

ORIGINAL ARTICLE

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Identifying seed cotton yield and abiotic stress response in cotton (*Gossypium hirsutum* L.) grown in the Arizona low desert

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Abstract

Cotton (*Gossypium* sp.) is an important natural fiber crop that supports a multi-billion-dollar textile industry worldwide. Improved breeding strategies are needed to develop heat- and drought-tolerant cotton. Six upland cotton entries were grown in the Arizona low desert at the Maricopa Agricultural Center, and seed cotton yields were recorded. Cotton responses to abiotic stressors, including high heat and low soil water content, were estimated from leaf chlorophyll and nitrogen content and chlorophyll fluorescence throughout the growing season. Statistical analysis identified important relationships and temporal patterns between the measured traits within each cotton entry. The data showed that leaf chlorophyll and nitrogen content and chlorophyll fluorescence can indicate degrees of abiotic stress tolerance along with improved seed cotton yields. These results agree with previous reports that low and stable leaf chlorophyll content and increased photochemical efficiency during heat stress are indicators of thermotolerance in cotton. The data also indicate that measurements collected just before and during peak flower are most informative for breeding programs when compared to a control.

Plain Language Summary

Two different growing seasons at Maricopa, AZ, provided an opportunity to examine the effects of record-breaking heat stress on seed cotton yield and influential physiological measurements compared to a “less” stressful year. The data showed that leaf chlorophyll, chlorophyll fluorescence, and nitrogen content can indicate degrees of heat and drought tolerance and are beneficial for breeders. The data also indicate that seed cotton yield improvement could plateau if thermotolerant characteristics are not incorporated.

Abbreviations: Chla, chlorophyll a; Chlb, chlorophyll b; DOY, day of year; GLM, general linear model; IRR, irrigation rate; PD, planting date.

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1 | INTRODUCTION

Cotton (*Gossypium* sp.) is an important natural fiber crop that supports a multi-billion-dollar textile industry worldwide. Upland cotton (*Gossypium hirsutum* L.) is the primary species produced in more than 80 countries and provides a main source of income to many farmers (FAS-USDA, 2024). In 2023, the United States was the fourth largest producer of cotton accounting for 11% of the global production, the majority of which was used for apparel (73%) and home goods (18%) (NCCA, 2024). In the United States, 17 states cultivate and produce cotton including Arizona (Walker & Nelson, 2023). In 2024, Arizona cotton growers harvested over 300,000 480-lb bales of upland cotton, making it a valuable commodity for the state (Ott, 2024).

Unfortunately, abiotic stressors worldwide threaten production of many agronomic crops, including cotton. A *DSSAT CSM-CROPGO-Cotton* model, using predicted future temperature and rainfall pattern data indicated fiber yield could be reduced by as much as 78% in the Arizona low desert (Ayankojó et al., 2020). Furthermore, increased air temperatures were predicted to be the primary cause of reduced fiber yields. These predictions are supported by several studies where high temperatures and/or low soil water content reduced cotton growth (Bange & Milroy, 2004; Reddy et al., 1991) and reproduction (Marshall et al., 1974; Norton, 2020) and caused abscission of flowers and bolls (Brown, 2008; Cook & El-Zik, 1992; Herritt et al., 2022; Reddy et al., 1992), thus reducing yields. Studies have found that altering planting date (PD) can potentially avoid heat stress, improve lint yield, and alter boll distribution patterns (Davidonis et al., 2004).

Optimum day/night temperatures for cotton growth and reproductive development are 30°C/20°C (Brown, 2008; Reddy et al., 1991), which are routinely exceeded in the Arizona low desert when cotton is grown. Response to high temperature has included reduced net photosynthesis (Hejrnák et al., 2015; Law & Crafts-Brandner, 1999) and chlorophyll content (Reddy et al., 2004; Snider et al., 2010; Thompson et al., 2022) as well as increased minimum chlorophyll fluorescence (van der Westhuizen et al., 2020; Wu et al., 2014) and inhibition of Rubisco activase (Law & Crafts-Brandner, 1999; Salvucci & Crafts-Brandner, 2004). Reduced net photosynthesis has also been found in cotton growing under low soil water conditions along with reduced stomatal conductance (Carmo-Silva et al., 2012; Radin et al., 1994) further limiting growth.

To improve cotton production, studies that examine the interaction between yield and cultivar-dependent response to environmental stressors, particularly high heat and low soil water content, are needed. Focus on the interaction with yield is particularly important because environmental response and resource use efficiency mechanisms that can improve yield in plants are complex and can impact each other, both positively and negatively (Singh et al., 2007). For example, regulation to

Core Ideas

- Abiotic stress response and seed cotton yields under high heat and low soil water content.
- Reduced chlorophyll and increased photochemical efficiency associated with higher seed cotton yields.
- Chlorophyll content and chlorophyll fluorescence measurements around peak bloom were more informative.

close stomata in response to low soil water content, an adaptation strategy that conserves water loss, is in competition with regulation to open stomata in response to increased temperatures, a strategy that reduces heat stress through evaporative cooling (Pandey et al., 2021) cause opposing effects on water use efficiency. Furthermore, evaporative cooling to avoid heat stress can cause depletion of soil water content in the root zone, leading to severe water deficit if supplemental irrigation is not provided (Carmo-Silva et al., 2012). Studies that examine cotton response to multiple stressors under dynamic growing conditions are needed to develop varieties that are tolerant to increased temperatures and low soil water content (Rivero et al., 2022).

The main goals of this research were to understand the effects of variable growing conditions on seed cotton yield in several upland cotton entries and examine relationships with abiotic stress response as measured by leaf nitrogen, chlorophyll content, and chlorophyll fluorescence traits. Previous findings by Thompson et al. (2022) found conflicting relationships between cotton fiber yield and chlorophyll content for entries grown in the Arizona low desert. The current research seeks to build upon previous results by including leaf nitrogen content and chlorophyll fluorescence traits to better understand nitrogen partitioning and light-absorption efficiency with yield. Understanding these relationships could provide useful phenotypes for cotton breeding strategies toward abiotic stress tolerance. The objectives were to (1) generate variable field growing conditions in which to evaluate cotton seed yields; (2) evaluate changes in leaf nitrogen, chlorophyll content, and chlorophyll fluorescence in response to the variable growing conditions; and (3) identify relationships among measured traits along with seasonal response patterns that can inform breeding decisions.

2 | MATERIALS AND METHODS

2.1 | Experimental design

Upland cotton (*G. hirsutum* L.) field trials were conducted in 2019 and 2020 at the University of Arizona, Maricopa

Agricultural Center (33.068° N, −111.971° W, 360 m above sea level), in Maricopa, AZ. This location is in an irrigated production area of the low desert that typically receives less than 100 mm of rainfall during the cotton growing season (April–September). The soil type is a Casa Grande sandy loam (fine-loamy, mixed, superactive, hyperthermic Typic Natrargids). The field was divided into three irrigation basins with 12 columns per basin; each basin was 118.5-m long and 12.2-m wide. Six upland cotton entries, Acala Daytona RF, DG2355B2XF, DP1549B2XF, NG4545B2XF, PHY499WRF, and Red Cotton, were grown in a (0–1) alpha lattice design with two PDs and three irrigation rates (IRRs) nested within the PD to create variation in the measured outputs. There were three replicates per IRR (PD) treatment for a total of 108 plots. Five of the entries were from the USDA-ARS National Cotton Variety Test program (USDA-ARS, 2023), representing upland cotton from several major cotton breeding organizations and thus chosen for this study. DP1549B2XF was used as the control for entry comparisons in the statistical analysis described below based on performance in Arizona variety trials prior to this study. Each plot included two 10.6-m rows with 1.02-m inter-row spacing and a density of approximately 13.2 plants m^{−2}. There was a 2.3-m alley between adjacent plots on the same row. The eastern and western plots of each basin were planted with a commercial cotton variety to reduce edge effects.

The planting and harvest dates and a list of other pertinent field activities are provided in Table 1. To germinate seed and establish plants after planting, the field was furrow flooded. After emergence, the irrigation method was switched to sub-surface irrigation via buried drip tape (Netafim), which was installed at a 20-cm depth prior to planting (Table 1). Valves were placed at the beginning and end of each column in each basin for independent irrigation control for each PD. Irrigations were scheduled from a daily crop water use and soil water balance model with IRRs of 60%, 80%, and 100% of the recommendation (Allen, 1998; Hunsaker et al., 2005). Irrigation was terminated on September 16, 2019 (day of year [DOY] 259) and September 14, 2020 (DOY 258). Nitrogen was managed and applied with two different methods in both years: the first as a granular application (urea 46-0-0) prior to planting (pre-plant) at a rate of 56 kg ha^{−1} N and the second as a liquid (urea-ammonium nitrate 32-0-0) delivered through the subsurface drip irrigation system (fertigation), during peak bloom, at a rate of 64 kg ha^{−1} N, totaling 120 kg ha^{−1} N in each growing season (Table 1). Plots were harvested by a two-row cotton picker on November 18, 2019 (DOY 322) and November 5, 2020 (DOY 310), and seed cotton weights were measured and adjusted to seed cotton yield in kg ha^{−1}. A barley cover crop was planted in December and terminated in March each year prior to planting to reduce soil erosion and deplete soil nitrogen between cotton plantings.

2.2 | Field and environmental measurements

Soil water content was monitored weekly using a neutron moisture meter (503E, InstroTek Inc.) with measurements collected every 20 cm to a depth of ~2 m within 5-cm steel access tubes that were installed after crop emergence. Each basin contained six access tubes for soil water measurements, three per PD within the irrigation treatment, totaling 18 tubes. The soil water content (%) was calculated to a depth of 120 cm using the drained upper (0.16–0.22 cm³ cm^{−3}) and lower (0.08–0.11 cm³ cm^{−3}) soil water limits (Thorpe et al., 2018) and the readings from the neutron moisture meter. The average soil water content to a depth of 120 cm was calculated for each IRR (PD) treatment within each year, starting on the first measurement date and ending at measurement termination (Table 1).

Meteorological data were obtained from the Arizona Meteorological Network (AZMET) weather station approximately 0.8 km away from the plots. The weather station measured hourly humidity, temperature, solar radiation, wind speed, soil temperature, and precipitation. Daily reference evapotranspiration in inches using the Penman–Monteith standardized equation was calculated and used within the irrigation scheduling tool. Heat units (30°C/12.8°C) were calculated using the daily maximum and minimum air temperatures with a sine curve computation approach (Brown, 1989, 1991; Snyder, 1985). The accumulated heat units were calculated for the first and second PDs within each year, starting on the PD and ending at harvest.

2.3 | Chlorophyll and nitrogen measurements

For chlorophyll extractions, six samples were taken from pre-marked, uppermost fully expanded leaves and collected in 1.5-mL safe-lock tubes (Eppendorf) from the eastern row of each plot between 08:00 and 12:00 (MST). Each sample consisted of two 0.283 cm² leaf discs (total area 0.565 cm²), taken from three plants per plot with two replicates per plant. The samples were kept in the dark on ice in the field until they could be stored at −80°C in the laboratory. Chlorophyll was extracted using methanol and measured using a fluorescence plate reader as described by Thompson et al. (2022). Chlorophyll a and b concentrations (µg mL^{−1}) from each sample were calculated following Porra et al. (1989). After extraction, the leaf discs were dried at room temperature (22.2°C) for 48 h and then weighed on an analytical balance. Chlorophyll concentrations were then converted to a ratio of chlorophyll and tissue masses (mg g^{−1}). Disc weights were not taken for the first collection of 2019 so chlorophyll concentrations could not be converted to mg g^{−1} and so data from this collection were not used in analysis. For leaf nitrogen extractions, three

TABLE 1 A timeline of events for the 2019 and 2020 field trials including the year, date, day of year (DOY), and calculated days after planting (DAP) for each event.

Year	Date	DOY	DAP (1,2)	Event
2019	Apr. 9	99	−7, −41	Pre-plant fertilizer
2019	Apr. 16	106	0, —	First planting
2019	May 6	126	20, —	First planting moisture measurement
2019	May 6	126	20, —	First planting drip
2019	May 20	140	—, 0	Second planting
2019	June 4	155	—, 15	Second planting drip
2019	June 10	161	—, 21	Second planting moisture measurement
2019	June 14	165	59, 25	Chlorophyll/nitrogen (1)
2019	July 5	186	80, 46	Chlorophyll/nitrogen (2)
2019	July 26	207	101, 67	Chlorophyll/nitrogen (3)
2019	July 29	210	104, 70	Fertigation
2019	Aug. 16	228	122, 88	Chlorophyll/nitrogen (4)
2019	Sept. 6	249	143, 109	Chlorophyll/nitrogen (5)
2019	Sept. 16	259	153, 119	Irrigation terminated
2019	Sept. 30	273	167, 133	Final soil moisture measurement
2019	Nov. 18	322	216, 182	Harvest
2020	Apr. 16	107	−7, −28	Pre-plant fertilizer
2020	Apr. 23	114	0, —	First planting
2020	May 14	135	21, —	First planting drip
2020	May 14	135	—, 0	Second planting
2020	May 20	141	27, —	First planting moisture measurement
2020	May 29	150	—, 15	Second planting drip
2020	June 8	160	—, 25	Second planting moisture measurement
2020	June 9	161	47, 26	Chlorophyll fluorescence (1)
2020	June 19	171	57, 36	Chlorophyll/nitrogen (1)
2020	July 9	191	77, 56	Chlorophyll fluorescence (2)
2020	July 10	192	78, 57	Chlorophyll/nitrogen (2)
2020	July 21	203	89, 68	Fertigation
2020	July 31	213	99, 78	Chlorophyll/nitrogen (3)
2020	Aug. 20	233	119, 98	Chlorophyll fluorescence (3)
2020	Aug. 21	234	120, 99	Chlorophyll/nitrogen (4)
2020	Sept. 11	255	141, 120	Chlorophyll/nitrogen (5)
2020	Sept. 14	258	144, 123	Irrigation terminated
2020	Sept. 28	272	158, 137	Final soil moisture measurement
2020	Nov. 5	310	196, 175	Harvest

uppermost fully expanded leaves from three different plants were collected in #2 paper bags (ULINE) from the western row of each plot between 08:00 and 12:00 (MST). Samples were kept in the dark on ice in the field until they could be processed in the laboratory. Bags were opened and placed in an oven set at 55°C for 48 h. Once fully dried, samples were pulverized using a Geno/Grinder and 15-mL short polycarbonate vials with two 11-mm steel grinding balls (Spex SamplePrep). The tissue powder was sent to a commercial laboratory (Ward Laboratories Inc.) for nitrogen content analysis. Chlorophyll and nitrogen collections were made on the same days between

June and September in 2019 for a total of four collections, and in June and September in 2020 for a total of five collections. Collections were made every 21 days after the initial collection. The initial collection started approximately 2-week prior to peak bloom in both years (Table 1).

2.4 | Chlorophyll fluorescence measurements

In 2020 only, chlorophyll fluorescence measurements were obtained with a fluorometer (FluorPen Z995-PAR, Quibit

Systems INC). Measurements were taken in the Acala Daytona RF, DP1549B2XF, and Red Cotton plots for each PD and irrigation treatment. To collect the measurements, a leaf clip was attached to a pre-marked (from chlorophyll collections) uppermost fully expanded leaf (three leaves per plot), avoiding the midrib. Leaves were dark adapted using the leaf clip for 20 min before data were captured using the fluorescence transient (OJIP) protocol between 10:00 and 14:00 (MST) with the fluorometer (Table 1). The OJIP protocol provided minimum fluorescence (F_0) and maximum fluorescence (F_M), which can be used to calculate variable fluorescence (F_V) and maximum photochemical efficiency (F_V/F_M). The protocol also provided estimates of electron transport rate per active reaction center (E_t_0/RC), and absorbance rate per active reaction center (ABS/RC).

2.5 | Statistical analysis of measured traits

The SAS for Windows software v. 9.3 (SAS Institute) was used for all statistical analysis. A general linear model (GLM) was used to determine if the accumulated heat units measured by the AZMET station and accumulated soil water content measured by the neutron moisture meter were significantly different between years and within each year. The model included either the heat units or the soil water content as the dependent variable (Y):

$$\text{Model 1 : } Y = \text{Year} + \text{Year} \times \text{PlantingDate} + \text{Year} \\ \times \text{Irrigation},$$

where all terms were fixed effects. The least squared means (LSMEANS) were calculated on the Year $\times$ Planting Date and Year $\times$ Irrigation terms and SLICED using the Year term to determine within year significance of the model terms.

A second GLM was used to determine if the measured traits, extracted chlorophyll a (Chla), chlorophyll b (Chlb), leaf nitrogen (N) content, and seed cotton yield, were significantly different between each year. The model included one of the measure traits as the dependent variable (Y):

$$\text{Model 2 : } Y = \text{Year} + \text{Year} \times \text{Entry} + \text{Year} \\ \times \text{Planting Date} + \text{Year} \\ \times \text{Irrigation (Planting Date)} \\ + \text{Replicate} \times \text{Irrigation (Planting Date)},$$

where Year, Year $\times$ Entry, Year $\times$ Planting Date, and Year $\times$ Irrigation (Planting Date) were fixed effects and Replicate $\times$ Irrigation (Planting Date) was designated as the random term.

Next, the data were assessed for outliers and removal with the following model:

$$\text{Model 3 : } \text{Entry} + \text{Planting Date} + \text{Irrigation} \\ (\text{Planting Date}) + \text{Entry} \\ \times \text{Planting Date} \\ + \text{Entry} \times \text{Irrigation (Planting Date)} \\ + \text{Replicate} \times \text{Irrigation} \\ (\text{Planting Date}),$$

where Entry, Planting Date, Irrigation (Planting Date), Entry $\times$ Planting Date, and Entry $\times$ Irrigation (Planting Date) were fixed effects and Replicate $\times$ Irrigation (Planting Date) was designated as the random term. Significant outliers were determined by setting an upper and lower limit for the studentized deleted residuals with a criterion of $\alpha = 0.05$ based on the total number of observations and model terms (Kutner et al., 2004).

Model 3 was used to determine the effect of cotton entry, PD, and irrigation treatment on seed cotton yield. The LSMEANS were calculated on the Entry $\times$ Irrigation (Planting Date) term and SLICED using the Entry term to determine the consistency of cotton entry performance across the irrigation and PD treatments. Overall entry performance was compared to DP1549B2XF using the LSMEANS statement on the Entry term with a Dunnett comparison.

Model 3 was modified to include the REPEATED statement to determine the effect of the collection day on the experimental parameters and the change in measured traits over time. The collection day (Table 1), designated as D1–D5 in the model, was used as the repeated measure with the Lecoutre (1991) correction. As above, LSMEANS were determined on the Entry $\times$ Irrigation (Planting Date) term and SLICED using the Entry term, and overall entry performance was compared to DP1549B2XF with a Dunnett comparison. Figures were developed using the Python “pandas” and “matplotlib.pyplot” packages (v. 0.9.0 and 3.5.3).

3 | RESULTS

3.1 | Field conditions and the effects of experimental parameters

The 2019 (DOY 106–322) and 2020 (DOY 114–310) field seasons were significantly different for accumulated heat units (30°C/12.8°C) ($p < 0.0001$) and soil water content ($p = 0.0162$), where heat units and soil water content were higher in 2020 (Figure S1, Table S1). Within year, the accumulated heat units for the first PD were significantly higher than the second PD (Table S1). The soil water content was highest in the 100% irrigation treatment and lowest in the 60% treatment but was not statistically different from each other

TABLE 2 The p -values ($Pr > F$) obtained from the general linear Model 2, using type three sums of squares, to determine the effect of year on measured traits and interaction with experimental terms cotton entry, planting date (PD), and irrigation rates (IRR) nested within PD.

Trait	Year	Year $\times$ entry	Year $\times$ PD	Year $\times$ IRR (PD)
Yield (kg ha ⁻¹)	<0.0001	<0.0001	<0.0001	0.756
Chla (mg g ⁻¹)	<0.0001	<0.0001	0.0001	<0.0001
Chlb (mg g ⁻¹)	0.2953	<0.0001	0.0014	<0.0001
Nitrogen (%)	0.0002	<0.0001	0.0003	<0.0001

Note: Significance was determined at $p \leq 0.050$.

Abbreviations: Chla, chlorophyll a; Chlb, chlorophyll b.

TABLE 3 The p -values ($Pr > F$) obtained from general linear Model 3, using type three sums of squares, to determine the effect of experimental treatments cotton entry, planting date (PD), and irrigation treatments nested within planting date (IRR [PD]) within each year (2019 and 2020) on measured traits yield, chlorophyll a and b (Chla and Chlb), leaf nitrogen content, and chlorophyll fluorescence traits.

Trait	Entry	PD	IRR (PD)	Entry $\times$ PD	Entry $\times$ IRR (PD)
2019					
Yield (kg ha ⁻¹)	<0.0001	<0.0001	0.0893	0.0584	0.9325
Chla (mg g ⁻¹)	<0.0001	0.8598	<0.0001	0.2111	0.9932
Chlb (mg g ⁻¹)	<0.0001	0.7401	<0.0001	0.0149	0.7668
Nitrogen (%)	<0.0001	<0.0001	<0.0001	0.1761	0.7748
2020					
Yield (kg ha ⁻¹)	<0.0001	<0.0001	0.0012	0.1734	0.0452
Chla (mg g ⁻¹)	<0.0001	0.0001	<0.0001	0.3307	0.5274
Chlb (mg g ⁻¹)	<0.0001	0.0008	<0.0001	0.3516	0.4258
Nitrogen (%)	<0.0001	<0.0001	0.0009	0.2324	0.9467
F_v^a	0.0071	0.4832	0.0688	0.9889	0.8865
F_M^a	<0.0001	0.4979	<0.0001	0.9186	0.9687
F_0^a	<0.0001	0.2920	<0.0001	0.8880	0.4566
F_v/F_M^a	<0.0001	0.0104	0.7604	0.5225	0.5175
Et_0/RC^a	0.3233	0.8703	0.5941	0.9958	0.2206
ABS/RC^a	0.5956	0.7643	0.7762	0.7383	0.6284

Note: Significance was determined at $p \leq 0.050$.

Abbreviations: F_0 , minimum fluorescence; F_M , maximum fluorescence; F_v , variable fluorescence; F_v/F_M , maximum photochemical efficiency; ABS/RC , absorbance rate per active reaction center; Et_0/RC , electron transport rate per active reaction center.

^aThese are chlorophyll fluorescence traits.

within year (Table S1). The output from Model 2 showed that year had a significant effect on all but one trait (Chlb), and significant interactions were found with most of the experimental treatments for all measured traits (Table 2).

Two outliers were identified in the dataset for leaf nitrogen content. One was identified in DP1549B2XF in 2019 and the other was in Red Cotton in 2020. Examination of traits within year (Model 3) determined none of the experimental treatments were significant for Et_0/RC or ABS/RC (Table 3). Cotton entry was significant for all other traits measured in both years, but the interaction with PD was only significant for Chlb in 2019, and the interaction with irrigation nested within PD was only significant for yield in 2020 (Table 3). PD was significant for yield and leaf N content in 2019 and in 2020 was significant for yield, Chla, Chlb, N, and maximum

photochemical efficiency (F_v/F_M) (Table 3). Irrigation nested within PD was significant for Chla, Chlb, and N in 2019 and in 2020 was significant for yield, Chla, Chlb, N, maximum fluorescence (F_M), and minimum fluorescence (F_0) (Table 3).

Examination of traits within year (Model 3), including the collection day as the REPEATED term, determined that collection day and interaction with the experimental treatments were not significant for Et_0/RC or ABS/RC (Table 4). Collection day was significant for all other measured traits in 2019 and 2020. Interactions between collection day and other experimental treatments were significant for several of the measured traits in 2019 and 2020 except for the interaction with the Entry $\times$ Irrigation nested within Planting Date term (Table 4).

TABLE 4 The p -values ($\text{Pr} > F$) obtained from the modified general linear Model 3 with the REPEATED statement, using type three sums of squares, to determine the effect of collection day (D) with experimental treatments cotton entry, planting date (PD), and irrigation treatments nested within planting date (IRR [PD]) within each year (2019 and 2020) on measured traits yield, chlorophyll a and b (Chla and Chlb), leaf nitrogen content, and chlorophyll fluorescence traits.

Trait	D	D × Entry	D × PD	D × IRR (PD)	D × Entry × PD	D × Entry × IRR (PD)
2019						
Chla (mg g^{-1})	<0.0001	0.0002	<0.0001	<0.0001	0.0037	0.9560
Chlb (mg g^{-1})	<0.0001	<0.0001	0.4003	<0.0001	0.0054	0.0366
Nitrogen (%)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.3385
2020						
Chla (mg g^{-1})	<0.0001	<0.0001	<0.0001	<0.0001	0.0619	0.2177
Chlb (mg g^{-1})	<0.0001	<0.0001	<0.0001	<0.0001	0.0446	0.3690
Nitrogen (%)	<0.0001	<0.0001	<0.0001	0.0028	0.1599	0.1112
F_v^a	<0.0001	0.1567	0.0969	0.0017	0.6207	0.2002
F_M^a	<0.0001	0.0938	0.2919	<0.0001	0.7145	0.3105
F_0^a	<0.0001	<0.0001	0.0468	0.0085	0.4769	0.6438
F_v/F_M^a	<0.0001	0.0547	0.0272	0.2706	0.5293	0.1004
Et_0/RC^a	0.3702	0.4226	0.3127	0.8399	0.6857	0.4768
ABS/RC^a	0.7145	0.4683	0.7492	0.9891	0.7157	0.5125

Note: Significance was determined at $p \leq 0.050$.

Abbreviations: F_0 , minimum fluorescence; F_M , maximum fluorescence; F_v , variable fluorescence; F_v/F_M , maximum photochemical efficiency; ABS/RC , absorbance rate per active reaction center; Et_0/RC , electron transport rate per active reaction center.

^aThese are chlorophyll fluorescence traits.

3.2 | Variation in seed cotton yield

In 2019 and 2020, yields ranged from 905.7 to 4134.8 kg ha^{-1} and from 150.6 to 2312.7 kg ha^{-1} , respectively. The SLICE analysis showed that yields varied significantly across the irrigation and PD treatments for all entries except DG2355B2XF (2) and NG4545B2XL (4) in 2020 (Figure 1b). In 2019, all entries except DG2355B2RF (2) and PHY499WRF (5) had significantly lower yields than DP1549B2XF (3) (Figure 1c). In 2020, all entries had yields significantly lower than DP1549B2XF (3) (Figure 1d).

3.3 | Variation in leaf chlorophyll a content

Chla content ranged from 2.71 to 9.46 mg g^{-1} in 2019 where the highest values were found on collection day 4 and the lowest were on collection days 3 and 5. The SLICE analysis showed all entries except Red Cotton (6) on day 2 varied significantly across PD and irrigation treatments on days 2, 3, and 5. On day 4, no entries varied significantly across PD and irrigation treatment (Figure 2, Table S2). On day 2 (DOY 186), all entries except for Acala Daytona RF (1) and PHY499WRF (5) had significantly higher Chla content than DP1549B2XF (3) (Figure 3, Table S3). On days 3 and 5, all entries except for Acala Daytona RF (1) and NG4545B2XL (4) had significantly higher content than DP1549B2XF (3). On day 4, only

DG2355B2RF (2) and Red Cotton (6) had significantly higher Chla than DP1549B2XF (Figure 3, Table S3). In 2020, Chla ranged from 2.66 to 12.69 mg g^{-1} where the highest values were found on collection day 3 and the lowest values were found on collection day 5. The SLICE analysis showed that only Acala Daytona RF (1) and Red Cotton (6) varied significantly across PD and irrigation treatments on day 1 (Figure 4, Table S2). On day 2, all entries varied significantly, while on days 4 and 5, only DG2355B2RF (2) varied significantly. On day 3, DP1549B2XF (3) and NG4545B2XL (4) were the only entries that did not vary significantly (Figure 4, Table S2). On days 2 through 5, all entries except for Acala Daytona RF (1) and NG4545B2XL (4) had significantly higher Chla content than DP1549B2XF (3) (Figure 3, Table S3). On day 1 (DOY171), all entries except for PHY499WRF (5) had significantly higher Chla content than DP1549B2XF (3) (Figure 3, Table S3).

3.4 | Variation in leaf chlorophyll b content

Chlb content ranged from 0.339 to 3.662 mg g^{-1} in 2019 with the highest values on day 5 and the lowest values on day 3. The SLICE analysis showed all entries varied significantly for Chlb across PD and irrigation treatments on days 2 (DOY 186) and 5 (DOY 249) except for Acala Daytona RF (1), which varied significantly on day 5 (Figure 2, Table S2). On day 4, no

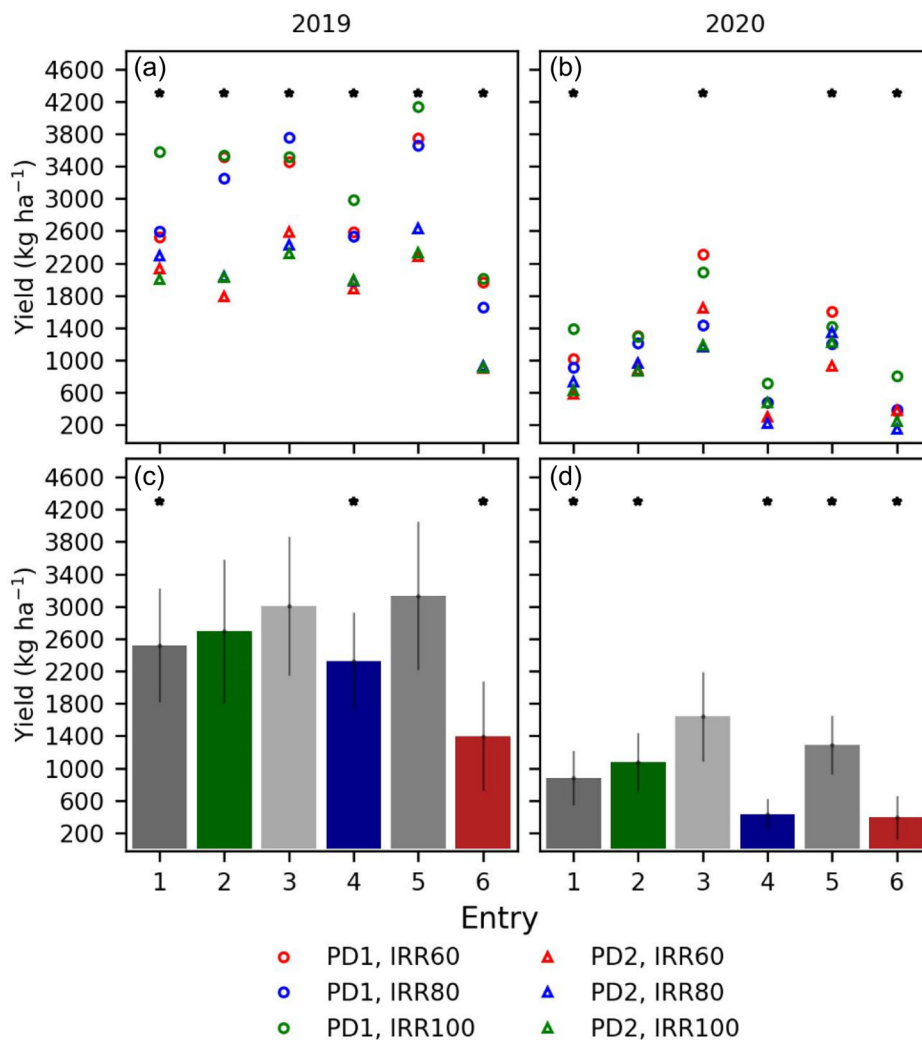


FIGURE 1 The LSMEANS estimates on seed cotton yield (kg ha⁻¹) from the Entry $\times$ Irrigation (Planting Date) term (Model 3) and SLICED using the Entry term to determine the consistency of cotton entry performance across the irrigation and planting date (PD) treatments in 2019 (a) and 2020 (b) field seasons. Entries (Acala Daytona RF [1], DG2355B2RF [2], DP1549B2XF [3], NG4545B2XL [4], PHY499WRF [5], and Red Cotton [6]) that had significant variation ($p < 0.05$) are designated by an asterisk (*). Overall entry performance was evaluated with a Dunnett comparison using DP1549B2XF as the control for the 2019 (c) and 2020 (d) field seasons. Entries that were significantly different ($p \leq 0.050$) from DP1549B2XF are designated by an asterisk (*).

entries varied significantly, while on day 3, only Acala Daytona RF (1), DG2355B2RF (2), DP1549B2XF (3), and Red Cotton (6) varied significantly across PD and irrigation treatment (Figure 2, Table S2). On days 2 through 5, Red Cotton (6) had significantly higher Chl b content than DP1549B2XF (3) (Figure 3, Table S3). NG4545B2XL (4) has significantly higher content on days 2 and 3, DG2355B2RF (2) was higher on days 4 and 5, while PHY499WRF (5) was higher on days 3 and 5, compared to DP1549B2XF (3) (Figure 3, Table S3). In 2020, Chl b ranged from 0.463 to 2.442 mg g⁻¹. Analysis showed all entries varied significantly across PD and irrigation treatments on day 2 (DOY 192), while no entries varied on day 5 (DOY 255) (Figure 4, Table S2). On day 1, only Acala Daytona RF (1) and Red Cotton (6) had significant variation, while on day 4, only DG2355B3RF (2) had variation

(Figure 4, Table S2). On days 2 through 5, DG2355B2RF (2), PHY499WRF (5), and Red Cotton (6) all had significantly higher Chl b content than DP1549B2XF (3). On day 1 (DOY 171), Acala Daytona RF (1), NG4545B2XL (4), and Red Cotton (6) had significantly higher content than DP1549B2XF (3) (Figure 3, Table S3).

3.5 | Variation in leaf nitrogen content

In 2019, all entries had significant variation across PD and irrigation treatments for leaf N content on days 2 (DOY 186) through 5 (DOY 249) except for PHY499WRF (5) on day 3. On day 5, Acala Daytona RF (1), DG2355B2RF (2), and PHY499WRF (5) had significant variation, while the other

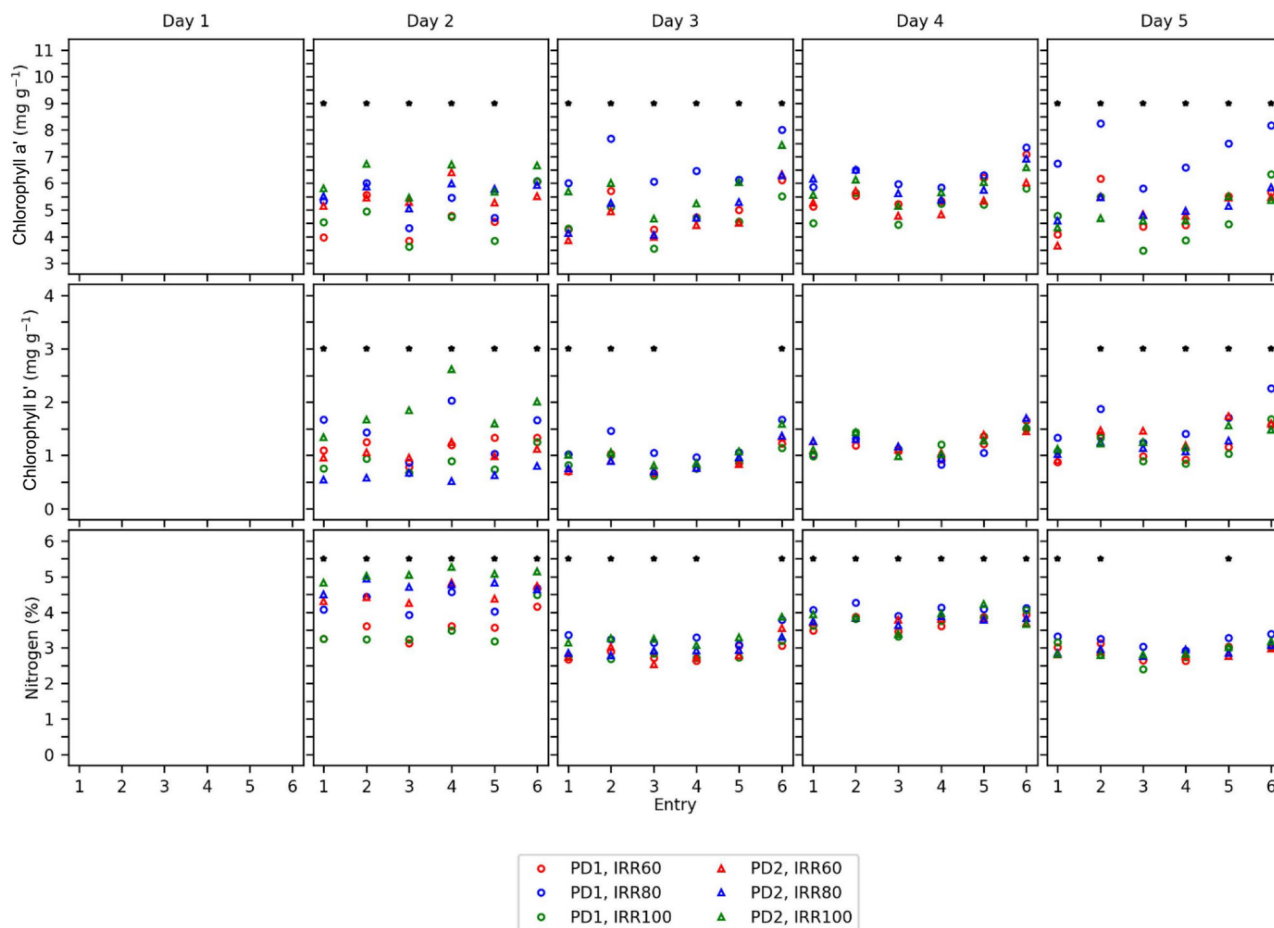


FIGURE 2 The LSMEAN estimates on leaf chlorophyll a and b and nitrogen content from the Entry $\times$ Irrigation (Planting Date) term (modified Model 3) and SLICED using the Entry term to determine the consistency of cotton entry performance across the irrigation and planting date (PD) treatments in 2019 for each collection day (1–5). Entries (Acala Dayton RF [1], DG2355B2RF [2], DP1549B2XF [3], NG4545B2XL [4], PHY499WRF [5], and Red Cotton [6]) that had significant variation ($p \leq 0.050$) are designated by an asterisk (*).

entries did not (Figure 2, Table S2). On days 2 and 3, all entries except for NG4545B2XL (4) and Red Cotton (6) did not differ significantly from DP1549B2XF (3) for leaf nitrogen content (Figure 3, Table S3). On days 4 and 5, all entries except for NG4545B2XL (4) had significantly higher N content than DP1549B2XF (3) (Figure 3, Table S3). N content ranged from 2.01% to 5.96% where the highest content was found on day 2 and the lowest on day 5 across entries and treatments. In 2020, all entries had significant variation across the PDs and irrigation treatments on day 2 (DOY 192), while on day 5 (DOY 255), no entries had significant variation. PHY499WRF (5) had the least amount of variation over the five collection days, while Acala Daytona RF (1), DG2355B2RF (2), and Red Cotton (6) had the most variation (Figure 4, Table S2). PHY499WRF (5) and Red Cotton (6) had significantly higher nitrogen content than DP1549B2XR (3) on all 5 days, while Acala Daytona RF (1) and NG4545B2XL (4) only differed from DP1549B2XF (3) on two of the five collection days (Figure 3, Table S3). N content ranged from 1.91% to 5.68%

where the highest content was on day 1 and the lowest on day 5.

3.6 | Variation in chlorophyll fluorescence

No significant differences were found for cotton entry, PD, or irrigation treatment with electron transport rate per active reaction center (E_t_0/RC) or absorbance rate per active reaction center (ABS/RC); therefore, no further analysis was performed (Tables 3 and 4). For minimum fluorescence (F_0), only DP1549B2XF showed significant variation across PD and irrigation treatment on collection days 1 and 2, while all three entries showed significant variation on collection day 3 (Table S2). On all three collection days, Acala Daytona RF was not significantly different than DP1549B2XF, while Red Cotton was significantly different on days 1 and 3 with lower values (Table S3). The highest F_0 values were found on day 2 (DOY 191) and the lowest were on day 1. With maximum

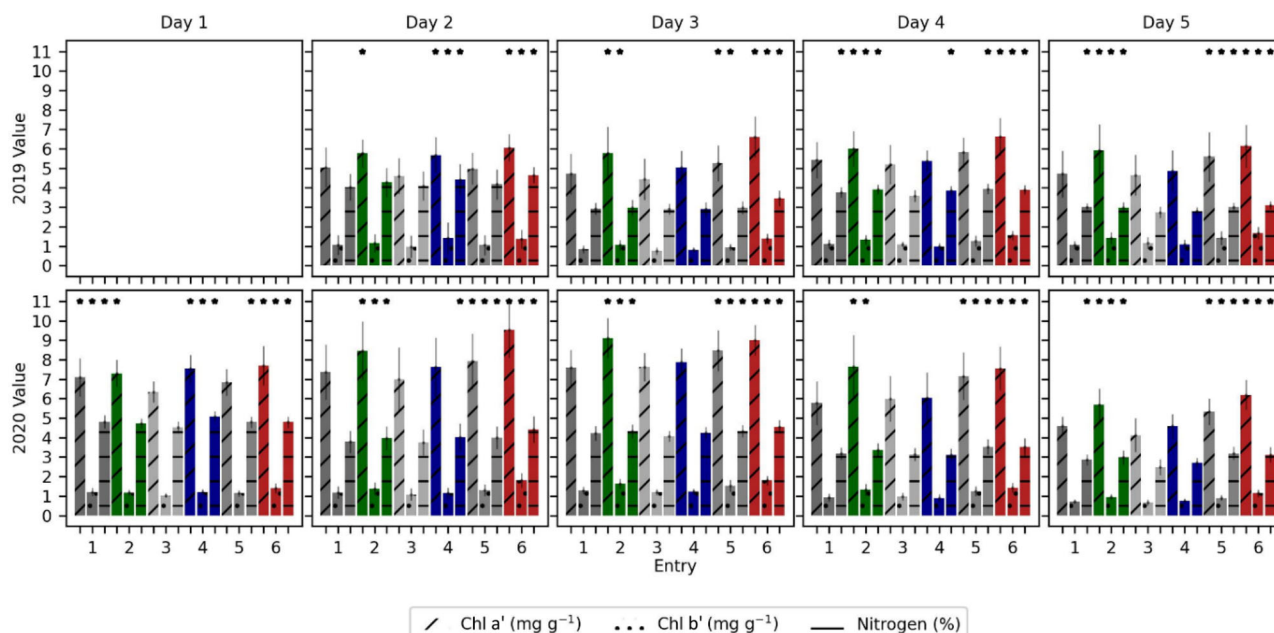


FIGURE 3 The LSMEAN estimates on leaf chlorophyll a and b and nitrogen content from the Entry $\times$ Irrigation (Planting Date) term (modified Model 3) to evaluate overall entry performance with a Dunnett comparison using DP1549B2XF as the control for the 2019 and 2020 field seasons for each collection day (1–5). Entries (Acala Dayton RF [1], DG2355B2RF [2], DP1549B2XF [3], NG4545B2XL [4], PHY499WRF [5], and Red Cotton [6]) that were significantly different ($p \leq 0.050$) from DP1549B2XF are designated by an asterisk (*).

fluorescence (F_M), significant variation across PD and irrigation treatments was only found on day 3 for all cotton entries examined (Table S2). Red Cotton was significantly different than DP1549B2XF on days 2 and 3 with lower F_M values, while Acala Daytona RF was only different on day 3 with lower values (Table S3). F_M values were lowest on day 1 and highest on day 3. With the variable fluorescence (F_V), calculated as the difference of F_0 from F_M , significant differences across PD and irrigation treatment were only found for DP1549B2XF and Red Cotton on day 3 (Table S2). Acala Daytona was significantly different from DP1549B2XF on days 2 and 3 with lower values (Table S3). The highest F_V values were found on day 3 and the lowest on day 2. The maximum photochemical efficiency (F_V/F_M) did not have significant differences across PD and irrigation treatment for the cotton entries examined except for Acala Daytona RF and DP1549B2XF on the first collection day (Table S2). No significant differences were found between cotton entries and the control except for Acala Daytona RF on day 2 (DOY 191), which had the lowest values (Table S3). The highest F_V/F_M values were found on day 3 and the lowest on day 2.

4 | DISCUSSION

In the last decade, there has been a surge in abiotic stress studies for important agricultural crops to understand and improve tolerance to increased temperatures and drought

while increasing global production for a growing population. Identifying the underlying causes of improved abiotic stress tolerance and the relationship with crop yield is no easy task due to their inherent complex nature. The purpose of this study was to examine relationships between seed cotton yield with leaf nitrogen and chlorophyll content and chlorophyll fluorescence traits, and to identify useful relationships that could improve breeding strategies for production of upland cotton (*G. hirsutum* L.) in variable temperature and soil water content scenarios. The 2019 and 2020 crop growing years at the Maricopa Agricultural Center (Maricopa, AZ) provided an opportunity to measure these traits under unique growing conditions, where the 2019 daily average lows and highs (18.32°C–35.9°C) were more typical of an Arizona low desert cotton growing season compared to 2020 (20.8°C–39.4°C) which had record-breaking heat stress conditions resulting in significant yield reductions (Thorp et al., 2020).

Previous studies in the Arizona low desert have shown that, in response to temperatures exceeding 40°C, cotton pollination will decline and/or developing bolls will be abscised, thus reducing yield (Norton et al., 2020). Pollen decline and boll abscission have been associated with reduced photosynthetic rates, photochemical efficiency, and chlorophyll pigments in the leaves (Carmo-Silva et al., 2012; Reddy et al., 1992; Snider et al., 2010), depleting energy reserves for developing flowers and bolls. Another possible source of yield reduction for 2020 likely came from the shorter growing season. Even though the 2020 season started later than the 2019 season,

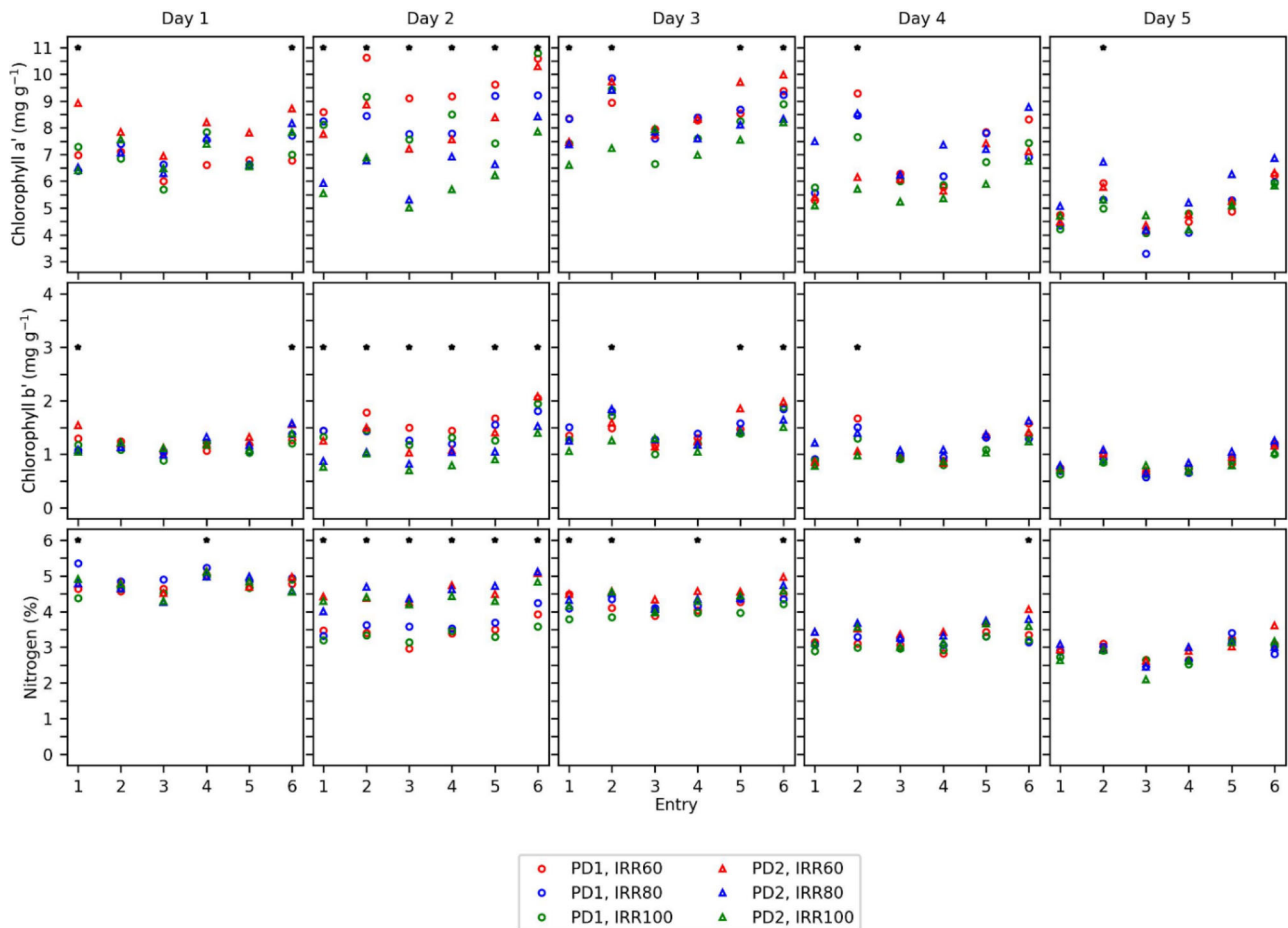


FIGURE 4 The LSMEAN estimates on leaf chlorophyll a and b and nitrogen content from the Entry $\times$ Irrigation (Planting Date) term (modified Model 3) and SLICED using the Entry term to determine the consistency of cotton entry performance across the irrigation and planting date (PD) treatments in 2020 for each collection day (1–5). Entries (Acala Dayton RF [1], DG2355B2RF [2], DP1549B2XF [3], NG4545B2XL [4], PHY499WRF [5], and Red Cotton [6]) that had significant variation ($p < 0.05$) are designated by an asterisk (*).

the plants were ready for harvest earlier in the 2020 season due to the increased temperatures. The shortened season likely decreased the time for fruit set and forced early boll maturity, resulting in a reduced number of bolls and lower boll weights (Bange & Milroy, 2004). The effect of a shortened season on yield is evident in the PDs where the first planting yielded greater than the second in both years.

Due to the reduced yields in 2020, the 2019 season had significantly higher seed cotton yields and lower leaf nitrogen and Chl a content across cotton entries, PDs, and irrigation treatments, which is why the years were assessed separately. In 2019, PHY499WRF and DG2355B2XF maintained yields comparable to the control DP1549B2XF. PHY499WRF maintained similar leaf nitrogen, Chl a, and Chl b content throughout the growing season as DP1549B2XF, where content was generally lower, suggesting similar heat and drought stress response strategies. DG2355B2XF also maintained similar leaf nitrogen and Chl b content but had significantly higher Chl a content compared to the control. The higher Chl a content suggests DG2355B2XF is less drought tolerant. Previ-

ous studies in peanuts (Arunyanark et al., 2008) and potatoes (van der Mescht et al., 1999) have associated increased Chl a content or density with drought stress as plants are attempting to maintain net photosynthesis with reduced stomata activity. However, neither PHY499WRF nor DG2355B2XF performed well in 2020 compared to DP1549B2XF where nitrogen and chlorophyll contents were higher, suggesting they are not tolerant to severe heat stress. While reduced chlorophyll content is not necessarily associated with thermotolerance (Rossi et al., 2017), Snider et al. (2010) found reduced Chl a/b ratios in the thermotolerant upland cotton line VH260. Hu et al. (2020) proposed that chlorophyll degradation might be a protective response to abiotic stressors to prevent more light energy from being adsorbed by the chlorophyll than can be used (Ort et al., 2011). In wheat, tolerance to long-term heat stress was attributed to less reduction in total chlorophyll and Chl b content (Almeselmani et al., 2012).

Interestingly, Acala Daytona RF maintained similar leaf nitrogen, Chl a, and Chl b content as DP1549B2XF, yet yielded significantly lower in 2019. It was hypothesized that while

Acala Daytona RF showed some measure of heat and drought stress tolerance by maintaining or reducing chlorophyll content, the entry was not able to utilize the captured energy for photosynthesis. In 2020, Acala Daytona RF was examined with chlorophyll fluorescence to determine the rate of photosynthetic efficiency compared to the control. Once again, Acala Daytona RF maintained similar leaf nitrogen, *Chla*, and *Chlb* content as DP1549B2XF as well as minimum fluorescence (F_0) values. However, the measured photosynthetic efficiency (F_v/F_m) and maximum fluorescence (F_m) in Acala Daytona RF were significantly reduced compared to DP1549B2XF on day 2 (DOY 191) during peak bloom when resource requirements are highest (Mullins et al., 2003). Higher F_v/F_m is an indicator of heat stress tolerance (Snider et al., 2015) and, along with increased F_m , has been associated with thermotolerant cotton (Hejrnák et al., 2015; Snider et al., 2010; van der Westhuizen et al., 2020; Wu et al., 2014), suggesting DP1549B2XF is utilizing a thermotolerance mechanism that enabled improved seed cotton yields. The reduced F_v/F_m values in Acala Daytona RF provide evidence that the light energy being absorbed is not being utilized for photosynthesis but rather being dissipated during initial fruit set, indicating less thermotolerance than the chlorophyll content alone suggested (Evans, 1989). Further examination of Acala Daytona RF is needed to determine if heat stress is causing degradation or inhibition of the photosynthetic machinery (Law & Crafts-Brandner, 1999; Salvucci & Crafts-Brandner, 2004). Comparison of chlorophyll content and chlorophyll fluorescence in this case highlights the importance of examining both traits to determine stress responses that not only support plant survival (reduced chlorophyll), but also improved performance (photosynthetic efficiency).

Red Cotton and NG4545B2XL had significantly lower yields than DP1549B2XF in both 2019 and 2020. Examination of NG4545B2XL showed that on collection day 2 in 2019 (DOY 186) and days 1 and 2 in 2020 (DOY 171 and 192), leaf nitrogen, *Chla*, and *Chlb* content were significantly higher than the control, whereas for later collections they were not significantly different. The timings of the changes in content are suspect as they coincide with the beginning of first bloom, when cotton plants are transitioning to reproductive branching. Previous studies have shown that cotton plants will mobilize nitrogen from the leaves to developing fruit, which are a strong sink for nutrient resources (B. O. Bondada, 1996; B. R. Bondada et al., 1997; Bourland, 1992), thus improving seed cotton yield. As chlorophyll is partially composed of nitrogen, a strong boll sink may also lead to catabolism of leaf chlorophyll to supply additional nitrogen for developing bolls. The increased nitrogen content in NG4545B2XL would suggest it does not have as strong a boll sink or is not as efficient at mobilizing nutrients as the control and the other top yielding entries. Previous research has found that heat stress can greatly reduce source and sink activities, affecting growth

and decreasing yields (Fahad et al., 2017). Soil water content is known to directly impact nitrogen adsorption and mobilization within the plant (Ullah, 2019). As many of the highest yields were found in the 80% and 100% irrigation treatments, it is possible plants were utilizing available water to mobilize nitrogen to developing bolls and may suggest NG4545B2XL is not as drought tolerant.

Further examination of Red Cotton showed leaf nitrogen and chlorophyll content were consistently higher than the control in both years. Red Cotton was also assessed for chlorophyll fluorescence traits showing no significant differences with DP1549B2XF F_v/F_m , but did show reduced F_0 and F_m on days 2 and 3. The higher nitrogen content can likely be attributed to the low yields as there would not be a strong sink for available resources. The higher chlorophyll content would suggest Red Cotton is not drought tolerant but may exhibit some heat tolerance as F_v/F_m was not significantly different than DP1549B2XF. If Red Cotton does indeed exhibit some thermotolerance, the decreased yields could further be attributed to drought intolerance. However, Red Cotton has not undergone extensive breeding and cultivation efforts like the other entries in this study; the reduced yield could simply be because Red Cotton is putting available resources toward biomass rather than yield.

This study supports previous findings that tolerance to heat and drought stress can be identified using chlorophyll content; however, adding the chlorophyll fluorescence traits provided a better understanding of thermotolerance. The control, DP1549B2XF, exhibited lower amounts of *Chla* and *Chlb* and maintained photosynthetic efficiency, indicating tolerance to both high heat and low soil water content. Acala Daytona RF also exhibited lower amounts of *Chla* and *Chlb*, indicating tolerance yet the photochemical efficiency was reduced, indicating less thermotolerance, which could be causing the reduced yields. Breeding programs that are seeking to incorporate tolerance to abiotic stress that also improve or stabilize yield should consider using chlorophyll content and chlorophyll fluorescence measurements. As it can be difficult to look at these measurements over time in a breeding program due to the large number of entries, the findings in this study suggest measurements prior to and during peak bloom are most informative when compared to a control.

5 | CONCLUSIONS

Two different growing seasons at Maricopa, AZ, provided an opportunity to examine the effects of record-breaking heat stress on seed cotton yield and influential physiological measurements compared to a “less” stressful year. The data showed that leaf chlorophyll, chlorophyll fluorescence, and nitrogen content can indicate degrees of heat and drought tolerance and are beneficial for breeders. The data also

indicate that seed cotton yield improvement could plateau if thermotolerant characteristics are not incorporated.

AUTHOR CONTRIBUTIONS

Alison L. Thompson: Conceptualization; data curation; formal analysis; funding acquisition; project administration; resources; supervision; writing—original draft. **Kelly R. Thorp:** Conceptualization; funding acquisition; methodology; resources; writing—review and editing. **Matthew T. Herritt:** Conceptualization; methodology; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The datasets generated and/or analyzed during the current are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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