define RUE. RUE refers to the efficiency with which the entire canopy converts intercepted or absorbed radiation into photosynthate or biomass. It can be measured by dividing the change in biomass over a defined period of time by the amount of radiation intercepted by the canopy in a given period of time. Alternatively, it can be expressed as cumulative whole canopy photosynthesis divided by intercepted or absorbed radiation. Research conducted decades ago in controlled environment soil-plant-atmosphere research facilities indicated that whole plant RUE ($\mu\text{mol CO}_2 \mu\text{mol}^{-1}$ photons) was not consistently affected by high temperature (35°C/27°C) between 64 and 70 days after emergence (V. R. Reddy et al., 1995). However, in another experiment, the investigators imposed heat stress for 48 consecutive days beginning during the flowering period (V. R. Reddy et al., 1991). Near the end of the experimental time frame, RUE (for whole plant CO_2 exchange) peaked at a maximum daily temperature of 35°C and declined as much as 26% for plants at a maximum daily temperature of 40°C.

Furthermore, other authors have indirectly exposed the cotton crop to different temperature conditions by manipulating either planting date or growing the crop in different environments. For instance, F. Wu et al. (2023) utilized six different sowing dates in two different growing seasons to generate substantial variation in environmental conditions at different growth stages. The authors documented negative correlations between yield and the mean or minimum temperature during the squaring (floral bud development) or seedling stage. However, RUE was not associated with yield variation, and the correlation between temperature variables was confounded by a negative correlation with soil water availability. Another study noted decreases in RUE in cotton plants grown in contrasting environments due to increases in vapor pressure deficit. Field-grown cotton plants in California (characterized by higher maximum temperatures and vapor pressure deficit) had lower RUE (1.52 g MJ^{-1}) than in Arkansas, with an RUE of 2.06 g MJ^{-1} (Gonias et al., 2012). However, in addition to temperature, the two environments also differed in relative humidity and total incident PAR, both of which could have driven RUE variation. Likely due to logistical constraints associated with conducting high-temperature experiments under field conditions, information on biomass-based RUE responses to directly imposed heat stress is incredibly limited. The experiment conducted by Álvarez et al. (2025) showed that experimentally imposed, yield-limiting heat stress reduced RUE by as much as 53% under field conditions.

Because RUE represents a measure of the photosynthetic efficiency of the canopy, it is tempting to speculate about canopy-level responses based on publications addressing single-leaf responses to temperature. There have been numerous reports documenting similar responses of single-leaf photosynthesis and whole-canopy assimilation or RUE (Earl & Davis, 2003; Kiniry et al., 1999; Rosati et al., 2004); however, single-leaf photosynthetic trends may not always agree with whole-canopy responses (Kiniry et al., 1999). This is likely because canopy structure can influence RUE, as can the partitioning of photosynthate to different types of macromolecules such as carbohydrates, lipids, and proteins (Kiniry et al., 1999; Rosenthal & Gerik, 1991). Thus, there is a clear need to develop functional frameworks that can be used to scale up from leaf level to canopy level responses, as discussed previously elsewhere (Milroy & Bange, 2003; A. Wu, 2023). Nonetheless, it is informative to gain a working knowledge of the impacts of heat stress on photosynthetic responses. First, there are numerous studies addressing the response of net photosynthetic rate (A_N) to high temperature. Generally, A_N declines when leaf temperatures reach somewhere between 35°C and 40°C (Table 1) (Crafts-Brandner & Salvucci, 2000; Law & Crafts-Brandner, 1999; Snider & Oosterhuis, 2015; Snider et al., 2009). Some of this decline is associated with the positive response of respiration to increas-

ing temperature, where the Q_{10} value (fold change for each 10°C increase in temperature) for respiration is 1.86 (Salvucci & Crafts-Brandner, 2004). However, care should be taken not to too broadly apply a Q_{10} response of respiration, as some studies have shown that plants alter their respiratory temperature response based on prior growth temperature (Snider et al., 2022; Way & Yamori, 2014). Nonetheless, acute high-temperature exposure does positively impact respiration up to leaf temperatures of at least 45°C (Salvucci & Crafts-Brandner, 2004). Photorespiration can also be considered a contributor to reduced assimilation rates under high temperatures since multiple authors have documented increases in photorespiratory carbon losses or decreases in the ratio of carboxylation to oxygenation under high temperatures (Parkash et al., 2024; Perry et al., 1983). Specifically, at 40°C , photorespiration accounted for 50% of net photosynthesis, compared to a temperature of 22°C , where photorespiration represented less than 15% of net photosynthesis (Perry et al., 1983). Additionally, at a high daytime air temperature of 40°C , the total electron flux partitioned to photorespiration increased by 36%, while the rate of electron flow driving CO_2 assimilation decreased by 14% as compared to an optimal day temperature of 30°C (Parkash et al., 2024). Photorespiration rates, defined by the percentage of Rubisco-oxygenase activity, increase by approximately 2.7% for every 1°C increase in leaf temperature (Guthrie et al., 1994). These decreases in Rubisco-specific carboxylase activity at high temperatures could be attributed to several factors not limited to the decreased affinity of Rubisco for CO_2 , lower specificity for CO_2 (Brooks & Farquhar, 1985; Jordan & Ogren, 1984), and a reduced ratio of CO_2 to O_2 solubility (Ku & Edwards, 1977).

In addition to increasing respiratory and photorespiratory carbon losses, high-temperature stress can also directly and negatively impact the photosynthetic apparatus. The exact cause of this photosynthetic inhibition was the subject of vigorous debate and study for decades. Unfortunately, one misconception that continues to appear in the peer-reviewed literature about heat stress is that photosystem II is the most heat-sensitive component of the photosynthetic apparatus (Paulsen, 1994; Pettigrew & Gerik, 2007; Saini et al., 2023). It is true that the total electron flux or actual quantum yield of electron transport through photosystem II under light-adapted conditions follows a similar temperature response to A_N (Armond et al., 1978; Berry & Björkman, 1980; Björkman et al., 1978). Similarly, it has been shown that photosynthetic carbon fixation and the actual quantum yield of photosystem II in cotton plants both declined at air temperatures above 36°C (Bibi et al., 2008). However, total electron flux under light-adapted conditions can be limited by several other processes occurring beyond photosystem II (Feller et al., 1998; Schrader et al., 2004). As a result, reductions in electron transport rate through photosystem II under light-adapted conditions only indicate that high temperatures limit

photosynthesis. Limitations to photosynthesis could occur at photosystem II, but they could also occur at sites beyond photosystem II, thereby limiting the efficiency of light-dependent electron transport. Importantly, dark-adapted, fluorescence-based measurements of the maximum quantum yield of photosystem II (F_v/F_m) allow researchers to determine the efficiency of photosystem II in the absence of other co-occurring processes (Maxwell & Johnson, 2000). In studies where dark-adapted fluorescence measurements have been taken alongside gas exchange measurements of A_N , photosystem II shows minimal inhibition, even at high-temperature extremes that drastically limit photosynthetic CO_2 assimilation or rubisco activity (Feller et al., 1998; Pettigrew, 2016; Salvucci & Crafts-Brandner, 2004). Photosystem II also readily acclimates to prevailing high air temperature conditions by shifting its high-temperature threshold upward to far exceed ambient temperature conditions (Hu, Snider, Chastain, et al., 2018; Kaur, Snider, Parkash, et al., 2023; Kaur, Snider, Paterson, et al., 2023; Snider et al., 2013). When the heat sensitivity of photosystem II, photosystem I, and intersystem electron transport are compared simultaneously, photosystem II and I are both significantly more thermotolerant than intersystem electron transport (Kaur, Snider, Parkash, et al., 2023; Kaur, Snider, Peterson, et al., 2023; Snider, Chastain, & Collins, 2015). This does not mean that photosystem II never shows reductions in efficiency under high temperatures; see previous reports for examples (Snider et al., 2010; Snider et al., 2015; Van der Westhuizen et al., 2020). However, when the thermotolerance of photosystem II is compared alongside other components, it becomes clear that it is among the least heat-sensitive processes.

Work conducted by numerous authors in multiple different species provided convincing evidence that rubisco activase was the weak link in photosynthetic temperature responses. First, the authors showed that in vivo carboxylation rates were equally as heat sensitive as net photosynthetic rates (Crafts-Brandner & Salvucci, 2000; Salvucci & Crafts-Brandner, 2004), while the maximum quantum yield of photosystem II was relatively insensitive to moderately high leaf temperatures ($<45^\circ\text{C}$) that limit CO_2 fixation (Crafts-Brandner & Law, 2000; Law & Crafts-Brandner, 1999; Salvucci & Crafts-Brandner, 2004). Second, isolated rubisco was far more heat tolerant than rubisco in combination with rubisco activase (Salvucci et al., 2001). In vitro activities of the latter could fully explain the heat sensitivity of gas exchange-based photosynthetic rates. Subsequent work conducted under field conditions and using natural variation in leaf temperature for Pima cotton indicated that ribulose-1,5-bisphosphate regeneration and electron transport were more heat sensitive than carboxylation (Wise et al., 2004). Furthermore, Schrader et al. (2004) showed that moderately high temperatures were sufficient to disrupt electron transport processes in thylakoid membranes. Based on these observations and, more recently,

those of Scafaro et al. (2023), it is likely that rubisco activase and electron transport (at sites other than photosystem II) co-limit photosynthesis under high-temperature conditions. For an overview of acute heat stress effects on photosynthesis, readers are referred to Figure 2.

4 | HEAT STRESS EFFECTS ON HARVEST INDEX AND YIELD COMPONENTS

Finally, we address HI, which is the ratio of economic yield (lint yield) to biological yield (total aboveground biomass). HI is influenced by the balance between vegetative and reproductive growth in addition to dry matter distribution to specific yield components. Vegetative growth is clearly less sensitive to high temperatures than reproductive development (Lokhande & Reddy, 2014; K. R. Reddy, Hodges, & Reddy, 1992; K. R. Reddy et al., 1992; K. R. Reddy et al., 1997; Snider & Oosterhuis, 2011, 2012). Specifically, K. R. Reddy, Hodges, and Reddy (1992) reported reductions in total plant biomass of 11.2% for cotton plants grown under a season-long high day/night temperature of $35^\circ\text{C}/25^\circ\text{C}$ compared to an optimal growth temperature of $30^\circ\text{C}/20^\circ\text{C}$. By comparison, reproductive growth measured by boll weight per plant declined by 88.3% under the same high-temperature condition. Additionally, the reproductive-to-vegetative growth ratio, defined as the fruit production efficiency, declined by 86.9% under the same temperature conditions. At $40^\circ\text{C}/30^\circ\text{C}$ day/night temperatures, the differences in heat sensitivity for vegetative and reproductive growth are even more drastic. High-temperature-grown plants exhibit near-complete loss (99.4%) of reproductive growth and yield (quantified by boll weight), while only a 31.2% reduction in vegetative growth was observed compared to the optimum temperature. V. R. Reddy et al. (1991) noted a 50% reduction in cotton dry weight at $40^\circ\text{C}/30^\circ\text{C}$ and 100% boll loss compared to an optimum temperature of $30^\circ\text{C}/20^\circ\text{C}$. Similar reports by the authors showed complete abscission of squares, leading to no boll formation for cotton plants grown under $40^\circ\text{C}/32^\circ\text{C}$ (K. R. Reddy et al., 1992). More recent work by Lokhande and Reddy (2014) similarly documented reductions in reproductive efficiency (ratio of reproductive to total biomass) as average daily temperature increased from 25.5°C to 29.5°C . While the observations made in previous studies would lead one to assume that HI must be one of the primary limitations to yield, very few studies have specifically documented the effects of heat stress on HI. Interestingly, a 3-year study by Pettigrew (2008) reported a 16% increase in HI in 1 year of their 3-year experiment for cotton plants grown under the warmer temperature regime ($\sim 1^\circ\text{C}$ higher than ambient). This could have been due to a higher crop maturity rate; however, statistically significant increases in HI were not observed in

Sensitivity of Photosynthetic Processes to Heat Stress

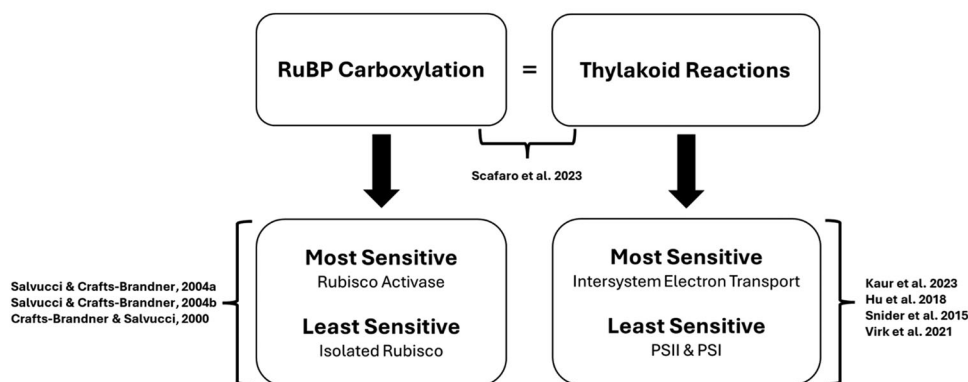


FIGURE 2 Relative sensitivity of photosynthetic processes to heat stress. Ribulose-1,5-bisphosphate (RuBP) carboxylation and photosynthetic electron transport during the thylakoid reactions are considered equally sensitive to high temperature and likely co-limit photosynthesis in most terrestrial plants. Rubisco activase is the most heat-sensitive factor driving high temperature-induced reductions in RuBP carboxylation. Within the thylakoid reactions, electron transport between the photosystems is the most heat sensitive. PS, photosystem.

years where yield was limited by elevated temperature. When an enclosure was used to induce temperature increases and cause yield loss for field grown cotton in Argentina, the heat induced reductions in HI ranged from 40% for pre-flowering heat stress to 60% for heat stress imposed during flowering (Álvarez et al., 2025). These declines are comparable to those observed for whole-canopy RUE in the same study, indicating that these yield-driving variables were equally important contributors to heat-induced yield loss. We note here that HI estimates in cotton are somewhat complicated by the fact that cotton is an indeterminate crop. This means that individual bolls on the same plant will reach maturity at different times. To avoid economic yield loss, it is necessary to wait until the uppermost harvestable bolls have reached maturity before harvest aids are applied (Gwathmey et al., 2016). Biomass assessments typically need to be conducted in the days immediately preceding harvest aid application to ensure maximum biomass accumulation (Conaty & Constable, 2020; Constable & Bange, 2015).

Moreover, economic yield (lint weight per unit land area), a component used to derive HI, can be defined as a product of boll density, individual boll weight, and lint percent (Hu, Snider, Wang, et al., 2018) or as the product of boll density, seed number per boll, and lint weight per seed (Snider et al., 2021). Hence, the impact of elevated temperatures on any or all of these components could influence HI or lint yield. When considering the yield components above, seed set and boll retention are probably the most heat-sensitive contributors to yield loss. For example, Pettigrew (2008) noted that declines in individual boll mass (6%) and the number of seeds per boll (7%) were the main drivers of the 10% decrease in lint yield observed under slightly elevated temperatures in the field. Since yield reductions were not associated with declines in boll numbers, an argument could be made

for seed number being the most heat-sensitive driver of yield. However, boll retention is well-known to be highly sensitive to elevated growth temperature (Hodges et al., 1993; Lokhande & Reddy, 2014; V. R. Reddy et al., 1991). Research conducted by Lokhande and Reddy (2014) documented 45% reductions in boll number per plant compared with only 24% and 25% reductions in seed number and seedcotton mass per boll as average daily temperatures increased from 25.5 to 29.5°C. Research conducted by Yang et al. (2024) showed that elevated temperatures (34°C daily maximum) were able to significantly reduce fruit retention, yet declines in fruit retention were offset by increases in boll mass, resulting in no reduction in lint yield. This response was attributed to carbohydrate redistribution within the plant. Where lint percent or lint mass per seed are documented under heat stress, these traits are less responsive to high temperature than boll retention and seed set. For example, the previously mentioned study by Lokhande and Reddy (2014) documented only 19% reductions in lint percent and lint mass per seed compared with 24%–45% for boll number and boll mass. Elevated temperature experiments in the field have shown relatively minimal changes in lint percent and lint mass per seed (0%–2.8%), even when heat-induced yield reductions ranged from 7% to 13% (Pettigrew, 2008). From five different reports in which yield loss and yield component responses were quantified, we have produced Figure 3 as a way to quantify the stress sensitivity of different yield components to high temperature. First, we identified studies in which heat stress treatments were imposed experimentally, where yield (per plant or per unit land area) was assessed, and where yield components were also assessed, leading to only a few publications from the peer reviewed literature. Since studies varied in their absolute treatment differences and the specific yield component variables quantified, the level of heat stress was expressed as

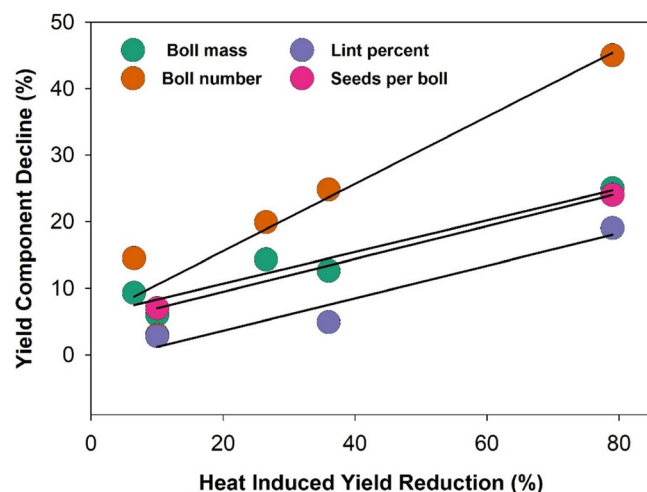


FIGURE 3 Percentage reduction in key yield components versus heat-induced yield loss in cotton. The following is a list of original research articles used to generate the summary graph: Lokhande and Reddy (2014), Pettigrew (2008), Saleem et al. (2018), Xin-Ying et al. (2013), and Yang et al. (2024).

relative yield loss for the heat stress treatment compared with the control treatment. Specifically, the *x*-axis in Figure 3 is the relative yield loss under high temperature, and the *y*-axis is the relative decline in one of four different yield component variables. Next, linear regression was used to define the responsiveness of each yield component variable to heat induced yield loss. Based on the slope and magnitude of the response, it is clear that boll number is the most sensitive yield component to yield-limiting heat stress, followed by seed number per boll and boll mass, which follow identical trends. Finally, lint percent is the least sensitive component to be affected by high temperature. It should be noted that boll number and seed number per boll are undoubtedly interrelated since ovule fertilization is required for seed set, and if an insufficient number of ovules are fertilized, the boll may abort (Stewart, 1986). The following section addresses the impacts of high temperatures on sexual reproduction in cotton.

The day of flowering is a critical event in seed and boll development and has been described extensively for decades. The following summary of reproductive events is heavily derived from Stewart (1986). The flower opens soon after sunrise, and pollination typically occurs within minutes of flower opening. The exact timing of flower opening and pollination is likely influenced by vapor pressure deficit as flower opening and pollination occurred earlier in the day when higher temperatures, and presumably lower relative humidities, are observed (Snider et al., 2011a). Thereafter, the pollen grains germinate on the surface of the stigma, and pollen tubes grow through the transmitting tissue of the style until they eventually reach the ovules inside the ovary. Once the pollen tube reaches the ovule, double fertilization occurs, and provided ovule abortion does not occur, the ovule is able to develop

into a fully mature seed. Thus, for yield to be produced, many processes must occur in a highly organized manner (Snider & Oosterhuis, 2011). While tissues such as the stigma, style, and embryo sac are all potential targets of heat-induced limitations to sexual reproduction (Snider et al., 2011a; Snider et al., 2009), they have received far less attention than viable pollen formation, germination, tube growth, and fertilization. As a result, the remainder of this review will focus on pollen-specific processes. Treatment of the subject will remain brief as the topic has been explored extensively in previous studies.

Pollen grain development begins with microspore meiosis. Subsequent mitotic divisions of haploid cells give rise to the microgametophyte (pollen grain). Microspore meiosis occurs somewhere between 2 and 3 weeks prior to flowering (Stewart, 1986), and high temperatures during this timeframe have been correlated with male sterility (Meyer, 1969; Stewart, 1986). Song et al. (2014) showed that prolonged exposure to temperatures in excess of 33°C during the squaring stage significantly reduced pollen viability (germination percentage) at the flowering stage in upland cotton. Masoomi-Aladizgeh et al. (2021) found that exposure of cotton to maximum air temperatures of 36°C for only 5 days during the tetrad stage of pollen development significantly reduced germination of mature pollen relative to a temperature of 28°C. Germination of otherwise viable pollen can be negatively affected by high-temperature exposure on the day of pollination. In vitro germination assays have traditionally been used to define optimal temperature ranges for the process. Using this approach, Burke et al. (2004) evaluated pollen germination at temperatures ranging from 20°C to 43°C. Temperatures greater than or equal to 37°C decreased pollen germination. Kakani et al. (2005) developed temperature response functions to estimate cardinal temperatures for pollen germination and concluded that 31.4°C produced the maximum percent germination. In vivo experiments under field conditions (using planting date to manipulate temperature) documented no reduction in pollen germination even at ambient temperatures near 35°C (Snider et al., 2011a). For pollen tube growth, research conducted by a number of researchers using in vivo and in vitro techniques indicates that the upper limit for optimal pollen tube growth is likely 33°C (Burke et al., 2004; Kakani et al., 2005; Liu et al., 2006; Snider et al., 2011a; Snider et al., 2011b). Figure 4 is a graphical summary of the peer-reviewed research discussed in the preceding text and is representative of most available original research on the topic. The lower temperature limit was defined as the lowest incubation temperature or lowest maximum daily temperature across all publications used here that still produced maximal values for a given process. The upper limit of the optimal temperature ranges represents the highest temperature evaluated across all publications used here that still produced maximum values for a given process.

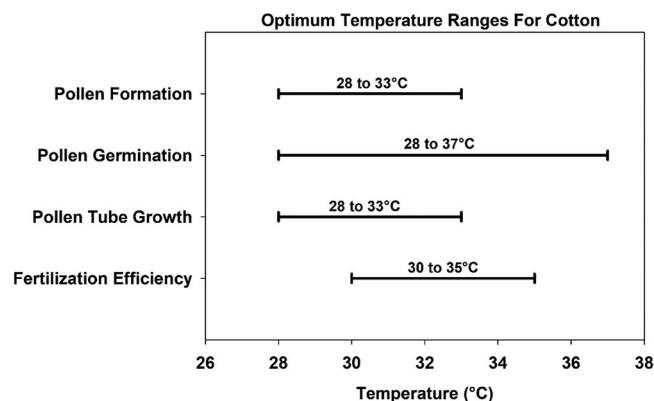


FIGURE 4 Optimum temperature ranges for key events in sexual reproduction for cotton. Bars represent the upper and lower temperature ranges at which each process has been shown to be maximal. Upper temperatures represent temperatures above which reductions in each process have been observed. In many instances, the lower end of the optimum temperature range only represents the lowest temperature tested. The following is a list of original research articles addressing heat stress effects: pollen formation (Masoomi-Aladizgeh et al., 2021; Song et al., 2014), pollen germination (Burke et al., 2004; Kakani et al., 2005; Snider et al., 2011a), pollen tube growth (Burke et al., 2004; Kakani et al., 2005; Liu et al., 2006; Snider et al., 2011a; Snider et al., 2011b), and fertilization (Snider et al., 2011a; Snider et al., 2011b; Snider et al., 2009).

5 | CONCLUSIONS

Extensive reviews have been written on the response of the cotton crop to high-temperature extremes (Majeed et al., 2021; Saini et al., 2023; B. Singh et al., 2020; R. P. Singh et al., 2007; Zahid et al., 2016). The current review is distinct in that it addresses the most heat-sensitive physiological contributors to yield in upland cotton within the conceptual framework of Monteith (1977). Specifically, we explore what is known about the heat sensitivity of canopy IPAR, RUE, and HI or their underlying processes.

1. The extent to which IPAR is affected by high temperature has received minimal attention in the peer-reviewed literature. However, leaf area (an important driver of IPAR) declines at temperatures between 35°C and 40°C, depending on the cultivar. As a result, IPAR could be negatively impacted by heat stress if the stress was experienced for an extended period of time prior to canopy closure. However, there is currently no evidence that yield-limiting heat stress has an appreciable impact on cumulative IPAR during a growing season (Álvarez et al., 2025). Limited expansion and radiation capture of key source leaves (subtending leaves) could contribute to heat-induced yield losses, even if whole-canopy IPAR is unaffected, but further study would be needed for this conclusion to be reached.

2. There are some data from controlled environment studies indicating that gas exchange-based RUE declines following chronic exposure to high temperatures of 40°C, but the declines only occurred during reproduction. Biomass-based RUE responses to high-temperature stress are extremely limited for field-grown cotton. In the one study where this was assessed, yield-limiting heat also caused substantial reductions in RUE. Thus, RUE is a likely contributor to yield reductions under elevated temperatures, yet temperature response experiments would need to be conducted in controlled field settings to define realistic upper temperature limits for RUE optimization. Net photosynthesis declines at temperatures between 35°C and 40°C, likely due to reductions in inter-photosystem electron transport rate or rubisco activase activity. By comparison, photosystem II is relatively heat-insensitive and readily acclimates to high temperatures.
3. HI is the ratio of economic yield to biological yield and represents the fraction of total biomass distributed to fiber. As with the other yield drivers, the impact of yield-limiting heat stress on HI is still underexplored, but HI is likely one of the most important contributors to heat-induced reductions in yield based on the following evidence. Reproductive growth is more heat-sensitive than vegetative growth, leading to more pronounced reductions in reproductive efficiency (reproductive biomass: total biomass) than vegetative biomass. In one of the only studies to document heat stress effects on yield and HI in field-grown cotton, HI was as negatively affected or more negatively than RUE when heat exposure occurred during reproduction (Álvarez et al., 2025). Fertilization of the ovules is required for seed set and may determine whether or not a boll is retained. Among the processes that lead to successful fertilization of the ovules, pollen formation (especially during microspore meiosis) or pollen tube growth are likely the most heat-sensitive processes. When yield reductions are observed with elevated temperature (per plant or per unit land area), boll number is the most heat-sensitive yield component, followed by seed set and boll mass, and distribution of boll biomass to fiber is the least sensitive.

6 | FUTURE DIRECTION

Despite extensive studies characterizing heat stress responses for complex physiological processes at the organ, plant, or cellular level in cotton (reviewed in Oosterhuis and Snider [2011], Saini et al. [2023], B. Singh et al. [2020], Snider and Oosterhuis [2011], and Snider and Oosterhuis [2012]), a number of research opportunities remain.

1. Research addressing the temperature responses of IPAR, RUE, and HI at the crop level are still needed. This is likely due to the constraints associated with conducting controlled heat stress experiments under field conditions. While some progress has been made through the use of heat tents or other enclosures in other crops (Cicchino et al., 2010, 2013; Hein et al., 2024; Shi et al., 2016), the deployment of these systems has been limited in cotton (Cottee et al., 2010), and only one paper that we are aware of has evaluated the aforementioned yield drivers in response to yield-limiting heat (Álvarez et al., 2025).
2. It has been argued that elevated night temperature poses a more significant threat to crop production than high day temperature (Sadok & Jagadish, 2020). However, the importance of night temperature in determining heat-induced yield reductions in cotton requires further exploration. In one of the only known field studies to explore the impacts of high night temperature (Soliz et al., 2008), yield reductions were not observed. Furthermore, the impacts of high night temperature on IPAR, RUE, and HI have not been evaluated.
3. Cultivar variation in heat tolerance of vegetative growth responses (Kaur, Snider, Parkash, et al., 2023; Virk et al., 2021), photosynthetic processes (Kaur, Snider, Parkash, et al., 2023; Kaur, Snider, Peterson, et al., 2023), and reproductive processes (Azhar et al., 2009; Kakani et al., 2005; K. Singh et al., 2018) have all been documented in controlled environment studies previously. Yield also exhibits cultivar variation in heat tolerance (Cottee et al., 2010; Xu et al., 2022; Zafar et al., 2023). Consequently, IPAR, RUE, and HI would be expected to exhibit cultivar-specific responses to temperature, yet this possibility remains an open question.

AUTHOR CONTRIBUTIONS

John L. Snider: Conceptualization; data curation; formal analysis; investigation; supervision; validation; writing—original draft; writing—review and editing. **Comfort O. Adegbenro:** Data curation; formal analysis; investigation; validation; visualization; writing—original draft; writing—review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data will be made available on request.

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