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Interactive effects of heat and drought on wheat yield change from synergistic to antagonistic as their severity increases

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ABSTRACT

Wheat yield is increasingly threatened by the co-occurrence of drought and heat stress, particularly under climate change. While both stresses independently reduce yield, their combined effects on wheat production remain under-explored. We meta-analysed 141 factorial combinations of heat and drought stress in field and controlled environment experiments. On average, combined stress led to 49% yield loss, indicating no between-stressor interaction as independent heat and drought caused 27% and 22% losses. However, combined stress impacts varied widely around this average value, but were predictable using a meta-regression model based upon the yield losses from independent stressors. Independent stressors causing relatively moderate yield losses led to greater losses in combination than expected from their independent effects. Conversely, severe stressors, more commonly applied in controlled environment experiments and resulting in extreme yield failure, interacted antagonistically. Our results therefore show that the impacts of combined stress will vary between contexts, requiring site-specific adaptation to future climate change, which can be informed by relatively simple experiments focusing on the independent stressors.

1. Introduction

Bread wheat (*Triticum aestivum* L.) and durum wheat (*Triticum turgidum* ssp. *durum*) are the most widely grown wheat species, covering over 220 million hectares worldwide, and contributing to global grain production with about 798 million tons annually (FAOSTAT, 2023). Climate change projections indicate that this global production is expected to face significant challenges in the coming years (IPCC, 2021). The frequency and severity of extreme temperatures and periods with reduced rainfall are projected to increase with climate change (IPCC, 2021). Each degree Celsius of further mean temperature increase could reduce global wheat production by approximately 6% (Asseng et al., 2015; Zhao et al., 2017). However, extreme weather events, such as heatwaves have effects beyond those of increased average temperatures (Barlow et al., 2015; Lobell et al., 2012; Pradhan et al., 2012; Ullah et al., 2022). For example, Liu et al. (2019) showed substantial reductions in grain number (45%) and fertility (33%) of wheat when heat stress (37 °C) was applied for 24 h post anthesis. Likewise, water deficit stress poses a significant threat to wheat yield (Daryanto et al., 2016; Farooq et al., 2014; Wang et al., 2017), especially in rainfed cropping systems where drought stress is projected to intensify causing an additional 9–12% yield loss in wheat by the end of this century (Leng and Hall, 2019).

The majority of research to date has focused on the impacts of drought stress or heat stress acting in isolation on wheat yield (Asseng et al., 2015; Barnabás et al., 2008; Farooq et al., 2011; Ullah et al., 2022). However, this narrow focus on individual stressors could risk maladaptation of global wheat production to combined drought and heat stress, which frequently occurs in farmers' fields (Côté et al., 2016) and with potential impacts beyond the individual stressors (Rizhsky et al., 2004). Research shows that while plants are sessile organisms, with adequate access to water, they can maintain an internal temperature safely below ambient through evapotranspiration, thus reducing the effects of heat stress (Fukai and Mitchell, 2022). This canopy temperature depression can depend on soil water conditions and can break down when water is limited, increasing plant temperature to harmful levels (Friedlhuber et al., 2011; Schumacher et al., 2019). Similarly, high temperatures may hasten the onset of drought stress by increasing evaporative demands (Miralles et al., 2019). Recent omics studies show that plants can detect water limitation and high temperature in different

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tissues (belowground and aboveground, respectively) and at different speeds, mounting different physiological responses to the individual and combined stressors (Xu et al., 2023).

Previous research that has investigated the effects of combined drought and heat stress on wheat yield has found inconsistent results (Cohen et al., 2021; Mahrookashani et al., 2017; Qaseem et al., 2019; Rizhsky et al., 2004; Sattar et al., 2020). Some studies report synergistic effects, where combined stress has a greater negative impact than is predicted by summing the individual stress impacts (Masruri et al., 2023; Alghabari et al., 2014), additive effects, where combined stress doesn't significantly vary from the sum of the individual stress impacts (Farooq, 2023), or antagonistic effects, where combined stress has a lower negative impact than the sum of individual stressors (Lama et al., 2023).

The different findings for the interaction of drought and heat stress could relate to methodological differences between experimental studies, for example, the timing or the severity of each stress (Shavrukov et al., 2017). Understanding how these stressors interact is essential to understand future threats to food security with climate change, with many existing climate change projection studies assuming only the independent effects of heat and drought (e.g. Harkness et al., 2020). Some of the contradictions that surround the interaction of these stressors may be due to statistical complications involved in quantifying interactions (Spake et al., 2023). Detecting statistically significant interactions requires larger sample sizes than those needed to detect the main effects (Burgess et al., 2022; Yang et al., 2022) and the nature of interactions can vary between additive and multiplicative (e.g. logarithmic) measurement scales (Duncan and Kefford, 2021; Spake et al., 2023).

To overcome these varied experimental and statistical barriers we sought to quantify the effects of drought stress, heat stress, and their combination on wheat yield and yield components using meta-analysis. Meta-analysis facilitates the comparison and synthesis of results from diverse studies, typically by converting them to a common scale (e.g. a ratio of yield in control and treatment conditions) and calculating an overall estimate that is often weighted to favour studies with greater replication and/or lower uncertainty (Hedges et al., 1999; Nakagawa et al., 2023). Meta-analysis can increase the statistical power (i.e., the probability to detect an effect) (Yang et al., 2022). Multilevel meta-analysis importantly also enables the quantification and exploration of the differences in effects both within- and between-studies (e.g. Bishop and Nakagawa, 2021).

Here, we used multilevel meta-analytic methods to synthesise empirical studies that have tested responses of wheat yield in 2 by 2 factorial combinations of drought and heat stress. We explored these interactions using effect sizes on both additive and multiplicative (log) scales, primarily focusing on pairwise comparisons, which measure the change in yield relative to control plants or relative to a stress treatment applied in isolation. Additionally, we conducted overall comparisons which measure the change in yield between treatments across factorial combinations (Gurevitch et al., 2000; Lajeunesse, 2011; Macartney et al., 2022; Morris et al., 2007). We then addressed three questions: i) do drought stress and heat stress interact to affect wheat yield and yield components? ii) if there is an interaction, is it synergistic or antagonistic? iii) which factors explain variation in the individual and combined effects of drought stress and heat stress on wheat yield and yield components?

2. Methods

2.1. Literature search and selection criteria

To identify relevant publications for our meta-analysis, we performed a systematic review using Web of Science and Scopus databases on 29th February 2024, searching publication titles, abstracts, and keywords with the following search strings: ["triticum OR wheat" AND "drought OR water OR moisture" AND "heat OR temperature OR hot" AND "yield" AND "stress"]. This search identified 3278 publications. We screened the 2483 unduplicated publications, first by title, then abstract and full text using the following criteria: it is an empirical study testing responses of wheat to at least 2 by 2 factorial combinations of drought and heat stress; treatments are randomly assigned to experimental units; it reports original results; it reports wheat responses using one or more of the following yield-related traits or yield components: grain number, harvest index, 1000 kernel weight, grain weight, spike length, number of spikelets and number of spikes.

Our screening process identified thirty-three publications. We then re-iterated the screening process on the reference lists of these publications, which resulted in a further three publications that met our inclusion criteria and a total of 36 publications with publication dates from 1984 to 2023 (Table 1a, 1b). See supplementary information for a PRISMA diagram (Fig. **S1**) and detailed reporting of our methods following PRISMA EcoEvo guidelines (O'Dea et al., 2021). Our analysis included experiments conducted in both controlled environments using pot-grown plants (Table 1a) and under field conditions (Table 1b). However, many field studies imposed high temperature stress by altering sowing dates between treatments (Table 1b), which can confound temperature treatments with other possible differences associated with sowing date and growing period. To understand the impact of these different approaches, the type of experiment (i.e., field vs. pot) was included as a moderator variable in the meta-regression (see Section 2.4).

2.2. Data extraction and compilation

We extracted descriptive statistics from text, tables, or figures (the latter using ImageJ software; Abràmoff et al., 2004). Publications typically reported plant responses to experimental treatments using more than one yield component (e.g., grain yield and grain number) for the same experimental unit (e.g. the same potted plant). We extracted all effect sizes and used random effects and variance-covariance matrices in our models to account for the resulting nonindependence (see Sections 2.3 and 2.4; Noble et al., 2017). Data were organised into four treatment combinations representing a 2 × 2 factorial design (control (C), drought stress (D), heat stress (H), and combined drought and heat stress (DH). One publication (Alghabari et al., 2014) reported results across multiple temperature treatments and we selected the two temperature levels closest to the mean control and high temperature levels in all other publications to avoid introducing dependence associated with shared-control comparisons (Noble et al., 2017). Where publications reported additional factors (e.g. nitrogen and compound application) we included only the control conditions. We did not categorise results based on these factors due to the limited number of studies, which limited our ability to account for the impacts of these factors. Our dataset for analysis comprised 458 rows for which we calculated effect sizes.

Some publications did not report standard deviation or a convertible alternative. We received data from some authors, but when contacting authors was unsuccessful, we imputed the missing SD values (179 data rows) using the HotDeck Nearest Neighbour method from the package metagear, which imputes SD from data with similar means using the function impute_SD (Lajeunesse, 2016). We conducted a sensitivity analysis to assess the impact of using these imputed SD in our meta-analytic models (see Section 2.5).

2.3. Calculating effect sizes

Our analysis focused on measuring the change in yield and yield components between plants exposed to stress treatments relative to control conditions, using log response ratio-based effect sizes (lnRR; Hedges et al., 1999).

$$\mathrm{lnRR} = \ln\left(\frac{\mathrm{M}_{\mathrm{treatment}}}{\mathrm{M}_{\mathrm{control}}}\right) = \ln(\mathrm{M}_{\mathrm{treatment}}) - \ln(\mathrm{M}_{\mathrm{control}}) \qquad (1)$$

Table 1a
Pot studies included in our meta-analysis. Field capacity (FC), plant available water (PAW), volumetric soil water content (VSWC), water potential (WP), not specified (-), control (C), drought stress (D), heat stress (H), and the combination (DH). We define progressive D and DH treatments as cases where plants are not re-watered during stress exposure such that soil moisture progressively decreases over time.

Reference	Country	C, D day/night temperature (°C)	H, DH day/night temperature (°C)	Photoperiod day/night (hours)	Duration of D (days)	Duration of H (days)	D/DH stress Intensity	Count of factorial combinations	Count of effect sizes	Stage of stress exposure
Farooq 2023	Oman	27/19	37/29	15/9	-	-	35% WHC	5	20	Stem elongation
Lama et al., 2023	Sweden	15/15	29/14	-	5	5	progressive	8	16	Heading
Masruri et al., 2023	Oman	25/18	37/28	15/9	-	-	35% FC	2	6	Stem elongation
Ru et al., 2023	China	26/16	36/26	14/10	12	12	45–55% FC	1	3	Grain filling
Ru et al., 2022	China	26/16	36/26	14/10	12	-	45–55% FC	2	6	Grain filling
Sattar et al., 2020	Pakistan	28/-	35/-	-	20	20	50% FC	1	5	Heading
Bakhshandeh et al., 2019	Australia	25/15	30/20	12/12	-	-	15% FC	4	4	Floral development
Li et al., 2019	Denmark	24/16	40/35	16/8	10	5	16% VSWC	2	10	Grain filling
Liu et al., 2019	Australia	22/12	37/27	12/12	-	1	50% FC	10	70	Booting & grain filling
Qaseem et al., 2019	Pakistan	25/15	36/30	-	16	16	30% FC	7	5	Heading
Qaseem et al., 2018	Pakistan	-	36/-	-	16	16	30% FC	1	20	Grain filling
Liu et al., 2017	Denmark	24/10	40/25	12/12	11	5	7.5–10% FC	1	4	Grain filling
Alghabari et al., 2014	England	20/12	33/25	16/8	3	3	progressive	17	28	Booting & anthesis
Rakszegi et al., 2014	Hungary	24/20	35/20	8/16	15	15	40–45% FC	3	3	Floral development
Pradhan et al., 2012	USA	21/15	36/30	18/6	16	16	progressive	6	30	Anthesis & grain filling
Balla et al., 2011	Hungary	24/20	35/20	8/16	15	15	40% FC	1	4	Floral development
Prasad et al., 2011	USA	24/14	31/18 or 34/22	16/8	18	18	progressive	2	8	Heading
Zhang et al., 2010	Canada	22/12	32/22	16/8	-	-	40% FC	2	4	Booting
Hassan 2006	Egypt	24/25	40 to 42/-	16/8	-	-	progressive	1	6	Flag leaf
Plaut et al., 2004	Australia	25/18	30/25	14/10	18	14	progressive	2	6	Grain filling
Auld and Paulsen 2003	USA	15/10	30/25	16/8	-	-	27% FC	1	5	Anthesis
Gooding et al., 2003	England	23/15	28/20	16/8	13	13	44% FC	1	3	Anthesis
Wardlaw, 2002	Australia	18/13	27/22	8/16	-	-	progressive	1	1	Grain filling
Baker, 1996	Canada	18/10	30/18	16/8	-	-	30% PAW	2	6	Stem elongation
Nicolas et al., 1984	Australia	23/15	28/20	16/8	10	10	progressive	1	6	Booting & anthesis

Table 1b
Field studies included in our meta-analysis. We define rainfed as cases where plants are grown without supplementary irrigation and receive only natural rainfall during the growing season. Late sowing describes the cases where heat-stress plants are sown later than normal to expose them to higher temperatures during targeted growth stages.

Reference	Country	D/DH stress Intensity	H imposition	Count of factorial experiments	Count of effect sizes	Stage of stress exposure
Kumar et al., 2021b	India	progressive	late sowing	4	24	Anthesis & grain filling
Yashavanthakumar et al., 2021	China	progressive	late sowing	2	6	Grain filling
Kumar et al., 2021a	India	progressive	late sowing	12	4	Anthesis
Qaseem et al., 2019b	Pakistan	35% FC	late sowing	1	4	Heading
Gurumurthy et al., 2019	India	rainfed	late sowing	1	2	Grain filling
Li et al., 2019b	China	rainfed	polytunnel	1	3	Grain filling
Barutcularl et al., 2017	Turkey	rainfed	late sowing	15	30	Anthesis
Milad et al.., 2016	Egypt	progressive	late sowing	14	84	Heading
Barutcularl et al., 2016	Turkey	rainfed	late sowing	1	1	Anthesis
Tahmasebi et al., 2014	Iran	progressive	late sowing	4	12	Booting
Li et al., 2012	China	rainfed	greenhouse	3	9	Grain filling

$$\mathrm{var}(\mathrm{lnRR}) = \frac{\mathrm{SD}^2_{\mathrm{treatment}}}{\mathrm{N}_{\mathrm{treatment}}\mathrm{M}^2_{\mathrm{treatment}}} + \frac{\mathrm{SD}^2_{\mathrm{control}}}{\mathrm{N}_{\mathrm{control}}\mathrm{M}^2_{\mathrm{control}}} \tag{2}$$

Using Eqs. (1) and 2, we calculated five pairwise effect sizes $\ln(M_D/M_C)$, $\ln(M_H/M_C)$, $\ln(M_{DH}/M_C)$ $\ln(M_{DH}/M_D)$ and $\ln(M_{DH}/M_H)$ which quantify the effect of each stress treatment type as a relative change in yield, in comparison to control plants, or in comparison to a stress treatment applied in isolation. A negative value indicates a lower yield in the numerator than the denominator. We used the formula exp(lnRR)-1 * 100 to calculate the percentage yield loss between the numerator and denominator (e.g., stress and control) for each effect size.

Other meta-analytic approaches exist for interpreting interactions (Gurevitch et al., 2000; Lajeunesse, 2011; Macartney et al., 2022; Morris et al., 2007) and we report results from these in the supplementary information (Section 1.4, 2.4, 3.4), but we note that these ‘overall’ effect sizes quantify the difference between all factorial combinations where a stress treatment is applied and where it is not, and therefore summarise yield loss against several different baseline conditions which is not of key relevance to our analysis.

We also calculated effect sizes using standardized mean difference (SMD) with heteroscedastic population variances in the two groups (Bonett, 2008, 2009), and a bivariate analysis which combines lnRR and SMD in the same model (Yang et al., 2024), and we report these results in the supplementary information (see Section 4). While lnRR quantifies the relative change in yield between numerator and denominator on the multiplicative scale, SMD makes comparisons on an additive scale and quantifies yield changes in units of standard deviation, which can lead to qualitatively different outcomes (Duncan and Kefford, 2021; Spake et al., 2023).

For each effect size, we calculated variance-covariance matrices (VCV) for each model using the impute_covariance_matrix function from the clubSandwich R package version 0.60 (Pustejovsky, 2025) to control for dependence of sampling variances that arises when yield is measured across multiple yield parameters on the same experimental unit (Pustejovsky, 2020). We assumed these sampling variances had a correlation coefficient of 0.5 and tested the sensitivity of model findings to other rho values (Bishop and Nakagawa, 2021). In addition, we explored using robust variance estimation to estimate the VCV matrix as an alternative approach (Pustejovsky and Tipton, 2022).

2.4. Meta-analysis and single moderator analyses

We ran meta-analytic models for all effect sizes in R version 4.2.2 (R Core Team, 2022; see supporting information for annotated R code) using the *metafor* package version 3.0.2 (Viechtbauer, 2010). We first ran null models to calculate cross-publication estimates for each effect size; these models included only random effects and no fixed effects (an intercept-only model). The optimal random effects were an individual effect size identifier (unique per data row), a publication identifier, and year nested within a publication (where a publication reported experiments conducted across multiple years). We also evaluated additional random effects, such as country, study latitude, and genotype nested within a study (where a study evaluated multiple genotypes), but these did not improve model fit based on Akaike’s Information Criterion (AIC) and were therefore excluded from the final models (see supporting information, Section 1.1, 2.1, 3.1). For each model, we estimated the heterogeneity in effect size (I^2) associated with random effects and remaining unexplained heterogeneity (Borenstein et al., 2019; see Table 2).

We assessed whether D and H act additively, antagonistically, or synergistically by summing the pairwise effect sizes $\ln(M_D/M_C)$ and $\ln(M_H/M_C)$, which represent the individual effects of D and H stress relative to C, and comparing this value to the combined stress treatment effect size $\ln(M_{DH}/M_C)$. If the sum of individual effect sizes for heat and drought stress was smaller than the pairwise effect size for the combined stress treatment, it would indicate that the stress treatments act synergistically, causing a greater than expected yield loss when occurring in combination. To assess the nature of the interaction, we used the “expected yield loss” (sum of individual effects) as a predictor of the actual yield loss with combined stress in meta-regression models and tested its explanatory power with likelihood ratio tests as below. We tested whether this relationship differed with experiment type (by including an interaction term) and whether it was curved or linear (by including a quadratic term). We did this analysis on the log scale (in which case summing is multiplicative; Kerkhoff and Enquist, 2009), on the scale of percentage yield loss (additive) by summing the back-transformed values, and on the SMD scale which is also additive.

Table 2
Pairwise comparisons of stress treatments drought (D), heat (H), and combined drought and heat stress (DH) vs. control (C) or a stress treatment applied in isolation across multiple effect sizes. Estimates, 95% confidence intervals (CI), and heterogeneity for random effects in ten models.

Model	Estimate	95% CI	Heterogeneity (I^2) for each random effect			
			Total	Study	Year in study	Residual
lnRR effect sizes						
D/C	**−0.25**	−0.20, −0.30	99.3	9.76	27.64	61.9
H/C	**−0.31**	−0.21, −0.40	99.6	34.38	32.32	32.91
DH/C	**−0.66**	−0.52, −0.80	99.7	23.9	40.58	35.17
DH/D	**−0.38**	−0.27, −0.49	99.4	38.09	36.62	24.70
DH/H	**−0.33**	−0.25, −0.40	98.9	32.10	28.74	38.03
SMD effect sizes						
D/C	**−3.95**	−2.80, −5.10	97.3	26.80	44.45	26.04
H/C	**−3.79**	−2.21, −5.36	98.11	66.78	24.54	6.79
DH/C	**−7.07**	−4.74, −9.39	98.77	68.46	23.86	6.45
lnRR_{Q10} effect sizes						
H/C	**−0.33**	−0.24, −0.42	99.5	31.52	26.21	41.8
DH/C	**−0.73**	−0.55, −0.90	99.7	45.61	21	33.14

Note: Bold values represent estimates that are significantly different from zero.

We conducted uni-moderator meta-regression analyses by adding moderators (fixed effects) to the three ‘pairwise’ random effect models (ModD.lnRR, ModH.lnRR and ModDH.lnRR; Table 2) to explain the heterogeneity in these effect sizes. The moderators we tested were (a) how yield is measured, (b) crop stage at stress, (c) pot volume, (d) drought duration, (e) drought treatment type, (f) heat duration, (g) difference between day temperature in H and control conditions, (h) treatment day temperature, (i) the type of the experiment, and (j) wheat species (see Table 3 and the supporting information for a detailed description of moderators).

We used likelihood ratio tests (LRT) to test the explanatory power of moderators by comparing models including each moderator to the null model for that effect size. We made these model comparisons using models fitted with maximum likelihood (ML) while we report results from models fitted with restricted maximum likelihood (REML). We also used the marginal R^2 to quantify the heterogeneity explained by each moderator (Nakagawa and Schielzeth, 2013).

2.5. Publication bias and sensitivity analysis

We used three approaches to test for publication bias. First, we used funnel plots to visually inspect the pattern of asymmetry of the residuals from full meta-analytic models that included all significant moderators. Second, we fitted ‘effective sample size’ as a moderator in the full models (Nakagawa et al., 2022). A significant sample size indicates

Table 3
The number of levels (df), effect sizes (k), likelihood ratio test statistic (LRT) and p-value, and marginal (R^2) for each moderator used in the single moderator analyses for each of the three pairwise meta-analyses: effect of drought stress (D), heat stress (H), and the combination (DH) in comparison to the control. LRT was used for all model comparisons.

	Pairwise effect: Drought stress				Pairwise effect: Heat stress				Pairwise effect: Combined stress			
Moderator	df, k	LRT	p-value	R^2 (%)	df, k	LRT	p-value	R^2 (%)	df, k	LRT	p-value	R^2 (%)
Response measure	4, 458	101.3	<0.001	16.87	4, 458	99.91	<0.001	9.38	4, 458	121.58	<0.001	11.74
Crop stage at stress	2, 458	1.22	0.54	0.92	2, 458	3.56	0.17	3.89	2, 458	7.38	0.02	7.14
Pot volume	2, 279	0.67	0.71	0.88	2, 279	1.73	0.42	3.13	2, 279	2.15	0.34	4.02
Drought duration	2, 157	5.63	0.05	12.70					2, 157	2.56	0.28	5.12
Drought treatment type	1, 458	0.28	0.60	0.36	1, 458	0.63	0.43	1.15	1, 458	0.09	0.77	0.15
Type of experiment	1, 458	2.64	0.09	3.33	1, 458	1.28	0.26	4.02	1, 458	3.72	0.05	6.76
Wheat species	1, 458	0.85	0.36	0.67	1, 458	1.08	0.001	6.08	1, 458	1.08	0.30	0.59
Heat duration					2, 21	7.70	0.02	18.04	2, 221	4.18	0.12	7.18
Heat exposure					1, 221	3.94	0.01	22.31	1221	1.15	0.28	4.44
Temperature difference					1, 279	0.44	0.81	0.81	1, 279	0.06	0.81	0.11
Treatment temperature					1, 427	0.41	0.52	0.92	1, 427	0.25	0.61	0.58

statistically significant asymmetry in the funnel plot (Egger et al., 1997). Third, we fitted the publication year as a moderator in the full models to test for time-lag bias where the magnitude of reported effect sizes changes over time.

We then tested the robustness of our findings from the three 'pairwise' effect sizes by conducting a series of sensitivity analyses. First, we examined the impact of varying the sampling correlation (rho) used in constructing the VCV by testing a range of rho values (0.3, 0.5, 0.7, 0.9) (Yang et al., 2024) and re-ran the three null models with each rho value. This allowed us to assess whether lnRR and SMD estimates were sensitive to the sampling correlation value. Second, we re-ran the three null models using data with only reported SD to understand the impact of imputing SD. Third, we conducted a 'leave-one-study-out' analysis by removing all effect sizes associated with a single publication from the dataset and calculating new meta-analytic means and 95% CIs. This allowed us to assess whether any individual publications had a strong effect on the pairwise effect sizes for D, H, and DH and in turn, our interpretation of whether these D and H act synergistically or additively when they co-occur.

To account for the difference in temperature between the numerator and denominator across the different publications we also re-ran the null meta-analytic models using two additional pairwise effect sizes ($\ln RR_{Q10}$ response ratio) for the effect of H stress and the combination of D and H stress in comparison with the control (Noble et al., 2022). $\ln RR_{Q10}$ effect sizes could not be applied to the pairwise effect size for drought because these and control treatments share the same temperature.

Finally, we re-ran the six multi-variate models (ModD.lnRR, ModH.lnRR, ModDH.lnRR, ModD.SMD, ModH.SMD, ModDH.SMD; Table 2) using the bivariate multilevel meta-analyses (Yang et al., 2024), a recently developed technique which combines lnRR and SMD in one model to reduce the number of models and the standard error in effect size estimates (see supporting information, Section 5).

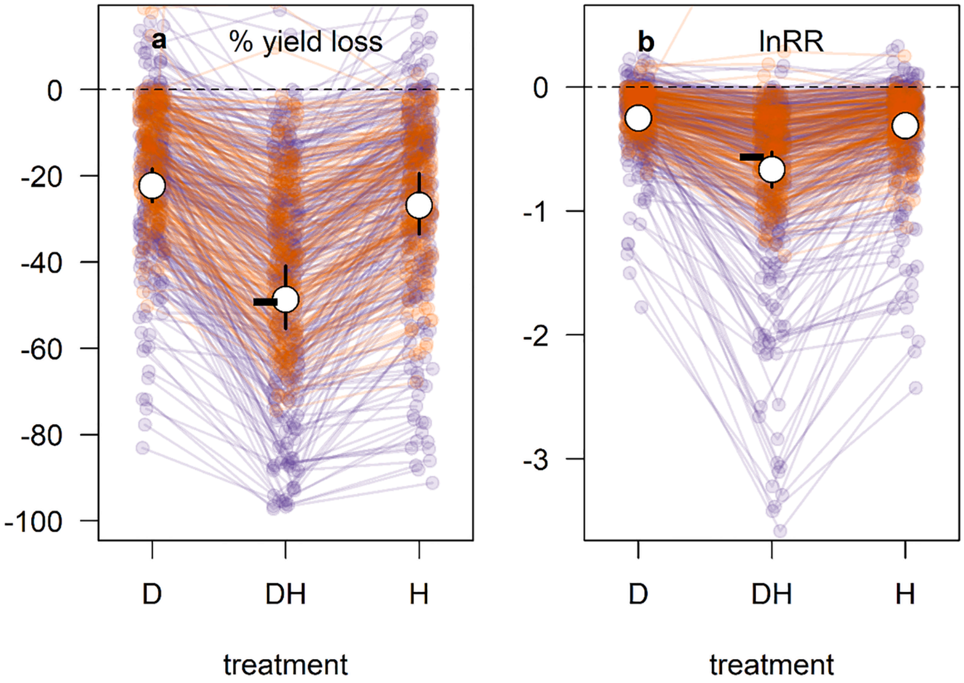

Fig. 1. Impacts of drought stress (D), heat stress (H), and their combination (DH) relative to control. Mean estimates and their 95% confidence intervals from pairwise meta-analytic models are illustrated by black outlined circles and vertical black lines. Negative values indicate that yield decreased in treatments relative to the control. An effect size of zero would indicate that there was no difference in mean yield between treatment and control. The bold horizontal lines is the sum of D and H mean estimates and indicates the expected effect size if D and H act additively. Purple and orange circles and lines show effect sizes from individual experimental comparisons from pot and field studies respectively (n = 458 for each treatment from 36 publications).

3. Results

Drought and heat stress caused greater yield losses in wheat when co-occurring than independently. Our pairwise lnRR models show that co-occurring drought and heat stress (DH) caused average losses of 48.6% compared to control conditions, while heat stress (H) and drought stress (D) in isolation caused 27% and 22% yield losses respectively (Fig. 1a).

Overall, our results indicate that co-occurring drought and heat stress act additively. The average yield loss due to DH, 48.6%, was near equal to the sum of percentage yield losses from D and H applied in the isolation, 49% (bold bar in Fig. 1a). The SMD effect sizes supported this finding (Table 2 and supplementary information Section 3.4). While on the log (multiplicative) scale the sum of the individual stressors (−0.56, bold bar in Fig. 1b) was smaller than the relative change in yield with combined stress (−0.66), it was within the confidence interval around this estimate (−0.52, −0.80; Fig. 1b; Table 2). This finding was consistent in a bivariate analysis of lnRR and SMD (see supplementary information, Section 5).

There was high heterogeneity in the pairwise effect sizes for D, H and DH ($I^2_{total} > 90\%$ in all models, Table 2). Experiments reporting smaller yield losses were more likely to show synergistic interactions between D and H, while experiments reporting greater yield losses were more likely to detect antagonistic interactions (Fig. 2a). Meta-regression analysis indicated that the interaction between D and H changed from synergistic to antagonistic when the sum of yield loss from independent D and H increases beyond 37% (Fig. 2a; note this threshold varied from 32.4 to 44% in various sensitivity analyses). The meta-regression model of actual yield loss with DH predicted by expected yield loss (sum of D and H yield losses) has slope 0.55 (confidence interval 0.52, 0.58) which is significantly different from a 1:1 relationship between expected and actual yield loss with DH (intercept is −16.7 (−19.6, −13.8)). The sum percentage yield loss caused by the two individual stressors exceeded 100 percent in 25 of the 458 effect sizes, which obligated an antagonistic interaction in these cases, as the sum of individual stressors will always exceed the actual yield loss from combined stress. An analysis using the SMD effect size, which is also on the additive scale, replicated this finding with a slope of 0.57 (0.53, 0.62), indicating that synergistic interactions were more likely when the independent stressors caused lower yield loss (intercept is −1.54). This effect was also present, but less pronounced, on the multiplicative (log) scale (slope 0.81 (0.76, 0.85) and intercept −0.18 (−0.25, −0.12)), where addition of D and H is assessed as proportional change and is therefore not subject to bounding (Fig. 2b). These relationships were consistent between controlled environment (pot studies) and field experiments; while an interaction term between experiment type and expected yield loss was marginally significant on the percentage yield loss scale ($p = 0.052$ on % loss scale, $p = 0.5$ on lnRR scale, $p = 0.81$ on SMD scale), indicating a slightly steeper slope for field experiments, this remained significantly different from the 1:1 line, see supplementary information, Section 4.3).

On the multiplicative (log) scale, there was a non-linear relationship between lnRR$_{DH/H}$ and lnRR$_{H/C}$, indicating that in experiments with greater yield losses due to heat stress in isolation, the effect of additional (combined) drought stress was diminished (Fig. 3a; Likelihood ratio test (LRT) comparing models with and without quadratic term $p = 0.002$). In contrast, the relationship between lnRR$_{DH/D}$ and lnRR$_{D/C}$ was linear (Fig. 3b; LRT comparing models with and without quadratic term $p = 0.45$). Both relationships were curved in models using SMD (additive scale) versions of the effect sizes (supplementary information, Section 4.3). Note these comparisons measure the additional yield loss with combined stress by using the yield following independent stress as the baseline, rather than yield in control conditions.

The ‘overall’ lnRR effect size for the interaction (see supplementary information for equations and further details, Section **3.4**) was significantly negative, indicating a synergistic interaction between D and H whereby an additional 8% (3%, 13%) yield loss occurred when D and H were combined, compared to plants exposed only to drought stress at control temperatures. In contrast, SMD effect size showed a significant positive value of 0.82 (0.03, 1.62, $p = 0.04$), indicating an antagonistic interaction between D and H.

3.1. *Single moderator analyses*

The way in which yield was measured explained more variation under D, H, and DH stress than the other tested moderators (marginal R^2 = 16.87%, 9.38%, and 11.74% respectively; Table 3). Grain yield was the most susceptible to stress with a loss of 31%, 36% and 59% under D, H, and DH respectively followed by grain number (Fig. 4). All other yield components (i.e., 1000 KW, harvest index, and spike attributes) responded to stressors similarly.

The extent of yield loss did not vary significantly with the magnitude of D, H and DH stress (Table 3), quantified as D duration, temperature difference (between H or DH and control conditions), and treatment day temperature (for H and DH). Withholding irrigation (progressive drought stress) had a similar effect on yield as pre-determined cycles of

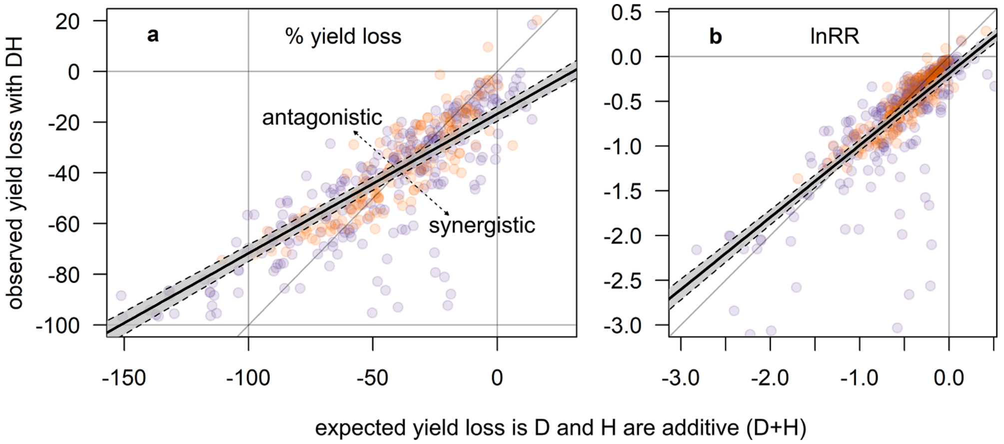

Fig. 2. Expected and observed yield loss due to combined drought and heat stress presented as a) % yield loss and b) multiplicative (log) scale response ratio (lnRR). Lines are estimates from meta-regression models (solid black line) and their 95% confidence intervals (dashed lines and gray shading) using expected yield loss (D + H) as a predictor. Diagonal solid grey line shows 1:1 line, above which the combined effect size causes less yield loss than the sum of individual stresses (antagonistic), on the 1:1 line, the combined effect size is equal to the sum of the individual stresses (additive), and below the 1:1 line, the combined effect size causes more yield loss than the sum of individual stresses (synergistic). Purple and orange circles and lines show effect sizes from individual experimental comparisons from controlled environment and field studies respectively.

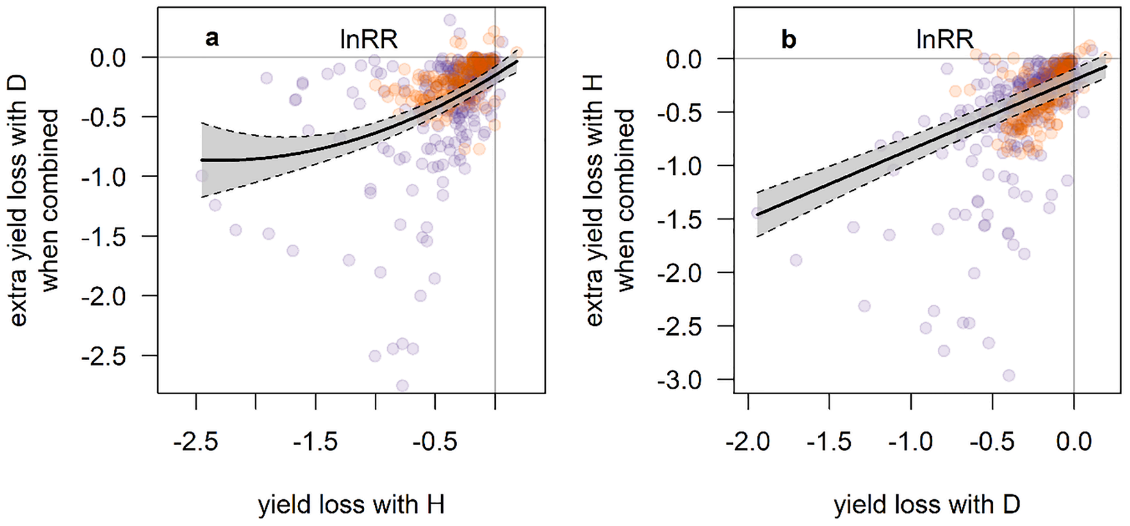

Fig. 3. Additional yield loss with combined stress in comparison to individual stressors, multiplicative (log) scale. a) y axis is pairwise $\ln RR_{DH/H}$ and x axis is $\ln RR_{H/C}$, **b)** y axis is $\ln RR_{DH/D}$ and x axis is $\ln RR_{D/C}$. Estimates from meta-regression models (solid black line) and 95% confidence intervals (dashed lines and gray shading). Purple and orange circles and lines show effect sizes from individual experimental comparisons from controlled environment and field studies respectively.

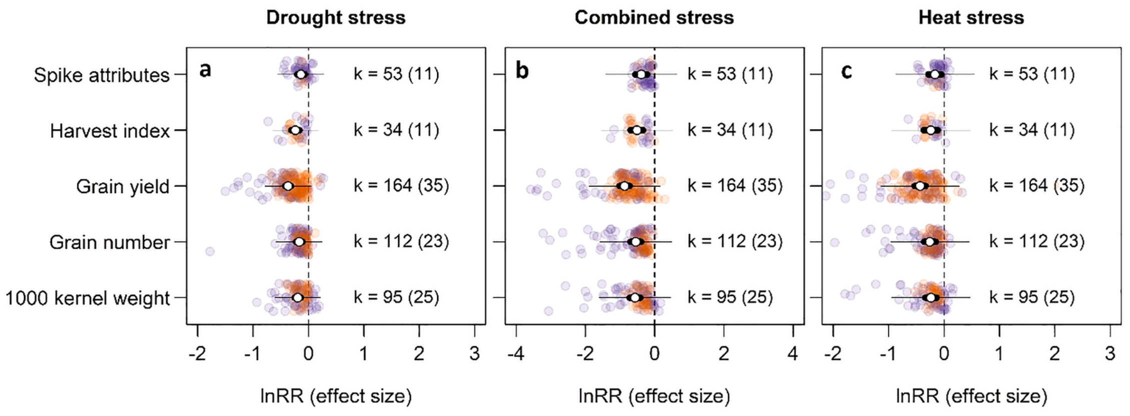

Fig. 4. The orchard plots showing the three different single moderator analyses on the pairwise comparisons. The moderator we tested was the response of wheat to a) drought, b) combined stress and c) heat stress with five categories (1000 kernel weight, grain number, grain yield, harvest index and spike attributes). Results are the proportional yield lost due to drought, heat stress and combined drought and heat stress in comparison with well-watered and optimum temperatures (control). The mean estimate values for each group are indicated as solid white circle, 95% confidence intervals (CI, horizontal thick black lines) and 95% prediction intervals (PI, horizontal thin black lines). Purple and orange circles show effect sizes from individual experimental comparisons from pot and field studies respectively. k shows the number of effect sizes and the number of studies reported the variable.

drying and re-wetting under DH (Fig. S28). The duration at which plants were exposed to high temperature stress explained some of the variation in the effect size under H and DH ($R^2 = 18.04\%$ and 7.18% respectively; Table 3). We also found some evidence that the effect of H stress varied with the duration of exposure to high temperatures ($p = 0.01$; Table 3). Our models produced similar estimates when we used temperature coefficient ($\ln RRQ_{10}$) in place of lnRR and SMD for the H and DH pairwise models, which accounts for the difference in temperature in the effect size calculation (supplementary information, Section 2.1, 3.1).

Wheat species also explained variation in heat stress responses ($R^2 = 6.08\%$; Table 3) but not in responses to D or DH. Greater yield losses were found in studies that used *Triticum aestivum* under heat stress, with an average of 28%, compared to 22% in *T. turgidum* ssp. *durum* (Fig. S20). Including genotype as a random effect did not improve the model fit for heat, drought and combined drought and heat stress (see supplementary information, Section 1, 2, 3).

We found some evidence that the impact of D and DH stress varied between controlled environment and field experiments ($p = 0.09$ and 0.05 respectively; Table 3). The effects of stress on wheat yield were relatively more severe in pot experiments with a loss of 24%, 32% and 53% relative to field studies which contributed to a loss of 17%, 22% and 38% under D, H, and DH respectively (Fig. S6, 19, 33). We found no significant evidence that effect sizes varied with pot size in the controlled environment experiments. Most experiments used small pots, with limited research conducted on medium or large pot sizes (supplementary information, Section 1.3, 2.3, 3.3). The developmental stage at which the crop plants were subjected to stress treatments explained some variation under DH stress ($R^2 = 7.14\%$) but did not explain significant variation in effect size under D and H stress (Table 3).

3.2. Publication bias and sensitivity analysis

There was no significant evidence of publication bias for any of our pairwise effects models (see supporting information for full details). Egger's regression did not identify significant slopes for the 'effective sample size' and similarly, the slope of year of publication was not significant ($p = 0.84$, 0.97 and 0.57) for drought, heat and combined stress, respectively (Supplementary information, Section 1.5, 2.5, 3.5).

We also observed that imputed missing standard deviations did not substantially influence the meta-analytic mean or 95% CI our pairwise effects models. Likewise, the model estimates with both lnRR and SMD did not change with different values of rho values assumed in constructing VCV matrixes (Table **S1** to **S6**).

The ‘leave-one-group-out’ sensitivity analysis, in which we re-ran our null models excluding the effect sizes from each individual publication in turn, indicates that our estimate from pairwise models using lnRR are not unduly influenced by the results of any individual publication (Fig. **S10, 23, 37**). We extended the leave-one-out analysis to test whether the effect sizes from individual publications affected our conclusions about the additive or synergistic nature of co-occurring water stress and heat stress. The confidence interval for the pairwise effect size always encompassed the additive estimate (the sum of drought stress and heat stress applied in isolation; Fig. 1a). Leave-one-out analyses using the SMD effect size corroborated this finding (supplementary information, Section 3.5). Similarly, when the meta-regression models in Fig. 2 were ran separately for pot and field experiments, the estimated yield-loss thresholds were 39.4% and 32.4%, respectively. Results from this leave-one-out sensitivity analysis showed that the threshold values ranged from 36.1% to 38.4%. When the analysis was restricted to grain yield data only, the estimated threshold increased to 44% (see supplementary information, Section 4.3.1.)

4. Discussion

Our results from an interaction meta-analysis of 141 fully factorial combinations of heat and drought stress on wheat from 36 publications show that drought and heat stress combined additively on average, but there was substantial variation, with experimental results spanning the full range of interaction types (Fig. 2a). With our meta-regression models, the impacts of combined stress can be predicted by the sum of yield loss caused by the individual stressors. Factorial combinations with smaller yield losses from individual stressors consistently showed that heat and drought stress interacted synergistically, with combined stress resulting in greater than expected yield losses. Meanwhile, combinations with greater yield losses from individual stressors showed antagonistic interactions between them. Our analyses indicate the latter occurs because total yield loss is bounded at zero yield. These relationships were qualitatively consistent across field and controlled environment experiments.

Considering our findings alongside modelled yield projections indicates that the interactions between drought and heat stress will range from synergistic to antagonistic in current and future climate conditions. We showed that the interaction between drought and heat changes from synergistic to antagonistic when the sum of yield loss from independent heat and drought increases beyond 37% (Fig. 2a; note this threshold varied from 32.4 to 44% in various sensitivity analyses). However, linking this impact threshold directly to physical climate properties is challenging and potentially misleading, because yield responses to a given temperature or soil moisture deficit depend on multiple interacting factors, including plant genotype, soil type, humidity conditions, and CO_2 concentration (Ainsworth and Long, 2021; Alghabari et al., 2014). Senapati et al. (2021) projected the 95-percentiles of yield loss due to heat and drought stress (the worst 1 year in 20) for rain-fed wheat at 13 sites across Europe in 2050 and reported median yield losses averaging 25% (45% at worst impacted site) for drought stress, and average median yield losses of 6% (16% at worst impacted site) for heat stress. Applying our meta-regression model, we predict that heat and drought stresses would interact synergistically at 7 of the 13 sites and antagonistically at the other 6, with the interaction form changing for some sites between baseline and projected future conditions (see supplementary information for details, Table **S7**; Section 4.4). While the experiments that we analysed were conducted for a range of purposes (e.g. to identify susceptible genotypes; (Alghabari et al., 2014), with many extreme yield loss values recorded, it could be more informative if the severity of stress applied was more closely linked to projected changes in extreme weather events. To facilitate this, there is a need for more readily accessible daily temperature and precipitation projections under different emissions scenarios (as is possible for monthly data via statistical packages such as geodata in R; Hijmans et al., 2023). Using more severe stresses than those projected could lead to underestimating the resilience and utility for adaptation of certain genotypes.

Our results highlight variation in stress responses between wheat species. We found that greater yield losses in response to heat stress were reported in *Triticum aestivum* than in *T. turgidum* ssp. *durum* (Table 3), consistent with previous reports of greater heat tolerance in some durum genotypes (Dias et al., 2011). However, various factors such as the duration and intensity of heat stress applied may have contributed to the differences observed between the two species. Responses to drought and heat stress are known to vary between genotypes (Singh et al., 2012), yet our analysis did not find significant genotypic differences. Genotypes were not consistently reported across the publications, and in some cases pooled results were reported across several genotypes, which limited our ability to robustly test genotype-level responses within and between publications and quantify the potential for adaptation. However, in studies where breeding lines were compared (e.g. Lama et al., 2023; Liu et al., 2019), some genotypes showed positive effect sizes, indicating increased yield under stress relative to control (Fig. 1). While this potentially reflects biological variation in stress tolerance, the majority of these effect sizes were likely not significant in the original studies and contributed little to our overall model estimates because they had low precision (characterised by high variance; see supplementary information Table **S8**; Section 4.7).

Interactions between drought and heat stress varied between additive and multiplicative (log) measurement scales, with the latter identifying some overall synergistic interactions between stressors (Fig. 3). Our analysis therefore supports the arguments made by other authors (Duncan and Kefford, 2021; Spake et al., 2023) that careful consideration of measurement scale is required when interpreting interactions. This is particularly important for authors in the growing field of interaction meta-analyses (e.g. (Gurevitch et al., 2000; Hu et al., 2024; Macartney et al., 2022) where there is an additional choice of the baseline from which to measure changes in an outcome. Reporting yield loss due to combined drought and heat on an additive scale (SMD or back-transformed lnRR) and relative to control yield may be more relevant to farmers, agronomists and researchers assessing future food security. In contrast, the multiplicative scale or the use of different yield baselines (e.g. comparing DH not to control, but to yield loss due to H or D in isolation) may be more relevant for those investigating the mechanisms of stress response, where proportional changes in yield, or yield loss from a reduced baseline may be more appropriate to understand survival and recovery responses including the regrowth of new stems and leaves after drought periods (Claeys and Inzé, 2013).

Plant responses to heat or drought stress are facilitated via opposing physiological mechanisms: drought triggers the closure of stomata to conserve water and heat stress causes the opening of stomata to facilitate cooling via evapotranspiration (Mittler and Blumwald, 2010). Previous studies have shown that the effect of drought on stomatal aperture overrides the effect of heat in needing to cool the leaf surface (Chaves et al., 2016; Fukai and Mitchell, 2022). Our findings using the baselines from the individual stresses as a comparator to their combined impact is informative, with a linear relationship between yield loss due to drought and additional yield loss from heat, and a non-linear relationship between yield loss due to heat and additional yield loss with drought (Fig. 3). This indicates feedback mechanisms (Miralles et al., 2019) with the effectiveness of heat stress response (i.e., stomatal opening for cooling) increasingly limited as the severity of drought increases, exacerbating the impact of heat stress on yield loss (Chaves et al., 2016).

We found that the most severe yield losses were visible in studies which measured grain yield, rather than other yield components (Fig. 4). This is surprising as acute stress is typically considered to act primarily upon reproductive processes such as spikelet initiation, differentiation of floral organs, male and female sporogenesis, pollination and fertilisation (Saini et al., 1984), which most directly influence grain number (Alghabari et al., 2014; Barnabás et al., 2008). The observed severe yield losses are generally associated with substantial reductions in both grain number and grain filling. Our finding may have occurred because grain yield integrates grain number (which heat impacts) and grain weight (which drought impacts). In our study, heat had on average more severe impacts than drought stress treatments, though this may be due to study methodology and the relative intensity of stress chosen by authors. Some studies used temperatures that are lethal to wheat (i.e., 40 °C) and this can trigger acute responses in wheat and dramatically reduce grain yield (Pradhan et al., 2012). In cropping regions prone to such high temperatures (e.g., Australia), wheat is typically grown in the cooler seasons to avoid prolonged exposure to extreme temperatures, particularly at critical growth stages like anthesis and grain filling (Cammarano et al., 2012; Lobell et al., 2015). Additionally, perhaps due to limitations of experimental facilities, heat stress in most of the studies was achieved by exposing plants to high temperature for a prolonged period (e.g., 16 h a day), while in real-world conditions, temperatures fluctuate throughout the day and night. Likewise, the field experiments in our analysis were not properly controlled comparisons and most elicited heat stress and combined stress by growing these plants in a different season, which can confound temperature effects with changes in radiation, photoperiod, and crop development, thereby reducing their robustness. While different methodological approaches have been used to elicit heat stress in field conditions without these confounding factors (e.g., infra-red heating; Martre et al., 2018), such experiments remain relatively rare and have not been combined with drought treatments. Further development of these techniques, especially in fully factorial designs would enhance our understanding of crop responses to combined stresses and perhaps allow the identification of additional useful genetic material for future breeding programmes.

Surprisingly few of the moderators that we tested allowed us to explain variation in response to stress. Cross-study comparisons of a single factor are challenging because each study in our analysis tested an individual combination of heat intensity, stress duration (1–20 days), drought type (progressive and predetermined cycles of re-wetting and drying), and pot size (0.2 – 28 L). Moreover, all but one publication that we analysed considered heat and drought as binary factors, preventing the identification of response surfaces or tipping points for crop yield, and limiting the integration of their results with future modelling studies. Smaller pots tend to exaggerate drought effects due to limited soil volume and nutrient availability (Hill et al., 2024; Poorter et al., 2012; Turner, 2019), and perhaps to overcome this, two-thirds of the publications in our analysis rewatered plants to maintain a pre-determined level of water availability. This may result in inaccurate responses as drought in the field typically occurs progressively (Turner, 2019) and co-occurring heat stress could hasten this drought through evapotranspiration. Not surprisingly, we found more severe yield losses in pot experiments compared to field studies under drought stress conditions. Larger pots might better simulate field conditions and could facilitate phenotyping of beneficial root traits (Hill et al., 2024).

Most publications that we analysed did not consider elevated atmospheric CO_2 as an experimental factor. Evidence from other empirical studies shows that elevated CO_2 can at least partially mitigate the effects of drought and heat stress in wheat by enhancing photosynthesis rates, improving water use efficiency, and maintaining higher PSII photochemical performance (Abdelhakim et al., 2021; Ainsworth and Long, 2005). It remains logistically challenging to consider the impacts of elevated atmospheric CO_2, alongside multiple levels of both heat and drought stress, particularly in controlled field conditions where it is challenging to elicit acute levels of temperature stress (Ainsworth and Long, 2021).

In conclusion, our analysis highlights the complex interplay between drought and heat stress on wheat yields, with interactions ranging from additive to synergistic, depending on the severity of individual stressors, measurement scale and experimental conditions. While pot studies may exaggerate stress effects compared to field studies due to constrained root volume and methodological choices, the high variability in outcomes highlights the importance of aligning experimental conditions with realistic field scenarios. Future research should focus on standardising stress application protocols e.g., guidelines for designing drought experiments in controlled conditions (Moshelion et al., 2024) and considering multiple scales of interaction measurement to fully capture the biological complexity of stress responses. This will provide more accurate predictions of how crops will respond to increasingly frequent and severe climate stressors.

Data and code availability

The code to reproduce the results of this study are available in the Supplementary information. We will archive the data in a permanent repository (Reviewer link: https://osf.io/fpj7z/?view_only=5f9e939e77e44cedb35d9d25e6b4fc8f).

CRediT authorship contribution statement

Arisede Chisaka: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **John P. Hammond:** Writing – review & editing, Supervision, Conceptualization. **Shinichi Nakagawa:** Writing – review & editing, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Jacob Bishop:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2026.111189.

Data availability

The data are available at doi.org/10.17605/OSF.IO/FPJ7Z

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