



Article Heat Stress Reduces Yield Through a Negative Effect on Radiation Use Efficiency during the Reproductive Phase in Cotton (Gossypium hirsutum L.) under Different Source Availabilities

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Abstract: Cotton is frequently exposed to high temperatures during the reproductive stage, which can negatively impact productivity. While previous research has shown that photosynthesis can decrease under heat stress, there is limited information on the effects of heat stress during the reproductive phase on crop variables such as radiation capture, use efficiency, and yield. This study aimed to: (i) assess the effect of heat stress on cumulative intercepted PAR radiation (IRcum), radiation use efficiency (RUE), harvest index (HI), and yield, and (ii) evaluate potential interactions between heat stress and source-sink relationships during the reproductive phase. Two field experiments were conducted, with heating treatments applied before and after flowering, and controls without temperature manipulation. In Experiment 1, two genotypes with contrasting growth cycles were compared, while Experiment 2 examined intact versus defoliated plants. Heat stress significantly reduced yield and HI, particularly during post-flowering. Source reduction (defoliation) further reduced yield, independent of temperature. Although IRcum was unaffected by treatments, RUE dropped sharply under heat stress in intact plants and was similarly low in defoliated plants under both control and heated conditions. These results suggest that heat stress, especially during post-flowering, exacerbates the effects on cotton productivity by reducing both total plant dry weight and HI. The study highlights that the relationship between RUE and yield strongly depends on the specific limiting factors, such as heat stress or source restrictions.

Keywords: cotton; heat stress; radiation interception efficiency; radiation use efficiency; harvest index; yield

1. Introduction

Climate change effects are observed across a wide range of ecosystems and species worldwide, associated with rising average temperatures and increasing annual fluctuations (Seneviratne et al., 2018). This process has been detected from pre-industrial times to the present, with an increase in heat stress periods and negative effects leading to crop yield losses (Bita & Gerats, 2013). In this context, high-temperature stress has a broad impact on plants in terms of physiology, biochemistry, and gene regulatory pathways, as temperature is a critical environmental factor controlling plant growth and development (Bhattacharya, 2019; Christiansen & Lewis, 1982). Thus, heat stress is linked to an increase in the maximum daily temperature above a threshold level sufficient to cause irreversible damage over the long term (Wahid et al., 2007).

Yield is the result of the product of cumulative intercepted photosynthetically active radiation (IRcum), Radiation Use Efficiency (RUE) (Andrade et al., 2005), and the harvest index (HI, the ratio between yield and total aboveground biomass). IRcum is the product of incident radiation and the crop's interception efficiency (IE). This is strongly influenced by the environment, not only through the amount of incident radiation but also through IE, as a consequence of the regulation of leaf area index (LAI, leaf area per soil area unit) (Naylor, 2012). Several studies conducted on annual crops such as wheat and maize suggest that temperature impact is associated with a decrease in RUE and HI (Cicchino, Rattalino Edreira, & Otegui,



2010; Rattalino Edreira & Otegui, 2012). However, little information is available about its effects on herbaceous perennial commodities like cotton.

Cotton (Gossypium hirsutum L.) is a perennial plant, although it is grown as an annual crop in commercial systems through agronomic management practices, and it is characterized by an indeterminate growth habit. During the crop cycle, its productivity is sensitive to variations in environmental conditions, such as water availability and extreme temperatures (Welsh, Taschetto, & Quinn, 2022). The effects of heat stress on vegetative growth and development during this crop's cycle have been well documented (Burke & Wanjura, 2010; Hodges, 1991; Loka & Oosterhuis, 2016; Loka et al., 2020; Pettigrew, 2016; Virk et al., 2021). Other studies on this species have focused on the reproductive phase, with most of them examining pollination inhibition or fruit retention (Echer et al., 2014; Phillips, 2012; Snider & Oosterhuis, 2012; Snider et al., 2009, 2018; Van der Westhuizen et al., 2020) which reduces HI and, consequently, yield. Furthermore, recent research conducted at various developmental stages has highlighted diverse mitigation responses in cotton genotypes to heat stress, such as the accumulation of sugars, proline, phenolics, flavonoids, and heat shock proteins, which could aid in developing and selecting heattolerant cotton cultivars (Dev et al., 2024; Majeed et al., 2021).

The planophile structure of the cotton canopy (spreading horizontally rather than vertically) creates a sharp radiation gradient across the canopy profile, especially under high plant populations. In this case, little radiation reaches the leaves in the lower leaf layers (Dauzat et al., 2008; Hearn, 1976; Lv et al., 2013). In fact, studies have shown that artificially shading crops during the reproductive phase, with a 32% reduction in incident radiation, results in a 47% yield decrease in cotton (Eaton & Ergle, 1954; Sorour & Rassoul, 1974).

The majority of studies evaluating the impact of heat stress on cotton have been conducted in controlled environments, limiting their relevance to real agricultural conditions (Saini et al., 2023). A recent publication on cotton grown under field conditions revealed that leaf photosynthesis rates under saturated irradiance were reduced by up to 35% due to heat stress (as a consequence of negative acclimation), while no response to instant temperature changes in the 35 to 43 °C range was detected (Mercado Álvarez et al., 2022). However, no information is yet available about the impact of heat stress during the reproductive phase on crop variables related to radiation capture, use efficiency, and yield. Additionally, it is known that growth can be modulated by the influence of reproductive sinks in several crops (Lambers, Chapin, & Pons, 2008), suggesting that the detrimental effect of heat stress on biomass accumulation could be influenced by genotype differences in source-sink ratios at the time of stress. Current cotton genotypes typically have shorter cycles, thereby reducing the source (leaf area per plant)/sink (potential yield per plant) ratio (Baker & Baker, 2010; Casuso, Tarragó, & Galdeano, 2016). Furthermore, no information is available about the interactions between source/sink relationships and the effects of heat stress on the crop variables mentioned above.

December 2016, for Experiments 1 and 2, respectively. Experiment 1 was conducted at the National Institute of Agricultural Technology (INTA) research station, located in Reconquista (29°15' S, 59°44' W, Santa Fe province, Argentina), and Experiment 2 at the experimental field of the Faculty of Agronomy, University of Buenos Aires, Argentina (34°35′ S, 58°29′ W). Two cotton genotypes (DP 402 BGRR, short cycle duration (from sowing to maturity), and DP 1238 BGRR, long cycle duration; INTA Reconquista, Argentina), hereafter referred to as Gs and Gl, respectively, were used in Exp. 1. Since no significant differences between genotypes were observed in this experiment, only the short-cycle genotype (DP 402) was used in Exp. 2. In both experiments, each experimental unit (microplot) consisted of an area of 3 \times 1.56 m, and the experimental design was completely randomized, with 3 replicates for each treatment combination. Seeds were hand-planted in rows 0.52 m apart, using a stand density of 20 plants m⁻².

For Exp. 1, daily mean temperature and daily radiation integral records were taken from an automatic meteorological station located 420 m from the experimental site. In Exp. 2, weather data were recorded by a meteorological station located 300 m from the plots. Air temperature and relative humidity (RH) inside the portable structures described below were recorded using temperature sensors connected to twochannel data loggers (Cavadevices, Buenos Aires, Argentina) located in the upper part of the canopy. Crops were grown under optimal water and nutritional conditions, with soil irrigated weekly to ensure field capacity in the top meter of the profile throughout the growing season, and preventive agrochemical applications were used to control diseases and insects. Insect damage was prevented through regular crop monitoring and strategic insecticide applications. Plots were fertilized with 100 kg ha⁻¹ of nitrogen, applied as urea at sowing. Herbicides were used for weed control (pendimethalin active ingredient, applied at 5 L ha⁻¹ preplanting, and glyphosate at 5 L ha⁻¹ post-emergence).

For both experiments, high-temperature treatments were imposed starting at the flower-bud stage (FB, Figure 1). Two heating treatments were applied: (i) a pre-flowering treatment

Based on the above exposed, the objectives of this study

are to evaluate (i) the impact of heat stress during the reproductive phase on IE, RUE, HI, and their contributions to

cotton yield under field conditions and (ii) the possible

interactions between heat stress and different source/sink

relationships during the reproductive phase. The reproductive

phase involves part of the critical period for yield determination in cotton, which ranges from the onset of floral bud

development to 10 days after the end of the effective flowering

Two experiments were conducted under field

conditions, with sowing dates of 24 November 2015, and 24

stage (EEF) (Paytas et al., 2023).

2.1. Plant material and experiments

2. Materials and Methods

of 14 days between FB and the flowering stage (FL) (H1), and (ii) a post-flowering treatment starting at FL and continuing until the end of the effective flowering stage (EEF) (H2). Control treatments were those without temperature manipulation during both phases (C1 and C2 for H1 and H2, respectively). Portable structures, consisting of an iron frame (3 m length, 1.3 m width, and 1.3 m height) covered with transparent polyethylene (150 µm thickness), were used for H1 and H2 treatments. The structures were closed on the top and sides, except for an aeration window of 20 cm at the base, to minimize potential artifacts associated with changes in humidity and carbon dioxide concentration (CO₂) resulting from transpiration and photosynthesis rates, respectively. The same structures were used for treatments C1 and C2, but in these cases, they were completely open on their sides, with the film deployed only on the roof. This setup was introduced to rule out possible artifacts associated with the structure itself and to quantify the extinction of radiation produced by the film.



Figure 1. Schematic representation of the heating and control treatments conducted in Experiments 1 and 2 using control (C1-C2) and heating (H1-H2) portable structures during the pre-flowering (C1-H1) and post-flowering (C2-H2) phases. Gray bars indicate the periods when the corresponding treatments were applied. S = sowing, FB = flower-bud stage, FL = flowering stage, EEF = end of effective flowering stage or cut-out, PM = physiological maturity.

To examine the interactions between source/sink relationships and heat stress effects proposed in this work, an additional source-sink ratio manipulation was applied in Exp. 2. The source-sink ratio was adjusted through partial defoliation treatments. Specifically, a reduced source-sink ratio treatment (D-) was applied to 50% of the replicates for both C and H treatments by removing 50% of the total leaves per plant, interspersed along the stem, immediately before applying the heat treatment. The leaf area in the remaining experimental units was left intact (D0) as a treatment without defoliation.2.2. Measured variables

In both experiments, the measured and estimated variables included total and organ dry biomass, LAI, IE, and RUE. These traits were measured at the FB, FL, and EEF stages, for both control (C) and heated treatments (H). LAI was quantified by scanning the green leaves of the same harvested samples used for measuring dry weight, using a Portable Leaf Area Meter LI-COR LI-3000C (Li-Cor Inc., Lincoln, NE). Each sample consisted of 5 plants located within the plot, excluding those at the borders. Samples were divided into the following organs: leaf blades, stems

(including petioles), flowers, and/or capsules (with seeds). LAI was estimated as the ratio of the sum of leaf area to the harvested soil area. Samples were dried at 60 °C for 7 days and weighed. Plant dry biomass measured at the end of the corresponding treatment (current dry weight, CDW) was estimated as the sum of all biomass fractions.

In each experimental unit, photosynthetically active radiation (PAR = 400-700 nm) incident and intercepted in lower strata was also measured using a 1-m long Li-Cor 191S line quantum sensor (Li-Cor Inc., Lincoln, NE, USA). IE was measured at solar noon by placing the linear sensor diagonally across the inter-row space, with the ends of the sensor window aligned with the center line of the rows. Five measurements were taken in each experimental unit, and the results were averaged.

RUE was initially estimated for each treatment using the overall reproductive phase (from FB to EEF) in which treatments were applied, as the slope of the biomass values from FB to EEF versus IRcum (Stöckle & Kemanian, 2009). RUE was also roughly estimated separately for the pre-flowering (from FB to FL) and post-flowering (from FL to EEF) phases, as the difference in biomass between two consecutive harvests divided by the corresponding amount of intercepted radiation during each phase (Sinclair & Muchow, 1999). IRcum was estimated by daily summing the product of daily PAR incident radiation and the IE estimated for the corresponding phase.

Raw yield (fiber + seeds) was estimated for each treatment after the plants reached 100% capsule opening, at 125 and 114 days after sowing (DAS) for Experiments 1 (Gs genotype only) and 2 respectively. Plants were harvested manually, and the raw yield was weighed. Additionally, in Experiment 2 only, seeds were separated from the fiber using a micro test gin with electric saws to determine fiber yield (kg ha⁻¹). Finally, for each treatment in that experiment, the harvest index (HI) was calculated as the ratio of raw yield to total aerial dry weight at harvest (DW).

2.3. Statistical analyses

Data were subjected to Analysis of Variance (ANOVA) using a two-way ANOVA (heat treatment x genotype for Exp. 1; heat treatment x defoliation for Exp. 2). Linear regressions were used to estimate RUE for the entire treatment phase as the slope of the cumulative total biomass versus cumulative intercepted radiation relationship. Statistical analyses were performed using Infostat software (Di Rienzo et al., 2011), and graphs were generated using GraphPad Prism 5 software for Windows (GraphPad Software, San Diego, CA, USA; www.graphpad.com, accessed on 25 Feb 2025).

3. Results

3.1. Location and treatments

Environmental conditions at the two sites were described in detail in (Mercado Álvarez et al., 2022). Briefly, mean, minimum, and maximum outdoor air temperatures in Experiment 1 (conducted in the northern subtropical location of Reconquista) were approximately 2 °C higher than those in Experiment 2, which was performed in Buenos Aires, Argentina. In both experiments, the average daily mean temperature during both heating phases (pre- and post-flowering) was 3.2 °C and 1.8 °C higher in the H treatment compared to the C treatment (Exp. 1 and 2, respectively; p < 0.05). Differences in average maximum temperatures between the H and C treatments (6.9 °C and 5.8 °C for Exp. 1 and 2, respectively; p < 0.05) were more pronounced, with the H treatment reaching a daily mean of 36.8 ± 0.8 °C and 37.9 ± 0.79 °C in Experiments 1 and 2, respectively (means ± standard errors). No differences in CO₂ concentrations at the top of the structures, leaf water potential, or vapor pressure deficit (VPD) were observed among treatments when measured at midday.

3.2. Leaf area index (LAI)

Although in Experiment 1 two genotypes with contrasting cycle duration between sowing and maturity were used, these differences were not reflected in the time from sowing to FB, as both reached this stage around 67 DAS. On the other hand, the duration of the same period in Experiment 2 was 50 DAS. LAI was affected in both experiments by heat (H), defoliation (D), and genotype (G) factors, with no interaction detected among these factors (Figure 2). In both experiments, initial values were lower than 1 in all treatments at FB, when the C1 and H1 structures were established (Figure 2A,C). In Experiment 1, LAI was unaffected by the

H factor at FL, when heat treatments concluded (Figure 2A). However, the negative impact became evident later, with a significant reduction of around 20% detected in the H1 treatment at EEF, while C1 reached values up to 2.7 in the Gl genotype. A similar pattern was observed in pre-flowering in Exp. 2, where the negative impact of heat was detected in H1 immediately after the treatment concluded, regardless of the defoliation treatment (Figure 2C).

Curiously, in Experiment 1, the negative impact of the H factor was detected (p < 0.05) very early, near FL, when the temperature treatments were applied during the post-reproductive phase (between FL and EEF, Figure 2B). The measurements were taken only a few days after the heat treatments were implemented, and this trend persisted at least until EEF, when the post-flowering treatments were removed. In contrast, no differences were found in Exp. 2 between the H2 and C2 treatments in LAI when measured a few days after FL, though this trait also showed a reduction of around 25% by EEF (Figure 2D).

In addition, LAI was approximately 20% and 30% lower in the Gs genotype compared to the Gl genotype for the pre-(C1-H1, Figure 2A) and post-flowering (C2-H2, Figure 2B) heat treatments, respectively (G factor, p < 0.05). In Experiment 2, LAI was around 30% and 70% lower in the defoliated (D-) treatment compared to the intact (D0) treatment during EEF for the pre- (C1-H1, Figure 2C) and post-flowering (C2-H2, Figure 2D) treatments, respectively (D factor, p < 0.05).



Figure 2. Leaf area index (LAI) as a function of the days after the onset of the flowering-bud stage (DAFB), for the short (Gs, \blacktriangle) and long (Gl, \blacksquare) genotypes, in Experiment 1 (**A**,**B**) and for the non-defoliated (D₀, \blacktriangle) and defoliated (D-, \blacksquare) treatments in Experiment 2 (**C**,**D**), subjected to control (entire lines) and heat (dotted lines) temperature treatments. Horizontal black bars indicate the period covered by the treatments between FB and flowering (FL) and between FL and the end of the effective flowering period or cut-out (EEF) for pre-flowering (**A**,**C**) and post-flowering (**B**,**D**) treatments, respectively. Two-way ANOVA analyses were performed for each measuring date and the results are indicate inside the Figure. H = temperature treatments, G = genotype, D = defoliation treatments, NS = non-significant.

3.3. Interception efficiency (IE)

There were significant differences between genotypes in IE during the overall pre and post reproductive phase in Experiment 1, regardless of the heat treatments (Figure 3A,B). IE showed a quick increase, with values from 60% in FB to 75% in EEF. In this phase, IE was slightly (although significantly) lower in the Gs than in the Gl genotype. An unexpected lack of a negative impact of heat treatment was detected when they were performed at pre-flowering (Figure 3A), while at post-flowering IE became significantly lower in the H treatment only at EEF (Figure 3B).

In contrast, strong temperature effects were detected in Exp. 2 for the H factor (p < 0.05). When treatments were applied during pre-flowering, significant effects were observed in H1 only at 27 DAFB, after the treatment was removed (Figure 3C). For the post-reproductive phase (C2-H2), this factor was significant at both the FL and EEF stages, with no interactions with the defoliation treatments (Figure 3D). Additionally, IE values were lower in D- compared to D0, as expected, although a clear recovery was observed in the former by EEF in the H1 treatment.

3.4. IR_{cum} and RUE estimated using slopes for the FB-EEF phase

Despite the negative effect of heat stress on IE shown in Figure 3, no differences in IRcum at EF were detected in either experiment compared to their respective controls, ruling out thermal stress effects on this trait (Tables 1 and 2). However, RUE was negatively affected by heat treatments in Experiment 1 during the pre-reproductive phase (Figure S1A,B,E,F; Table 1), regardless of genotype. For the postflowering treatment, RUE also decreased, but this reduction was significant only in the Gl genotype (Figure S1C,D,G,H; Table 1). CDW was near 50% lower under heat stress in both genotypes, at both pre and post-flowering periods.

In contrast, in Experiment 2, RUE remained the same across all treatments, as neither the slopes nor the accumulated intercepted radiation and CDW differed among treatments when measured throughout the entire FB-EEF phase (Figures S2 and S3; Table 2).



Figure 3. Interception efficiency (IE) as a function of the days after the onset of the flowering-bud stage (DAFB), for the short (Gs, \blacktriangle) and long (Gl, \blacksquare) genotypes, in Experiment 1 (A,B) and for the non-defoliated (D₀, \blacktriangle) and defoliated (D-, \blacksquare) treatments in Experiment 2 (C,D), subjected to control (entire lines) and heat (dotted lines) temperature treatments. Horizontal black bars indicate the period covered by the treatments between FB and flowering (FL) and between FL and the end of the effective flowering period or cut-out (EEF) for pre-flowering (A,C) and post-flowering (B,D) treatments, respectively. Two-way ANOVA analyses were performed for each measuring date and the results are indicate inside the Figure. H = temperature treatments, G = genotype, D = defoliation treatments, NS = non-significant.

Table 1. Radiation use efficiency (RUE) values, Cumulative Intercepted PAR Radiation (IR_{cum})) and Current dry weight (CDW), for the different thermal treatments (control: C and heat H) estimated during FB to EEF phase. Data are presented for the short cycle (Gs) genotype DP402 and for the long cycle (Gl) genotype DP1238 in Exp.1. Statistical analyses were performed for each trait using two-way ANOVA tests (n = 3). RUE values were estimated as the adjusted slopes of the functions fitted in Figure S1. Asterisks indicate significant differences from their respective control treatment.

	Gs			Gl		
Treatments	RUE (g MJ ⁻¹)	IR _{cum} (MJ m ⁻²)	CDW (g m ⁻²)	RUE (g MJ ⁻¹)	IR _{cum} (MJ m ⁻²)	CDW (g m ⁻²)
C1	4.83 ± 0.62	221.64	834.84	3.81 ± 0.46	241.11	733.03
H1	0.72 ± 0.11 ***	202.51 ns	250.6 ***	2.05 ± 0.14 **	237.98 ns	421.06 ***
C2	2.64 ± 0.13	222.39	527.2	3.39 ± 0.48	250.35	704.29
H2	$1.79\pm0.15\ ns$	205.30 ns	380.42 ***	1.60 ± 0.15 **	244.83 ns	341.52 ***

** *p* < 0.01; *** *p* < 0.001; ns = non-significant.

Table 2. Radiation use efficiency (RUE) values, Cumulative intercepted PAR radiation (IR_{cum}) and Current dry weight (DW), estimated during FB to EEF period, for the different thermal (control: C and heat H) and defoliation (D-) and without defoliation (D₀) treatments in Exp.2. Statistical analyzes were performed for each variable using two-way ANOVA tests (n = 3). The values were obtained through the adjusted slopes of the functions in Figures S2 and S3. ns = non-significant.

		D ₀			D-	
Treatments	RUE (g MJ ⁻¹)	IR _{cum} (MJ m ⁻²)	CDW (g m ⁻²)	RUE (g MJ ⁻¹)	IR _{cum} (MJ m ⁻²)	CDW (g m ⁻²)
C1	2.76 ± 1.28	221.47	868.86	4.67 ± 0.75	182.83	982.22
H1	$3.88\pm0.86\ ns$	222.38 ns	1153.33 ns	$3.66 \pm 1.21 \text{ ns}$	182.95 ns	922.22 ns
C2	2.47 ± 0.60	262.82	1067.78	1.08 ± 0.40	251.99	648.44
H2	1.60 ± 0.45 ns	268.8 ns	760.0 ns	1.07 ± 0.51 ns	257.14 ns	646.66 ns

ns = non-significant.

3.5. Radiation use efficiency (RUE) estimated separately for the pre and post reproductive phases

With the aim of increasing the precision of the RUE analysis, this trait was also separately estimated for the FB to FL (pre-flowering) and FL to EEF (post-flowering) subphases. In Experiment 1, the heat treatment clearly decreased RUE in both genotypes. However, significant interactions between heat treatments and genotypes were detected, with RUE values 80% and 20% lower than the control ones in the Gs and Gl genotypes, respectively, when applied during preflowering (Figure 4). Thus, the effect was considerably more detrimental in the shorter-cycle genotype than in the longercycle one. Interestingly, an opposite trend was observed when heat stress was imposed during the post-reproductive phase, as the negative effect was more pronounced in the longer-cycle genotype. Indeed, reductions of around 30% and 70% were detected in the Gs and Gl genotypes, respectively. Nevertheless, this outcome is a consequence of the extremely high RUE value, close to 6 g MJ⁻¹, estimated for the C2 treatment.

Unlike the RUE estimated for the entire FB to EEF phase (Table 2), significant effects and interactions between temperature and defoliation factors were detected in Exp. 2 (Figure 5). When D0 plants were exposed to high temperatures, a drastic reduction in RUE values of 60% was observed in both

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the pre- and post-reproductive phases, compared to their respective controls. However, in the defoliation treatment (D-), RUE drastically decreased to values close to 1 g MJ^{-1} , regardless of the heat treatment or phase.



Figure 4. Radiation use efficiency (RUE, g MJ^{-1}) estimated for the period FB-FL (pre-flowering; C1-H1)) and FL-EEF (post-flowering; C2-H2)) for control (C1-C2) and heat (H1, H2) treatments. Data are presented for the short cycle (Gs) genotype DP402 and the long cycle (Gl) genotype DP1238 in Experiment 1. Vertical bars are standard errors for means (n = 9) and different letters indicate significant differences among treatments (p < 0.05).



Figure 5. Radiation use efficiency (RUE, g MJ^{-1}) estimated for the period FB-FL (pre-flowering; C1-H1) and FL-EEF (post-flowering; C2-H2)) for controls (C1-C2) and heat (H1, H2) treatments. Data are presented for the undefoliated (D₀) and defoliated (D-) treatments in Experiment 2. Vertical segments are standard errors for means (n = 9) and different letters indicate significant differences among treatments (p < 0.05).

3.6. Yield

Control yield was approximately 2700 kg ha⁻¹ in Exp. 1 and was differentially reduced by heat stress, decreasing by 66% and 42% in H1 and H2 plants, respectively, compared to their respective controls (Gs genotype, Figure 6A). Surprisingly, in Exp. 2, conducted in Buenos Aires, raw yield reached up to 6000 kg ha⁻¹ in the control treatments (Exp. 2, Figure 6B), more than double the yield obtained in Experiment 1. This result is noteworthy, given that Buenos Aires lies outside the traditional cotton cultivation region in Argentina, whereas Experiment 1, conducted in Reconquista, is located within that region. No significant interactions were detected, and the yield reduction due to heat stress was more pronounced when heat was applied during the post-flowering phase (approximately 75%) compared to the 50% reduction observed during the pre-reproductive phase (Figure 6B). Additionally, defoliation had a negative impact, independent of temperature, resulting in average losses of 15%. As expected, fiber yield followed a similar pattern, representing an average of 35% of the raw yield, with the overall pattern remaining consistent (Figure 6C).

3.7. Harvest index (HI) and total dry weight (DW) al harvesting

In general terms, the harvest index (HI) in Exp. 2 was approximately 0.32 in control treatments and significantly decreased under high-temperature exposure during both treatment periods (H1 and H2) when leaf area was not manipulated (D0), with average decreases of 40% and 65% for the pre-flowering (C1 and H1) and post-flowering (C2 and H2) thermal treatments, respectively (Figure 7). Similar trends were observed for both D0 and D- plants, ruling out interactions with the thermal treatments. Reductions in DW also contributed to the yield decrease caused by heat stress (around 23%, averaged across H1 and H2 treatments for both D0 and D- plants, Figure 8). A similar effect was observed for defoliation treatments, regardless of the thermal regime.



Figure 6. Raw yield (fiber + seeds) in Exp.1 (**A**, short cycle genotype only) and Exp.2 (**B**), and fiber yield for Exp.2 (**C**) for their respective control (C1-C2) and heat (H1, H2) treatments. Data are presented for the undefoliated (D₀) and defoliated (D-) treatments in Experiment 2. Vertical segments are standard errors for means (n = 24). Two-way ANOVA analyses were performed in Exp. 2 for temperature (H) and defoliation (D) treatments, and the results are indicated as insides. In Exp. 1, different letters indicate significant differences among treatments (p < 0.05). In Exp. 2, asterisks indicate significant differences for the H factor respect to their respective controls (* = p < 0.05; ** = p < 0.01).



Figure 7. Harvest index in Exp.2 for control (C1-C2) and heat (H1, H2) treatments, for the undefoliated (D0) and defoliated (D-) treatments. Vertical segments are standard errors for means (n = 24). Two-way ANOVA analyses were performed for temperature (H) and defoliation (D) treatments, and the results are indicated as insides. Asterisks indicate significant differences for the H factor respect to their respective controls (* = p < 0.05; ** = p < 0.01).



Figure 8. Total aerial dry weight in Exp.2 for control (C1-C2) and heat (H1, H2) treatments, for the undefoliated (D₀) and defoliated (D-) treatments. Vertical segments are standard errors for means (n = 24). Two-way ANOVA analyses were performed in Exp. 2 for temperature (H) and defoliation (D) treatments, and the results are indicated inside.

4. Discussion

Knowledge about the impact of high-temperature episodes on crop variables related to radiation utilization in cotton has been quite limited, with most research focusing on the effects on water use efficiency (Conaty et al., 2015; V. R. Reddy, K. R. Reddy, & Hodges, 1995). Previous studies on temperature stress have primarily concentrated on its impact on harvest index, particularly failures in the pollination process (Abro et al., 2023; Snider et al., 2009; Snider & Oosterhuis, 2012). The reproductive phase encompasses a significant portion of the critical period for yield determination in cotton, spanning from the flower bud (FB) stage to 10 days after the end of the effective flowering period (EEF) (Paytas et al., 2023), Thus, the effect of heat stress on raw and fiber yield (Figure 6) was closely associated with similar reductions observed in the harvest index (Figure 7). The stronger yield and harvest index reductions during the post-reproductive phase support the idea that heat stress exacerbates the detrimental effects on pollen viability and fertilization when applied during this stage, as flowers are fully exposed to pollination and fertilization processes (K. R. Reddy, Hodges, & V. R. Reddy, 1992).

Interestingly, our results clearly reveal an additional detrimental effect of heat stress on yield due to a reduction in plant size (total aboveground dry weight) at harvest, (Figure 8). This finding is particularly relevant, as total dry biomass has been a key trait for improving cotton productivity over the past 65 years of breeding. Modern cultivars require increased biomass accumulation to achieve higher yields (Singh et al., 2023). This contrasts with approaches used in other crops (such as wheat during the Green Revolution), where dwarfing genes were introduced and harvest index was enhanced rather than plant size (Ferrero-Serrano, Cantos, & Assmann, 2019). Although LAI and interception efficiency were significantly affected by heat stress (Figures 2 and 3, respectively), a surprising lack of differences caused by temperature treatments was observed in both experiments regarding cumulative intercepted PAR radiation, measured

from floral bud to the end of the effective flowering stage (Tables 1 and 2). Therefore, our results suggest that yield reduction cannot be attributed to diminished radiation capture, at least under the 20 plants m^2 density used in the experiments, higher than the 15 plants m^2 typically employed by farmers in Argentina (Scarpin et al., 2022, 2023).

Fiber yield in the control treatments of Experiment 2 was around 2200 kg ha⁻¹, conducted in Buenos Aires, a site located outside the traditional cotton cultivation region in Argentina (Figure 6C). This productivity aligns with other reports from irrigated cotton in Australia (Grundy, Yeates, & Bell, 2020; Yeates, Constable, & McCumstie, 2010a) and the USA (Hu et al., 2018; Siegfried et al., 2023). Paradoxically, yield was 38% lower in Experiment 1, carried out in Reconquista, a location within the traditional cotton-growing region of Argentina. However, lower lint yields of 1171 and 1135 kg ha⁻¹ for the Gs and Gl genotypes, respectively, were also reported by (Scarpin et al., 2022) in that location, supporting the idea that yield may be higher in non-traditional regions compared to traditional ones. Further research is needed to understand the physiological basis underlying these productivity differences.

RUE estimated during the critical period of yield determination emerged as the main determinant of the detrimental effects on yield, produced not only by heat stress but also by the reduction of source availability generated in our work through defoliation (Figures 4 and 5). Certainly, this aligns with findings in cotton subjected to reductions in other resource availabilities such as nitrogen, radiation, or waterlogging (Milroy & Bange, 2013; Pokhrel et al., 2023; Yeates, Constable, & McCumstie, 2010a). However, this contrasts with a report on potato, conducted across a broad range of genotypes, which revealed that radiation interception played a more significant role than radiation use efficiency in determining yields (Sandaña & Kalazich, 2015). In fact, the RUE estimations reported in this work are the first for the species under heat stress. Our results for control treatments ranged between 2.47 and 4.83 g MJ⁻¹ in both experiments throughout the reproductive phase (Tables 1 and 2), which is consistent with the approximately 3 g MJ⁻¹ values reported by (Yeates, Constable, & McCumstie, 2010b) during the prereproductive phase at 27 °C, as well as other studies on the same species (Grundy, Yeates, & Bell, 2020; Pokhrel et al., 2023). Much higher values (up to 6 g MJ⁻¹) were obtained when estimated separately for the pre- and post-reproductive phases in both experiments (Figures 4 and 5). This discrepancy is presumably due to the estimation methodology (calculating the difference in biomass between two consecutive harvests divided by the corresponding amount of intercepted radiation), which can introduce errors associated with the calculated differences. Furthermore, the growing rate could have differed along the crop cycle (Sinclair & Muchow, 1999). Although further research is needed to determine more accurate RUE values for the pre- and post-reproductive phases separately, the methodology used in this work was sufficiently precise to detect differences not only among heat stress treatments but also across different source/sink relationships.

In general terms, no interactions between heat stress and source/sink relationships were found in the study, with the notable exception of RUE. Thus, unlike the much smaller reductions in yield caused by defoliation compared to heat stress (without interactions between factors) (Figures 6-8), RUE was dramatically affected in Exp. 2 by defoliation to the same magnitude in both heated and non-heated plants (Figure 5). Therefore, the causes of RUE depletions could be explained through different mechanisms: while the decrease due to source restriction may be produced by a higher proportion of the canopy subjected to saturating irradiance, as observed in other crops such as sunflower (Lambers, Chapin, & Pons, 2008; Trapani et al., 1992) or wheat (Tao et al., 2022), lower photosynthesis rates likely contribute to RUE reduction under heat stress in cotton, as indicated by recent research (Mercado Álvarez et al., 2022; Yousaf et al., 2023). Thus, the impact of RUE reductions on cotton productivity, during the reproductive phase, strongly depends on the nature of the limiting factor.

The results from Experiment 1 significantly contributed to consolidating the knowledge regarding the role of heat stress on the studied traits. However, the behaviors of both genotypes (with different cycle durations) were not sufficiently contrasting to generate solid trends about how source/sink relationships affect the variables analyzed in our study. Fortunately, this was achieved in Experiment 2 by introducing a manipulative defoliation treatment, which reduced yield by approximately 15%, regardless of temperature (Figure 6). Our results contrast with the increases in cotton fiber yield observed by (Liu et al., 2024), who performed partial leaf removals after the crop reached its maximum LAI. One possible explanation is that, in that study, LAI was adjusted from a maximum level close to 6 to an optimum level near 3, which would enhance crop architecture and, hence, RUE. Such values are significantly higher than the 3 and 0.5 LAI values observed in unheated plants of Experiment 2 for intact and defoliated plants, respectively (Figure 2). Thus, the results obtained in our work contribute to the understanding of the effect of source/sink relations on cotton productivity. Our results clearly demonstrate that when reductions in LAI fall below an optimal level, productivity would be reduced not only associated to a decrease in RUE (Figure 5) but also to interception efficiency (Figure 3).

5. Conclusions

Heat stress drastically reduced raw and fiber yield by 50% and 75% during the pre- and post-reproductive phases, respectively. The defoliation treatment also diminished yield by 20%, without interacting with the thermal regime. The effect of

heat stress was closely linked to reductions in harvest index, with lesser total plant dry weight also contributing to yield reduction due to both heat stress (21% reduction in the pre- and postreproductive phases) and source reduction (25%) compared to unheated and intact plants, respectively. No impact on cumulative intercepted radiation during the pre- and postflowering periods was observed from temperature or defoliation treatments at the given plant density, despite significant reductions in LAI detected in this study. Interestingly, strong interactions between heat and defoliation treatments were observed for RUE, supporting the notion that the association of this variable with cotton yield greatly depends on the nature of the limiting factor. This work represents a significant advancement in understanding the crop variables involved in yield generation in cotton subjected to heat stress under different source/sink relationships during the reproductive phase. However, further research is needed to determine the impact of these combined treatments on the number and weight of capsules, as well as the spatial distribution of capsules along different reproductive branches.

Supplementary Materials

The additional data and information can be downloaded at: https://www.sciltp.com/journals/PlantEcophys/2025/1/518/s1.

Author Contributions

K.M.A. developed the initial conceptualization and investigation, carried out the methodology and formal analysis, and wrote the original draft. H.D.B. contributed to the conceptualization, supervised the activities, and assisted in manuscript writing. M.J.P. conducted part of the methodology, supervised the activities, and revised the manuscript. E.L.P. managed the project and resources, supervised the conceptualization and activities, and wrote the revised manuscript. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

Data are available upon request from E.L.P.

Conflicts of Interest

The authors have no conflict of interest to declare.

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