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Point stresses during reproductive stage rather than warming seasonal temperature determine yield in temperate rice

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Abstract

Climate change is predicted to shift temperature regimes in most agricultural areas with temperature changes expected to impact yields of most crops, including rice. These temperature-driven effects can be classified into point stresses, where a temperature event during a sensitive stage drives a reduction in yield, or seasonal warming losses, where raised temperature is thought to increase maintenance energy demands and thereby decrease available resources for yield formation. Simultaneous estimation of the magnitude of each temperature effect on yield has not been well documented due to the inherent difficulty in separating their effects. We simultaneously quantified the magnitude of each effect for a temperate rice production system using a large data set covering multiple locations with data collected from 1995 to 2015, combined with a unique probability-based modeling approach. Point stresses, primarily cold stress during the reproductive stages (booting and flowering), were found to have the largest impact on yield (over 3 Mg/ha estimated yield losses). Contrary to previous reports, yield losses caused by increased temperatures, both seasonal and during grain-filling, were found to be small (approximately 1–2% loss per °C). Occurrences of cool temperature events during reproductive stages were found to be persistent over the study period, and within season, the likelihood of a cool temperature event increased when flowering occurred later in the season. Short and medium grain types, typically recommended for cool regions, were found to be more tolerant of cool temperatures but more sensitive to heat compared to long grain cultivars. These results suggest that for temperate rice systems, the occurrence of periodic stress events may currently overshadow the impacts of general warming temperature on crop production.

KEYWORDS
climate change, cold sterility, respiration, rice, temperature, yield potential

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Abbreviations: CA, California; CI, Credible interval; VPD, Vapor pressure deficit

1 | INTRODUCTION

There has been considerable focus in recent years on the role of increased temperatures on grain yield in agricultural systems, including rice (e.g., Baker, 2004; Peng et al., 2004; Sheehy, Mitchell, & Ferrer, 2006; van Groenigen, van Kessel, & Hungate, 2013; Wang et al., 2016; Welch et al., 2010; Zhang, Zhu, & Wassmann, 2010). This focus is, in part, driven by the accumulated scientific evidence predicting that temperatures will increase between 1 and 5°C caused by climate change (Stocker et al., 2013). Warmer temperatures increase maintenance respiration and thereby decrease the amount of carbohydrate available for yield formation (Amthor, 2012). Previous literature has suggested that T_{min}, which is linked to nighttime respiration, is particularly important as a driver of yield losses compared to T_{max} (Peng et al., 2004; Wang et al., 2016). However, using field observations to estimate the impact of seasonal warming stress on crop yield has proven difficult, with conflicting estimates of the magnitude of the effect on crop yields in rice. Reported yield losses from increased seasonal T_{min} have ranged from large (e.g., 10% per °C; Peng et al., 2004; Wang et al., 2016), to modest (e.g., 6% per °C or less; Rehmani et al., 2014; Sheehy et al., 2006; Welch et al., 2010), to little loss (e.g., Zhang et al., 2010).

One challenge in estimating the consequences of high temperatures is the presence of other temperature-driven mechanisms which also impact yield. One such mechanism is the reduction in crop yield components (i.e., the number of plant organs available to develop into grain) by high or low temperature point stresses during critical times. In rice, reproductive crop stages (booting and flowering) are particularly sensitive to these point temperature stresses. Booting follows panicle initiation and ends when the panicle emerges from the boot (i.e., the flag leaf sheath), while flowering starts when the panicle emerges from the boot and ends when the spikelets have completed anthesis (Counce, Keisling, & Mitchell, 2000). Early in booting, the developing panicle is low on the plant, often at or below flood water in paddy rice, and protected by plant tissue. Yet cold temperature during this stage has been shown to damage cells undergoing meiosis (Board, Peterson, & Ng, 1980; Farrell, Fox, Williams, & Fukai, 2006; Peterson, Lin, Jones, & Rutger, 1974), specifically as microspores release from tetrads in the early microspore stage (Mamun, Alfred, Cantrill, Overall, & Sutton, 2006). This sensitive phase of booting begins approximately 7 days following panicle initiation and lasts approximately 15 days (Peterson et al., 1974) (hereafter referred to as simply as "booting"). During the flowering stage, the spikelets have emerged and are exposed at the top of the plant, where they have been shown to be sensitive to both cold and high temperature injury (Farrell et al., 2006; Horie, 1993; Van Oort, Saito, Zwart, & Shrestha, 2014). Yield reduction can be the result of damage to pollen grains or failure of pollen grains to release from the anther (Farrell et al., 2006; Maruyama, Weerakoon, Wakiyama, & Ohba, 2013; Wassmann et al., 2009). These reproductive point stress mechanisms have been described as response to accumulated degrees above (heat) or below (cool) a threshold, often referred to as the "cooling-degree index" (Uchijima, 1976). The occurrence of these point stresses can correlate with overall seasonal mean T_{min} and T_{max}, confounding the estimation of either point stress or seasonal warming yield loss mechanisms. At issue when using field data, as opposed to growth chamber data, to simultaneously estimate these effects is the reliance on natural variability to provide the needed combination of temperatures required to separate the effects. For example, there is no guarantee of heat stress at flowering during an otherwise cool year, or vice-a-versa.

Rice systems in the Sacramento Valley, California (CA), USA, provide an ideal environment to quantify the impact of these yield loss mechanisms. The climate in CA is characterized as a temperate Mediterranean climate, with cool, wet winters and dry, warm summers. Due to the influence of cool air originating from the San Francisco Bay, there exists a natural temperature gradient south (cool) to north (warm), while, unlike rice production systems in more humid areas, the arid environment results in potentially large diurnal changes in temperature (e.g., T_{max} and T_{min} in season of over 40°C and under 12°C, respectively). This natural gradient allows comparisons between different locations within and between seasons, which increases the likelihood to observe the aforementioned required combination of temperatures. Furthermore, the production system in CA is highly intensive and has low pest and disease pressure, resulting in yield limited primarily by environmental factors. Lastly, both short and medium grain types (temperate *japonica*, typically regarded as cold tolerant), and long grain types (temperate and tropical *japonica*, typically regarded as heat tolerant and cold sensitive) (Lu et al., 2005; Mackill & Lei, 1997) are grown in CA, allowing for comparisons of the impact of point stresses between sensitive and tolerant cultivars.

The primary objective of this study was to simultaneously estimate the magnitude of the effects of two temperature-driven mechanisms on grain yield: (1) point stresses of warm and cool temperature events during the reproductive stages of booting and flowering, and (2) warm temperatures during the entire growing season and during grain-fill specifically. Secondarily, this study sought to estimate the temperature thresholds for the three major grain types (long, medium, and short grain) below or above which yield losses occur during the sensitive crop stages of booting and flowering.

2 | MATERIALS AND METHODS

2.1 | Site and yield data description

Crop performance data were collected from the CA Statewide Rice Variety Trials from 1995 to 2015. These trials were conducted annually in seven to nine commercial rice fields located throughout the Sacramento Valley. Each trial was implemented using a completely randomized design with four replicates and an average of 50 different entries per location, including 4–12 checks (i.e., commercially available cultivars of known performance for comparison to the experimental lines). Seven cultivars ("A201," "Calmochi-101," "M-202," "M-205," "M-401," "M-402," and "S-102") were present in the trials for the entire study period (including years as test entries). Experimental plots were 14.0–18.5 m^2 and were planted similar to commercial practice by either broadcasting pregerminated seed into flooded field plots or by drill seeding into unflooded fields. Drill-seeded plots were flooded approximately 21–30 days following planting. Field preparation, fertility, pest control, and water levels were managed by farmers using conventional practices. For each plot, the date when 50% of the plants reached the heading stage (referred to as "50% heading" hereafter), plant height, percent lodging, and moisture content at harvest were recorded. As the observed date of panicle initiation was not observed, it was estimated using a thermal time model calibrated for CA rice cultivars by Sharifi, Hijmans, Hill, and Linquist (2016), who found little difference among cultivars in thermal time from planting to panicle initiation. For the purposes of defining crop stages, the vegetative stage was assumed to last from the date of planting to panicle initiation, the sensitive boot stage from 7 days after panicle initiation until 7 days prior to 50% heading, the flowering stage from 7 days prior to 50% heading to 7 days after 50% heading, and grain-fill from the date of 50% heading to 30 days following. As seeds in drill-seeded locations were not pregerminated and were planted into unflooded fields, development from planting to panicle initiation for drill-seeded plots was assumed to take an additional 7 days (typical of side-by-side comparisons of water vs. drill seeding in CA; University of California Cooperative Extension, unpublished data). All plots were harvested at maturity with a small-plot combine and corrected to 14% moisture prior to reporting.

2.2 | Weather data

As sites were located proximate to several weather stations, temperatures for each site were estimated as a weighted average of temperatures from the nearest weather stations. Input weather data were retrieved from eighteen weather stations throughout the Sacramento Valley (Figure 1, Table S1). Stations were chosen to ensure coverage over CA rice growing area and sites and with at least one station within 30 km of each site, prioritizing weather stations not located in urban areas or airports when possible. The site temperatures were estimated using an inverse distance weighted average according to the formula:

$$T_i = \sum_{j}^{n} w_{ij} * T_j \quad (1)$$

where

$$w_{ij} = d(x_i, x_j)^{-\rho} \quad (2)$$

where T_i is the estimated temperature (minimum or maximum) value for site i, w_{ij} is the weight for weather station j at site i, and T_j is the observed temperature at weather station j. The weights for weather station j at site i were determined by the inverse distance d between site i and weather station j. The power parameter ρ controls the degradation of weights as stations become more distal to the site and needed to be optimized before estimating the site temperatures. The optimum value of ρ was determined via ninefold cross-validation (i.e., two stations held out for each fold). The best predictions (lowest cross-validation error) were achieved with $\rho = .75$. This value was again verified using temperature data collected in-field at each site during the 2015 season, with $\rho = .75$ also having good predictive accuracy for the in-field data. Where there were missing values in the source data, the weight for that source was set to zero and the weights recalculated with the remaining stations. Geographic distances between stations were calculated using the Vincenty Ellipsoid method.

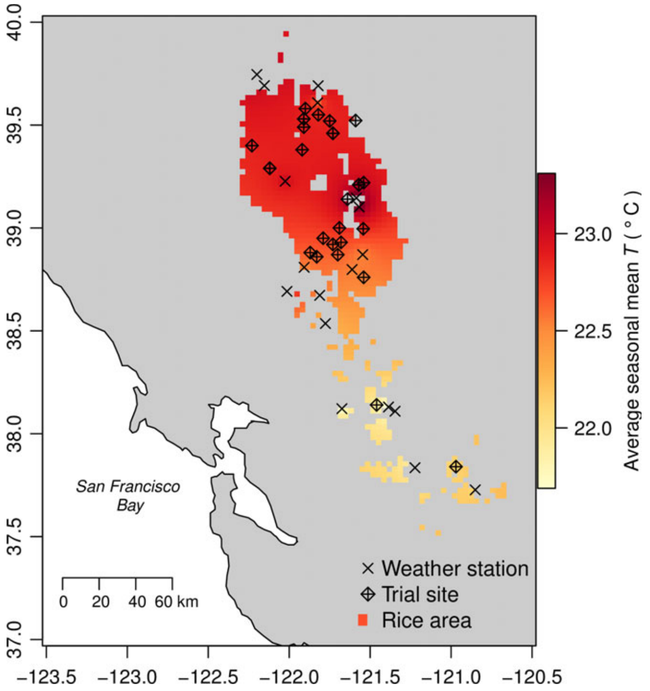

FIGURE 1 Locations of weather stations, trial locations, and seasonal mean temperatures for rice production areas averaged over the period 1995 to 2015, in the Sacramento Valley, California, USA. Not all trial locations and weather stations had data for each year

2.3 | Model description

Data were analyzed using a probability-based linear model. To control for possible confounding effects and differences between observations (Gelman et al., 2013), inferences were conditioned on relevant covariates (site, year, site: year interaction, cultivar, county, grain type, plant height, days to heading, planting date, annual trends). As this production system is known to experience high solar radiation, with little to no cloud cover during the growing season (Yoshida, 1981), solar radiation was not included in the model and so the effect of solar radiation, if any, would fall into the more general site, year, and site: year effects. Low correlation between solar radiation and other variables of interest suggests little possibility of solar radiation confounding other estimates (Fig. S1). Observations where either yield or covariates were not recorded were excluded from the regression. Additionally, instances where 50% heading occurred earlier than 70 days following planting (the 1% quantile of days to 50% heading) were also excluded (n = 179) because panicle initiation in these instances is not well estimated by the thermal time model, leading to a final data set of N = 27,021 observations. To enforce sparsity in the regression and mitigate issues with overfitting and collinearity, hierarchical shrinkage priors were implemented using the HS_3 parameterization (Piironen & Vehtari, 2016). Hierarchical shrinkage priors result in predictive performance similar to Bayesian model averaging (BMA) (Carvalho, Polson, & Scott, 2010), often considered a gold-standard of predictive accuracy in statistical models (Madigan, Raftery, Volinsky, & Hoeting, 1996; Raftery, Madigan, & Hoeting, 1997). Furthermore, to make the model robust to outliers, errors were assumed to be t-distributed with five degrees of freedom (Lange, Little, & Taylor, 1989).

Due the difficulty in joint estimation of both the threshold and impact of cool and heat point stress, the thresholds at which yield is negatively impacted by temperature stress were determined prior to assessing the impact of point stresses. To assess these thresholds, simple cooling/heating-degree stress models were included inside the linear regression. These models are based on the "cooling-degree concept" (Uchijima, 1976). The submodels calculate the cooling or heating stress experienced by the crop as a function the accumulated number of degrees below or above a threshold during the crop stage. The accumulated cooling or heating stress was calculated as:

$$\sum_{i}^{n} f(T_i) = \begin{cases} \theta - T_i, & T_i \geq \theta \\ 0, & T_i > \theta \end{cases} \tag{3}$$

and heating stress as,

$$\sum_{i}^{n} f(T_i) = \begin{cases} \theta - T_i, & T_i \geq \theta \\ 0, & T_i > \theta \end{cases} \tag{4}$$

where T_i is the daily $T_{\min}$ or $T_{\max}$ for day i in the crop stage of length n d, and θ is the estimated threshold. These submodels assume that there is zero effect on yield above (cool) or below (heat) the threshold. Values of the temperature thresholds were determined by grain type by including the above submodels into the regression model and optimizing for the most likely value of each threshold. To safeguard against settling on a local optimum, eight instances were initiated at different starting values and convergence to similar solutions was confirmed. These estimated thresholds were used to calculate the accumulated cooling stress experienced by each observation prior to fitting the final model. Although more complex, physiological models exist for cooling and heating stress (e.g., Julia & Dingkuhn, 2013; Van Oort, de Vries, Yoshida, & Saito, 2015; Van Oort et al., 2014), a simple linear response to accumulated stress was assumed due to the empirical nature of the model.

The model was constructed incrementally and tested against simulated data before adding additional parameters to verify that the model could recover a known signal. The final model was likewise tested against multiple simulated data sets representing different scenarios, including (1) no effect of either mechanism (point stresses or warming temperature effects), (2) similar effects and thresholds by major rice grain types, and (3) differing effects by major rice grain types. The model was able to reliably recover simulated parameters across all simulated data sets, suggesting that the model would converge to the correct solution with observational data. To fit the final model to observations, eight parallel instances were initialized at different points, and convergence to the same solution was verified. To ensure the model estimates were not being unduly influenced by the inclusion of sites known a priori to be cooler than typical (i.e., the southern sites; Figure 1), the analysis was also run excluding these sites. Similarly, the analysis was run excluding long-duration cultivars due to concerns about those possibly being out of sequence with the main field variety for which the trials were managed. Lastly, all model diagnostics and posterior predictive checks were investigated for issues prior to reporting the results.

2.4 | Data processing and model fitting

All data were programmatically transferred from the original data sheets, error checked, and manipulated using the R statistical language (R Core Team, 2016). Vincenty Ellipsoid distances between sites and weather stations were computed using the "geosphere" package for R (Hijmans, 2016). The model was fit using the Stan probabilistic computing language (Stan Development Team, 2017b), which implements the No-U-Turn sampler, a variation on Hamiltonian Monte Carlo sampling. Stan was chosen primarily due to its flexibility fitting user-specified models. Threshold values were determined using Stan in optimization mode using the L-BFGS optimizer. The final model was run using "cmdstan," a command-line interface to the Stan sampler (Stan Development Team, 2017a). To ensure robust sampling and full exploration of the posterior distribution, the Stan tuning parameters "adapt delta" and "maximum treedepth" were increased. Model diagnostics were checked using the "shinystan" package for R (Gabry, 2016). Relative effect sizes were determined via a weighted parameter approach, where each parameter was estimated as:

$$\beta_{ij} = z_{ij} * w_i \tag{5}$$

where β_{ij} is the parameter for effect j in parameter group i, z_{ij} is the parameter on a normalized scale, and w_i is the weight, or relative effect size for the parameter group i. All predictors were standardized to z-scores to allow for easier comparison between parameters. Yield loss in response to temperature stresses was calculated as the difference between predictions with and without each stress. Ninety percent credible intervals (CI), defined as the interval that contains 90% of the posterior density, were determined by the quantile method. Ninety percent CIs are presented because 95% CIs show high sampling variability (see https://groups.google.com/d/msg/stan-users/zAr3EXpIe14/tHzmIZ_nAAAJ and http://andrewgelman.com/2016/11/05/why-i-prefer-50-to-95-intervals/for further discussion of this issue). The entire analysis, code, and supporting data are publicly available through the Open Science Foundation (Espe, 2017).

3 | RESULTS

The temperature thresholds below or above which the crop experienced yield losses varied by grain type (Table 1). Medium and short grain types were estimated to have better tolerance to cooling stress during the booting stage, with temperature thresholds of 13.0°C and 13.8°C, compared to long grain types (17.2°C; Table 1). However, all three grain types were estimated to have similar thresholds (XoC) for cooling stress at flowering (Table 1). Long grain types were estimated to have better tolerance to heat during flowering and only experienced yield losses above an estimated threshold of 38.7°C, while medium and short grains were estimated to experience yield loss at lower temperatures (35.7 and 36.6°C, respectively) (Table 1), although the total impact of heat during flowering was low (Table 1).

The impact of point stresses during the reproductive stages of booting and flowering was estimated to be approximately fivefold higher than the impact of seasonal warming losses (Figure 2 and Fig. S2). The largest estimated temperature-driven effect was found to be cool stress during the booting stage, followed by cool stress at flowering, heat stress during flowering, seasonal mean $T_{\max}$, seasonal mean $T_{\min}$, mean $T_{\max}$ during grain-fill, and lastly mean $T_{\min}$ during grain-fill (Figure 2; Fig. S2). For medium grains (the dominate grain type in CA), the model estimated yield losses from point stresses of 64.6 kg/ha per °C below 13.0°C during booting, 34.0 kg/ha per °C below 10.9°C during flowering, and 19.8 kg/ha per °C above 35.7°C (Table 1, Fig. S2). Long grain types were estimated to experience larger losses from cooling stress during booting (14.4 kg/ha per °C below 17.2°C) and flowering (38.9 kg/ha per °C below 11.9°C), while short grains were estimated to experience less yield loss from cool stress at booting (24.2 kg/ha per °C below 13.8°C), and higher losses compared to long and medium grains due to cold at flowering (31.9 kg/ha per °C above 36.6°C). All grain types were estimated to have low losses due to heat at flowering, and hence, there was little estimated difference in total yield loss due to heat stress during flowering by grain type (data not presented). The occurrence of $T_{\min}$ below the estimated thresholds (a cool event) for booting and flowering increased late in the season, with minimum cool events observed during July (Figure 3a). Following Aug 1, the occurrence of cool temperatures increased. Compared to observed booting and flowering crop stages, relatively few observations of booting and flowering occurred as early as July 1, but many observations occurred following August 1 (Figure 3b).

There was no evidence in the observed data of increasing seasonal mean temperatures or decreasing occurrence of days below the estimated cooling thresholds in this region, even going back to 1985 (i.e., 10 years before the study period; see Figure 4). While northern sites were warmer compared to southern sites (Figure 1), cool temperature events during critical periods were experienced even at the northern sites (e.g., the “Durham” station (Figure 4) is in the northern end of CA rice area). The importance of point stresses relative to seasonal warming losses was preserved even when known cool sites were excluded from the regression ($N = 24{,}869$), although the magnitude of the effects of cool stress was decreased slightly (data not presented). As the inclusion of cool sites allowed greater precision in estimating the impact of cooling effects, only the results of the model including all sites are presented ($N = 27{,}021$). Similarly, exclusion of very late maturing cultivars did not have a significant impact on the estimates (data not presented).

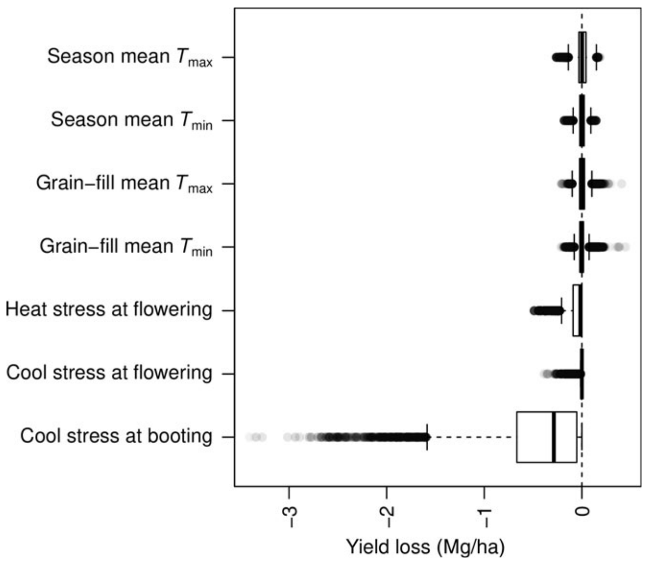

FIGURE 2 The estimated yield losses in rice of reproductive point stresses (cool stress during booting, cool stress during flowering, and heat stress during flowering) and seasonal warming losses (mean $T_{\min}$ and $T_{\max}$ over the season and during the grain-fill stage). Boxes cover the quartile of the marginal posterior distributions of the losses from 27,021 observations over the period 1995 to 2015 in the Sacramento Valley, California, USA

TABLE 1 The estimated impact of cool and heat stress during the reproductive stages of booting and flowering for rice, the threshold below (cooling) or above (heating) which the crop is estimated to experience stress, and the maximum accumulated degrees below or above the threshold observed over the period 1995 to 2015 in the Sacramento Valley, California

	Median	90% CI	Threshold (°C)	Max. accum. (∑>°C)
	(kg ha^{-1} °C^{-1})			
Cooling at booting				
Long	14.4	13.2–15.6	17.2	267
Medium	64.7	59–70.5	13	52
Short	24.2	19.7–28.6	13.8	83
Cooling at flowering				
Long	38	20.5–56.5	11.9	21
Medium	34.3	7.8–63.1	10.9	11
Short	25.4	4.9–53.5	11.6	18
Heating at flowering				
Long	70.8	44.9–97.4	38.7	7
Medium	19.7	14.6–24.8	35.7	31
Short	31.7	23.1–40.3	36.6	21

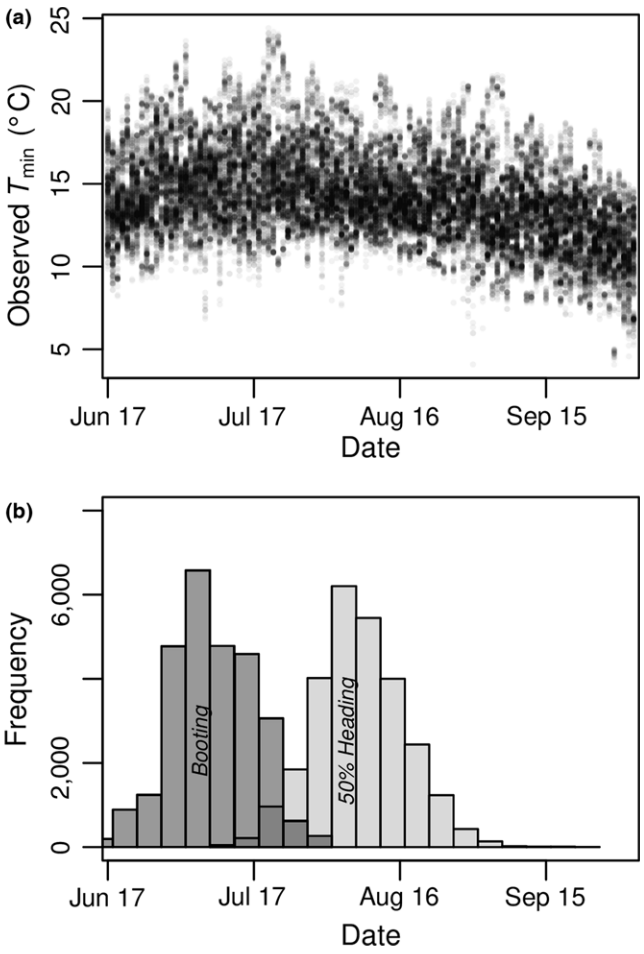

FIGURE 3 Observed T_{min} during the reproductive crop stages of booting and flowering (a) and observed frequency of booting (dark gray) and flowering (light gray) during the study period (b)

4 | DISCUSSION

Simultaneous estimation of the impact of point stresses and seasonal warming losses revealed that the impact of point stresses is many times greater than the impact of seasonal warming losses in this system. Similar to estimates from other subtropical rice systems (Zhang et al., 2014), point stresses during reproductive stages had a large impact on yield (Figure 2). Furthermore, stress events were found to be a persistent threat (Figure 4), and evidence that climate change is increasing the occurrence of these extreme temperature events (Buckley & Huey, 2016) makes it crucial to accurately estimate the impact of these events. Yield losses to these point stress events are a threat to yield stability and an important obstacle to meeting the challenge of feeding the estimated five billion people who rely on rice as a staple in their diet (Battisti & Naylor, 2009; Hatfield et al., 2011; Khush, 2005; Tubiello, Soussana, & Howden, 2007). In the latest report, the International Panel on Climate Change clearly stated that the "first step towards adaptation to future climate change is reducing vulnerability and exposure to present climate variability (high confidence)" (Stocker et al., 2013). Therefore, increased awareness of the current stressors on yields in temperate cereal production systems is needed as a critical component of climate adaptation and should not be overshadowed by long-term planning for a warmer planet.

Based on these results, it is reasonable to question how the effect of seasonal mean T_{min} on yield, often speculated to reflect respiratory losses, has been previously hypothesized to be a large mechanism of yield loss (10% decrease per °C; Peng et al., 2004), while there was a negligible effect estimated in our study (estimated losses of approximately 1–2% per °C, Figure 5). Although the seasonal mean T_{min} values observed in this temperate system (11.7–15.7 °C; Figure 5) were substantially lower than the T_{min} values observed in tropical and subtropical systems (19–25°C, Wang et al., 2016; 22.0–23.8°C, Peng et al., 2004), it is unlikely that the temperate systems used in this study were too cool to experience significant yield losses from respiration given the current understanding of the mechanisms involved. The impact of maintenance respiration is expected to be nonlinear (Amthor, 2012), and based on the temperature coefficient concept (with the typical assumption of $Q_{10} = 2$), maintenance respiration is expected to double per 10°C increase in temperature (Lambers, Chapin, & Pons, 2008), or conversely, halve per 10°C decrease in temperature. Hence, if it is assumed that 10% yield decrease per °C is correct for the range 19–25°C, the effect of warming temperatures on yield would be expected to be reasonably strong at 12–16°C. To reconcile both 10% per °C at higher temperatures and the negligible effect seen here, maintenance respiration would need to triple or quadruple per 10°C (i.e., Q10 of 3–4). However, acclimatization to higher temperatures (expected during a warm season) decreases seasonal warming losses (Atkin, Bruhn, & Tjoelker, 2005; Lambers et al., 2008), and recent research suggests the temperature coefficient for rice might be closer to 1.5 (Peraudeau et al., 2015). Lastly, and most critically, the estimates here for the impact of seasonal T_{min} are similar to estimates from controlled experiments where temperatures were tightly controlled by researchers (as compared to observational studies) (2.6% per °C; Rehmani et al., 2014). Therefore, based on this accumulated evidence, it is possible that 10% yield loss per °C is an overestimate. Although direct attribution of seasonal warming losses to respiratory mechanisms requires further study, climate change scenarios assuming 10% yield loss per °C may require revision.

One explanation for this discrepancy in the estimated importance of seasonal warming losses is that many of these previous efforts (e.g., Peng et al., 2004; Wang et al., 2016) failed to include possible confounding factors into the analysis, such as site, year, and cultivar effects. By not including these effects, previous analyses are implicitly relying on the strong assumption that given the environmental variables (e.g., temperature), other differences between observations are ignorable (Gelman et al., 2013). If that assumption is invalid, which is likely given the preponderance of literature on site, year, and variety effects in agricultural systems, the estimates are unlikely to transfer beyond the original data set. In contrast to a priori assumptions that these confounding effects are "relatively small" (Wang et al., 2016), the analysis here conditions inference over uncertainty induced by many possible covariates, including but not

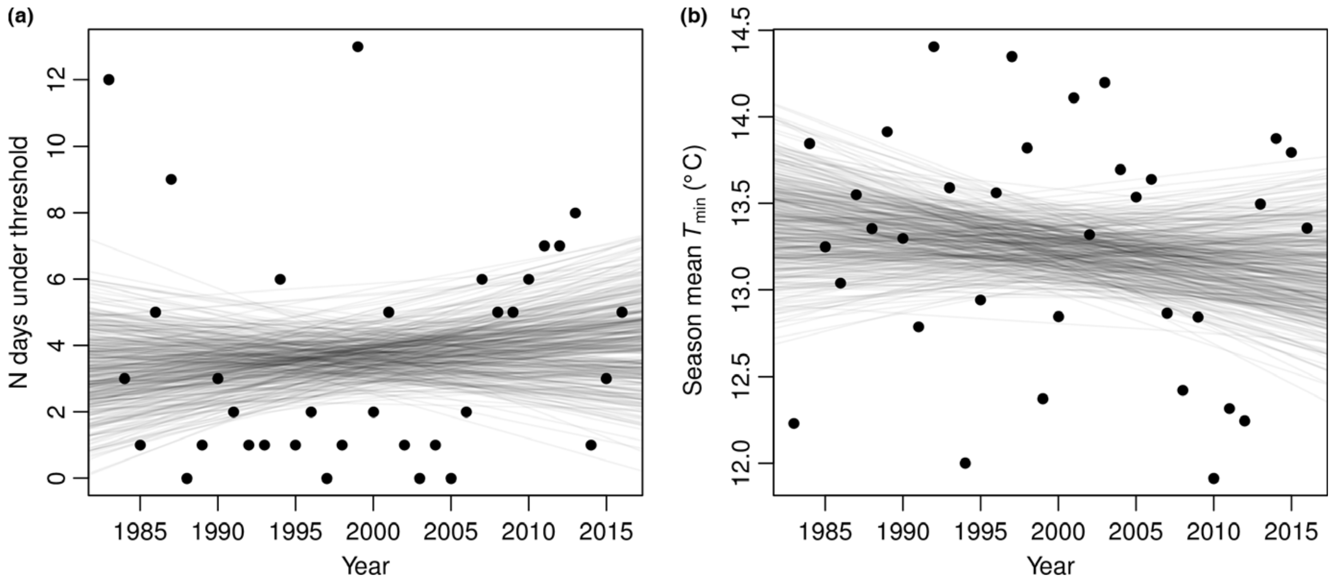

FIGURE 4 Number of occurrences below the mean estimated threshold (14.0°C) during the period when booting typically occurs for medium grain cultivars (a) and the mean seasonal T_{min} over a typical season (b). Data are from the Durham weather station, located in the northern part of the Sacramento Valley, California, USA, from 1985 to 2015. This station is located in an area generally considered warmer than the southern part of the Sacramento Valley. Light gray lines are predicted regressions

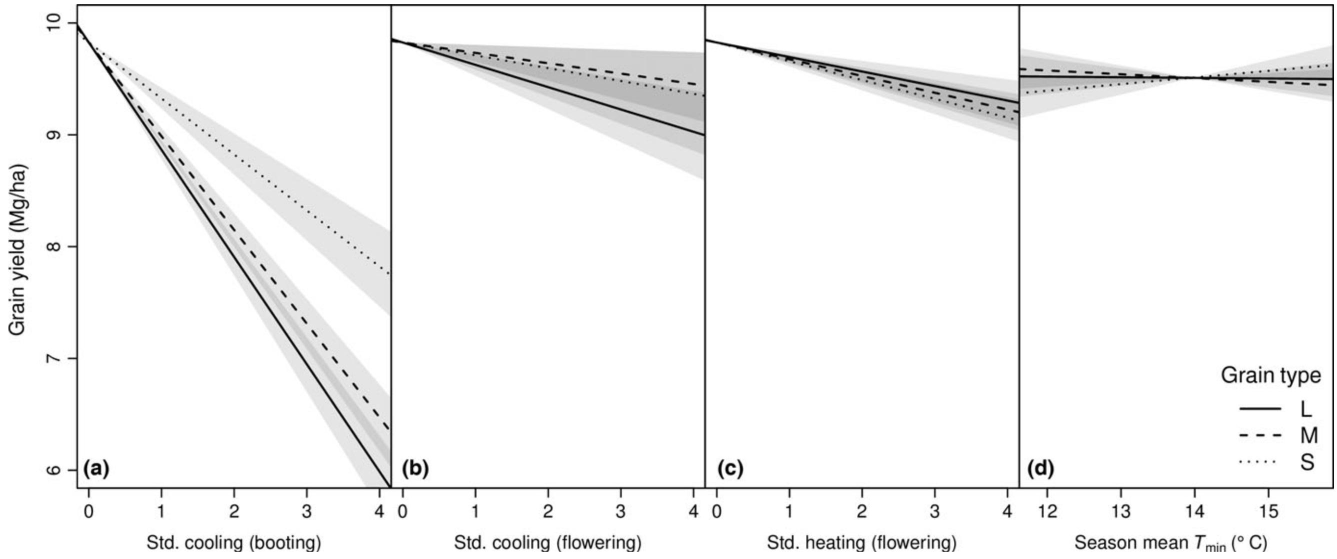

FIGURE 5 The estimated effects of cool during the booting stage (a), cool during the flowering stage (b), heat during the flowering stage (c), and season mean temperatures (d) on yield of long (L), medium (M), and short (S) grain rice cultivars in California, USA, from 1995 to 2015. Cool and heat stress (a–c) have been standardized to be from 0 (no stress) to 4 (maximum stress) to make comparisons between stressors possible. Presented estimates are the effect averaged over uncertainty in the other parameters in the model. The shaded areas are the 90% credible intervals

limited to systematic differences between sites, cultivars, and years. By conditioning on these differences between observations, the estimates here rely on fewer strong assumptions for validity. Second, in this study the effects of point stresses and seasonal warming losses are simultaneously estimated, with the conclusion that once the amount of cool and heat stress during booting and flowering is taken into account, seasonal mean T_{min} does not explain much additional variation in yield. As the effects of point stresses and seasonal warming losses tend to be correlated, it is possible that previous estimates were attributing yield loss to the wrong mechanism. Lastly, these differences might be due to differences between the data sets used to make inferences; at $N = 27{,}021$, the data set used for this analysis is orders of magnitude larger than the data sets used by these previous efforts, and, as stated previously, were observed in a system uniquely situated to separate these temperature effects.

The results here confirm medium and short grain cultivars bred for temperate rice production systems are tolerant of cool temperatures relative to long grain cultivars (Kim & Tai, 2011; Lu et al., 2005; Mackill & Lei, 1997; McKenzie, Johnson, Tseng, Oster, & Brandon, 1994). The estimate for medium grain types (14°C) is similar to previous estimates (12.5–15°C; Board et al., 1980). However, due to differences between collecting temperature data in-field, where temperatures are buffered by the large mass of flood water and plant matter verses at near-by weather stations, the estimates here should be taken as approximations. These estimates also confirm long grain cultivars are not as tolerant of cool temperatures and begin to experience yield loss at a higher temperature (16.3°C; Table 1). It is notable that long, short, and medium grain types were estimated to have similar tolerance of cool temperatures during the flowering stage (Table 1), suggesting lower genotypic variability in cooling tolerance during flowering compared to cooling tolerance during booting. Although long grains were more tolerant to heat during flowering compared to short and medium grains (Table 1), heat stress was estimated to have relatively low impact compared to the cooling stress at booting (Figure 2 and Fig. S2, Table 1); hence, medium and short grain types will continue to be the most suitable grain types for this system. It is worth noting, however, that high vapor pressure deficit (VPD) in CA's arid climate may have resulted in significant transpirational cooling of the panicles (Julia & Dingkuhn, 2013; Van Oort et al., 2014, 2015). Thus, rice may not have experienced as severe heat-induced sterility compared to similar temperatures in a more humid climate. Furthermore, it has been shown that there can be large genotypic variation in the ability of different rice cultivars to cool the panicles through this mechanism (Julia & Dingkuhn, 2013). Therefore, the estimate for the relative impact of heat stress during flowering may not be accurate for humid areas with low VPD. Lastly, although the estimates for point stresses represent the average sensitivity by major grain types and significant differences within grain types may exist (Julia & Dingkuhn, 2013) and could present opportunities for improvement in these traits through plant breeding. Evidence here suggests greater resistance to point stresses would increase yield stability in these systems.

The findings here can provide a foundation for future work. Although collecting the data for this study from a single geographic region with highly intensified management decreased confounding effects compared to using data generated from more varied systems, it introduces some uncertainty when extrapolating beyond this system. Follow-up work confirming these estimates in tropical and other temperate systems could further improve the accuracy of these estimates and support climate change impact assessments. Second, this analysis is intrinsically empirical, and while the results provide estimates for the magnitude of various temperature effects, mechanistic models need improvement to better capture the effects estimated here. As noted elsewhere, the current ability of physiological models to capture these mechanisms is limited (Espe, Yang, et al., 2016; Van Oort et al., 2015). Improved physiological models would allow better understanding of the yield potential in these systems (Espe, Cassman, et al., 2016; Zhang & Tao, 2013; Zhang et al., 2014) and allow better simulation-driven investigation of not only the future impacts of climate change but also the current vulnerability of these systems to current climate variability. Lastly, while this study has been concerned with the impact of temperature-driven effect, the estimation of the impact of other factors, such as solar radiation, can be made more accurate by controlling for the confounding influence of point stresses.

The ability of agricultural systems to continue to feed the world's population relies on producing more food in the face of uncertainty, both current and future. Previous literature has identified seasonal warming losses due to increased temperatures as a key concern for agricultural systems in the future. However, evidence here suggests that point stresses during the reproductive stages are currently impacting agricultural yield in temperate rice production systems more than seasonal warming losses. Point stresses have a direct effect on yield stability; hence, efforts to increase the resilience and continued improvement of agricultural systems need to account for this current state of affairs, even while planning for the future. Evidence of genetic variability in the response of different grain types to these stresses suggests opportunities for breeding programs to increase yield stability in the face of a changing world.

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