1 **Systematic review of heatwave experiments on plant health and survival**

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15 Title: Systematic review of heatwave experiments on plant health and survival

16 Running title: Experimental Insights on Plant Heatwaves

17 **Abstract**

18 **Background**: Heatwaves, which are becoming more intense and more frequent due to global

19 warming, are a major threat to the stability of plant populations and ecosystems. Safeguarding

20 ecosystem function requires a clear understanding of vulnerability to these extreme events. Yet

21 vulnerability cannot be reliably inferred from experiments that manipulate only mean

22 temperatures or from standard thermal tolerance assays. These limitations have spurred a

23 growing body of research specifically simulating heatwaves and studying their effect on plants.

24 **Method**: Here, we present a systematic review of empirical studies on plant responses to

25 heatwaves.

26 **Results**: Regional biases are pronounced, reflecting the logistical and financial challenges of

27 conducting these costly experiments. Likely for similar reasons, studies have largely been

28 restricted to seedlings, with little attention to adult plants and wild species in the reproductive

29 stage. Experimental approaches are also highly diverse, particularly in how heatwaves are

30 simulated, creating major hurdles for cross-study comparison. More than half of the studies

31 (53/84) incorporated at least one interacting factor—most commonly drought (23/84)—yet

32 other ecologically important interactions, such as grazing and microbial associations, remain

33 underexplored.

34 **Implications**: This review offers a comprehensive resource to guide the next generation of

35 heatwave experiments, highlighting underrepresented plant groups and geographic regions,

36 and underscores the pressing need for greater standardisation in experimental approaches to

37 facilitate a synthetic understanding of heatwave effects globally. Such coordination will

38 improve our ability to identify heatwave-sensitive species and better predict ecological

39 responses to climate extremes.

1. Introduction

Heatwaves pose a major and growing threat to plants and ecosystems. In recent decades, intense and prolonged heatwaves have become more frequent and severe, leading to widespread plant dieback and mortality (Steffen *et al.*, 2014; Breshears *et al.*, 2021). These extreme climatic events have raised serious concerns about the persistence of plants and the broader consequences for biodiversity and ecosystem stability (Evans *et al.*, 2025). As global temperatures continue to rise, the frequency and severity of heatwaves are projected to increase further as well (Trancoso *et al.*, 2020), potentially triggering ecological collapse in vulnerable systems (Urban, 2015). Natural heatwaves are challenging to study (Ummenhofer & Meehl, 2017; Thakur *et al.*, 2022), so researchers have increasingly used experimental simulations of heatwaves to investigate plant responses and identify species and systems most at risk (Davies *et al.*, 2018). These experiments have deepened our understanding of heat stress physiology, recovery mechanisms, and thresholds of vulnerability.

Heatwave simulations differ widely in their design, which limits comparability across studies. Biological effects of heatwaves can differ markedly from those caused by gradual, moderate warming (Jagadish *et al.*, 2021; Bernacchi *et al.*, 2023). While moderate warming may promote growth by accelerating metabolism, heatwaves often exceed critical thresholds, causing irreversible tissue damage (Bernacchi *et al.*, 2023). Although definitions vary, heatwaves are generally described as several consecutive days of abnormally high temperatures (Perkins & Alexander, 2013), and experimental simulations often adopt conditions that are hotter and shorter than those in warming studies, yet milder than acute heat shock treatments (Jagadish *et al.*, 2021).

An important complexity is that simulated heatwaves may vary in many dimensions. Studies differ in their experimental settings—ranging from tightly controlled climate chambers to field-

based manipulations—each offering different advantages and limitations (Notarnicola *et al.*, 2021; Arnold *et al.*, 2025a). Field experiments can better reflect real-world interactions, such as the combined effects of high radiation and low humidity (De Boeck *et al.*, 2010, 2016), but they are difficult to implement in variable climates. Controlled-environment studies offer greater precision but may exclude important ecological complexity. Simulated heatwave experiments also differ in the traits measured, the life stages and plant functional groups targeted, and the inclusion (or omission) of interacting factors, such as drought, herbivory, and microbial interactions (Breshears *et al.*, 2021; Trivedi *et al.*, 2022).

To understand this growing body of research, we conducted a systematic review of empirical heatwave studies on plants. Our goal was to identify key dimensions of variation across experiments and highlight underexplored areas of research. Specifically, we examined which plant types, experimental methods, regions, traits, and interacting effects are most studied. This synthesis provides a foundation for developing more standardised and ecologically meaningful heatwave experiments, which are urgently needed to improve cross-study comparisons, strengthen predictive models, and inform conservation efforts under increasing climate extremes.

We addressed the following research questions:

1. What are the most frequently used characteristics of simulated heatwaves in experimental studies?

2. Which plant growth forms and life stages are investigated in heatwave studies?

3. Which physiological and morphological traits are measured to evaluate plant responses?

4. Which regions and habitats are represented in current heatwave experiments?

5. What other environmental factors (e.g., drought, elevated CO_2) are included as interacting effects in heatwave studies?

2. Material and methods

Our methodology was described in our pre-registration (Mu *et al.*, 2024), and we adhered to it as much as possible. However, we adjusted several elements. These adjustments are mentioned below when applicable (see also online Appendix 1 for a summary of these adjustments). We broadly followed the guidelines of PRISMA-EcoEvo (O'Dea *et al.*, 2021) to report this study (Supporting Information SI1). We report author contributions using MeRIT guidelines (Nakagawa *et al.*, 2023) throughout this manuscript and the CRediT statement (McNutt *et al.*, 2018) at the end of the manuscript.

2.1. Literature searches

X.M. conducted literature searches using four different sources, all on August 12, 2024. First, X.M. conducted a main database search using Scopus and Web of Science (Core Collection), both accessed through the University of New South Wales, Sydney. For this, all authors jointly created strings with keywords aimed at capturing empirical studies on wild plants that cover one or more topics relevant to heatwaves (Table S1). Second, to find relevant grey literature, X.M. used similar keyword strings in Bielefeld Academic Search Engine (BASE), applying a filter to include only theses (doctype:18*). Third, X.M. conducted several searches in Google Scholar using translations of a simplified English string into Italian, Portuguese, Simplified Chinese, and Traditional Chinese, which were languages that at least one person from our team could understand (Table S1). However, we only screened the first 10 results from each of these Google Scholar searches, sorted by relevance. We planned to screen 10 more if at least half of the previous 10 contained relevant articles, but that was not the case for any language. A pilot conducted before our pre-registration found that these searches retrieved relevant benchmark articles (see Mu *et al.*, 2024), ensuring that our searches were comprehensive.

114

2.2. Screening process and inclusion criteria

116 Our screening criteria are summarised in Table 1 and in Figure S1 (slightly different from our

117 pre-registration; see Mu *et al.*, 2024). We used Rayyan QCRI (Ouzzani *et al.*, 2016) for both

118 the initial and the full-text screenings. P.A., P.P., R.N. and X.M. conducted the initial screening,

119 i.e. assessed the title, abstract, and keywords of retrieved studies. The full-text content of

120 studies that passed the initial screening was then assessed by two people: X.M. (100%) and

121 either P.A., P.P. or R.N. (33%, 34%, 33% of the cases, respectively). In both initial and full-

122 text screening, authors resolved conflicts through discussion until consensus was reached. Full-

123 text screening decisions are shown in Supporting Information SI2.

124

125 Table 1. Scope of our systematic review on topics related to the impact of heatwaves on plants,

126 according to the population, intervention/exposure, comparator, outcome, and study-design

127 (PECOS) framework (Richardson *et al.*, 1995; Foo *et al.*, 2021).

Population	Wild terrestrial plants (not cultivars)
Exposure	Simulated heatwaves (including artificially controlled passive and active heating)
Comparator	Control group without heating
Outcome	Survival, morphological or physiological measures, or heat shock protein expression
Study design	Empirical studies in the lab or the field

128

2.3. Data extraction

X.M. extracted all data from empirical heatwave studies included in our systematic review. P.P. cross-checked around 20% of the extracted data to ensure replicability. The extracted data (Fig. 1) included plant growth forms, life stages, simulated heatwave characteristics, response variables (survival, physiological, morphological, or molecular traits), the habitat and region of the plants, and other environmental factors tested under heatwaves. Notably, we adopted a broader classification of plant growth forms (woody *vs* herbaceous) rather than more specific types (e.g., tree, shrub, herb, climber), given the plasticity of growth forms across lifespans and regions. This classification was implemented in R (version 4.4.0) using the package *growthform* (Taseski *et al.*, 2019).

Notably, X.M. used the temperature difference between treatment and control groups to quantify heatwave intensity, rather than relying on absolute heating temperatures. This relative measure accounts for global variability in baseline temperatures across latitudes and elevations. X.M. prioritised mean temperatures over maximum temperatures, as many studies incorporated ramping patterns and (diel) temperature fluctuations, rendering maximum temperatures a relatively poor proxy for thermal exposure. Because heating temperatures were reported in various formats (e.g., text, figures, schematics), X.M. estimated mean temperatures as accurately as possible based on the available information. For instance, when studies specified different day and night heating temperatures with ramping rates according to photoperiods, X.M. calculated daily mean temperatures by weighting the day and night temperatures by their respective durations (e.g., mean daily temperature = (mean day temperature × day duration + mean night temperature × night duration) / 24 hours). Maximum temperatures were recorded only as an alternative when mean temperatures could not be reliably estimated.

152   X.M. recorded the country where each study was conducted based primarily on the described

153   experimental location. If no specific location was provided, X.M. used the country of the first

154   author's institutional affiliation. For plant measurements, X.M. extracted the measurement

155   names from figures, tables, or datasets provided by authors. X.M. categorised these

156   measurements as multilevel traits—spanning morphological, physiological, and molecular

157   categories—and further subcategorised them according to their relevance to key metabolic

158   processes and core plant functions (as shown in Fig. 1). Although some measurements are

159   associated with multiple metabolic pathways, X.M. assigned each to the category most critical

160   to plant health and survival. For example, although stomatal conductance is linked to both

161   water relation and carbon flux, X.M. classified stomatal conductance as water relation because

162   transpiration may be more vital than photosynthesis for plant survival under heatwave
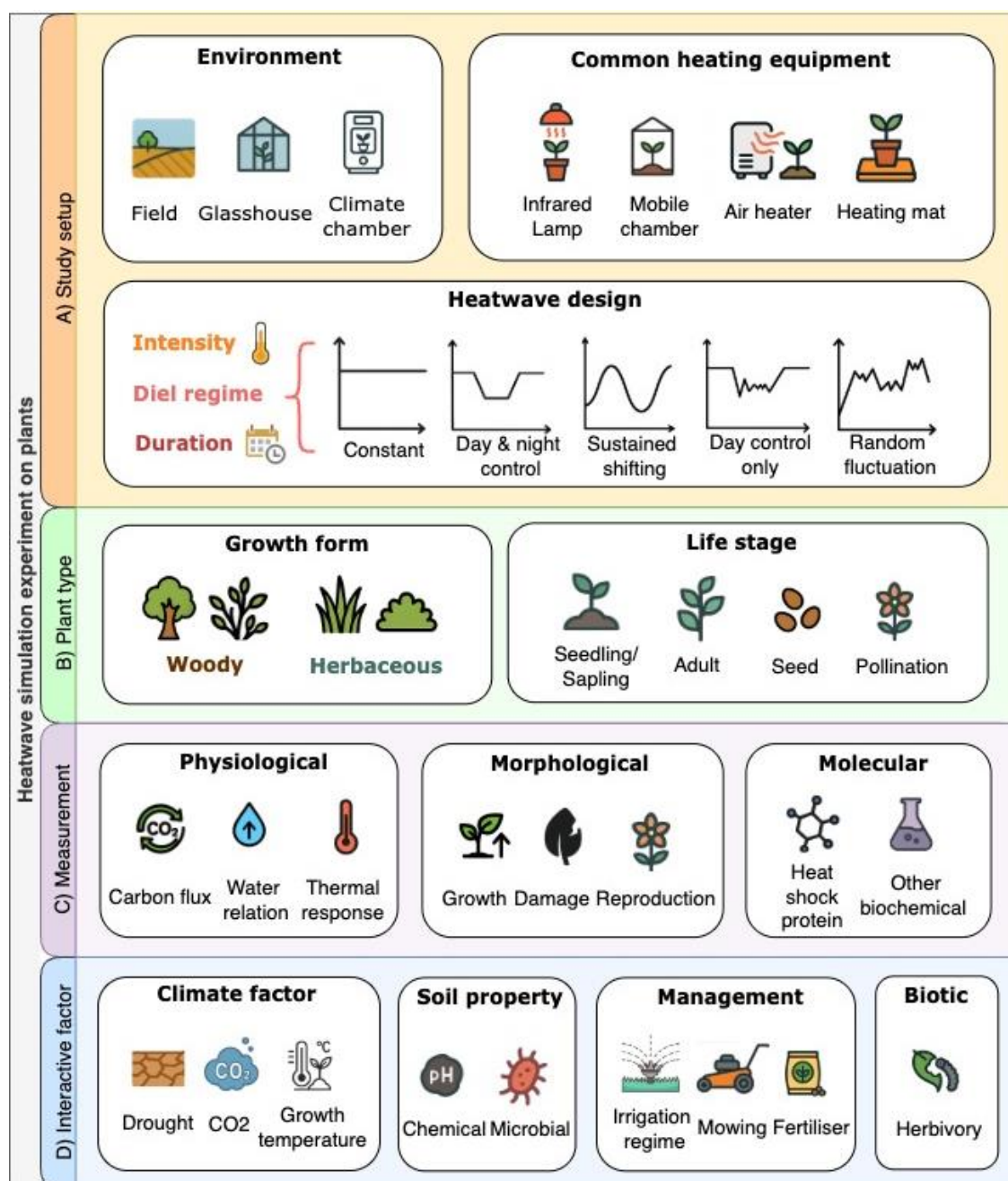
163   conditions.

164

Fig. 1 Conceptual diagram illustrating the categories used in this study as meaningful proxies

for sources of variation in heatwave experimental designs. Variation may arise from: (A) Study

setup (yellow section), including aspects of the study environment, heating equipment, and

temperature control; (B) Plant type (green section), covering growth form and life stage; (C)

Conducted measurements (purple section), encompassing physiological, morphological, and

molecular traits, which are further classified into eight functional processes: carbon flux, water

relations, thermal response, growth, damage, reproduction, heat shock protein expression, and other biochemical indicators (e.g., chlorophyll a and b); (D) Co-factors (blue section) studied alongside heatwaves, including climate factors, soil properties, management practices, and biotic interactions. These co-factors are further divided into nine categories: drought (reduced water supply), CO_2, growth temperature, precipitation (including increased water supply, water regime, and irrigation method), chemicals, microbial activity, mowing, fertilisation, and herbivory.

3. Results and discussion

3.1. Number of eligible studies

Our screening process is summarised in Figure S2. Searches from all sources retrieved a total of 3093 records, 1170 of which were duplicates. We assessed the title, abstract, and keywords of the remaining 1923 articles, from which 193 met our initial selection criteria (i.e. were initially included). After examining the full text, we excluded 108 studies that did not meet our selection criteria. Specifically, 72 studies simulated heatwaves that did not meet the defined heat conditions (e.g., heat intensity was insufficient, duration was inappropriate, or descriptions were unclear); 12 focused on cultivars or crops rather than wild species; seven lacked relevant measurements of plant morphological, physiological, or heat shock responses; four full-text articles could not be retrieved; eleven did not include a control treatment, making it impossible to assess the heatwave intensity; and two were published in languages outside those we could assess (see also Fig. S2). One additional record (Zhu, 2017) was a thesis that included a relevant published chapter that was captured in another record (Zhu *et al.*, 2024) (duplicated); these were considered a single study. Another record (Backes, 2022) was a thesis with two relevant chapters, one of which lacked a control treatment, so this was also counted as a single study.

195   In total, this process resulted in the inclusion of 84 eligible studies in the systematic review

196   (see the list of studies in Appendix 2 and details in Supporting Information SI3). The first study

197   on the effects of a simulated heatwave on plants was published in 2004.

198

199   *3.2. Geographic spread*

200   Although the 84 studies in our systematic review reported experiments globally, the majority

201   were conducted in only a few countries (Fig. 2). The uneven distribution we found regarding

202   heatwave experiments is probably due to institutional bias (Zvereva & Kozlov, 2021), the

203   availability of research funding (Luukkonen *et al.*, 1992), and research attention driven by the

204   impacts of historical extreme climate events (Steffen *et al.*, 2014). Notably, three studies were

205   conducted in tundra regions within polar zones, demonstrating the feasibility of simulating heat

206   events even under extremely low temperatures. In contrast, tropical regions (including large

207   parts of Africa and South America) remain severely understudied, despite their high levels of

208   plant diversity (Raven *et al.*, 2020). While this distribution pattern is consistent with studies

209   measuring thermal tolerance in wild plant species (Geange *et al.*, 2021), current empirical

210   research on the effects of heatwaves on plants remains notably restricted in geographical scope.
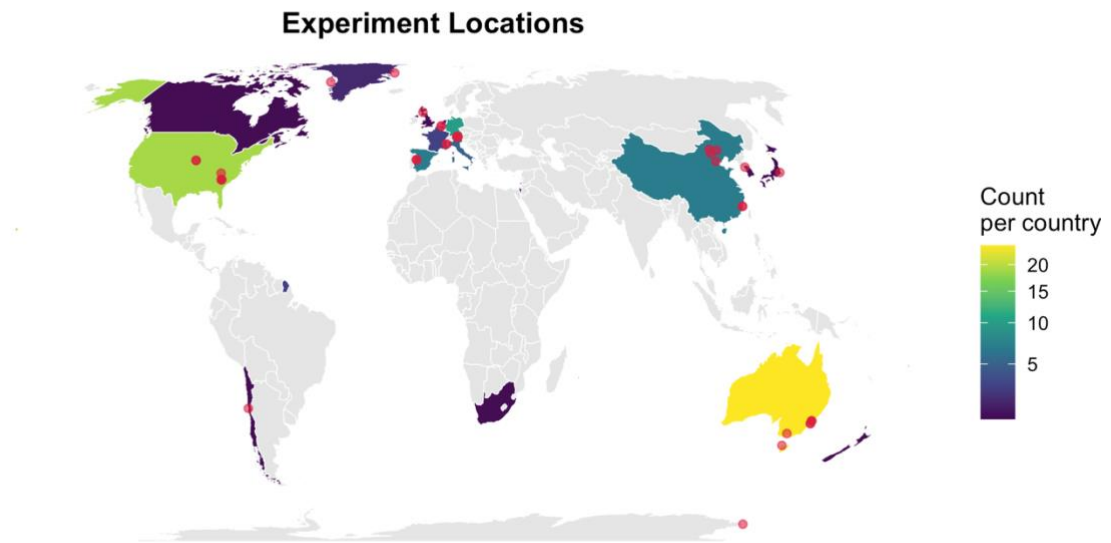
Experiment Locations

211

212 Fig. 2 Global distribution of 84 heatwave studies (field and laboratory). Red dots mark the

213 specific experiment locations where such information was available. Detailed information is

214 provided in Supporting Information SI3.

215

216 3.3. Heatwave design

217 Transparent reporting of temperature regimes is essential as thermal settings and their

218 interaction with ambient conditions may critically influence plant responses. Yet

219 approximately 39 out of 84 studies (46.4%) described the heatwave regime only in the text.

220 Some of these studies reported only a mean or maximum temperature, obscuring diurnal shifts

221 and the true heat load experienced by plants (Fig. 3a). In contrast, 34 studies (40.5%) included

222 graphical representations (raw data traces or schematic diagrams), which more effectively

223 convey temporal fluctuations. Only 11 studies (13.1%) showed the temperature information in

224 a table and one study in a datasheet (1.2%).

225   Studies included in our systematic review varied considerably both in the number and

226   characteristics of the simulated heatwaves they conducted. Most studies applied a single

227   heatwave treatment, typically characterized by a specific temperature pattern maintained over

228   a continuous period. However, a subset of studies included multiple heatwave events, either by

229   varying key characteristics such as intensity and duration, or by repeating heatwaves over

230   intervals spanning days (French *et al.*, 2019; Birami *et al.*, 2021), weeks (Ahrens *et al.*, 2021;

231   Liu *et al.*, 2023), months (Yu *et al.*, 2023), or even up to a year (Qu *et al.*, 2020; Li *et al.*, 2021).

232   Heatwave intensity (i.e. temperature difference between heatwave and control groups) ranged

233   widely across studies, from 1°C to over 20°C, with the majority of studies applying increases

234   of 10°C or less (Fig. 3b). Although we only included studies applying at least 4°C increase in

235   maximum temperature under heatwave conditions compared to a control condition in our

236   systematic review, peak temperatures (i.e., maximum values) may only be sustained briefly

237   due to ramping protocols or temperature fluctuations (Fig. 1) and we thus focused on mean

238   temperature differences (see section 2.3).

239   The duration of the heatwaves simulated by studies ranged from three days (minimum required

240   for inclusion in this review) to as long as 99 days, with most experiments clustering around one

241   week in length (Fig. 3c). This heatwave duration is consistent with the natural heatwaves

242   observed in both historical records and current climate conditions (Perkins-Kirkpatrick &

243   Lewis, 2020; Trancoso *et al.*, 2020). As heatwaves are projected to become increasingly

244   prolonged under future climate scenarios, studies simulating durations longer than one week

245   are particularly relevant for assessing plant persistence under extreme conditions in coming

246   decades (Trancoso *et al.*, 2020). Notably, six studies imposed heatwave treatments lasting more

247   than three weeks, perhaps exceeding the length of recommended heatwaves by experimental

248   guidelines proposed by Breshears *et al.*, 2021. However, these long heatwaves may be plausible

249   under certain regional projections, high-emission scenarios, or late-century timeframes

250   (Trancoso *et al.*, 2020). Given that extended heat exposure can increase the risk of cumulative

251   stress or trigger acclimation responses in plant (Marchand *et al.*, 2005), these studies may yield

252   distinct physiological or ecological outcomes and should therefore be interpreted with caution

253   when comparing results across studies.

254   Regarding the location of the experimental simulation of heatwaves, studies were mostly

255   conducted in climate chambers, greenhouses, and field settings (natural sites and common

256   gardens). These markedly differ in their temperature-control capacity (from precise regulation

257   to fully dynamic fluctuations), ambient conditions (e.g., light intensity, humidity), plant growth

258   context (*ex situ* vs *in situ*), and experimental scale (e.g., number of plants, species diversity,

259   interacting factors). The choice by researchers reflects trade-offs among their objectives,

260   priorities, and logistical constraints. Interestingly, we found that simulated heatwaves were

261   applied relatively evenly across the three experimental locations, from tightly controlled

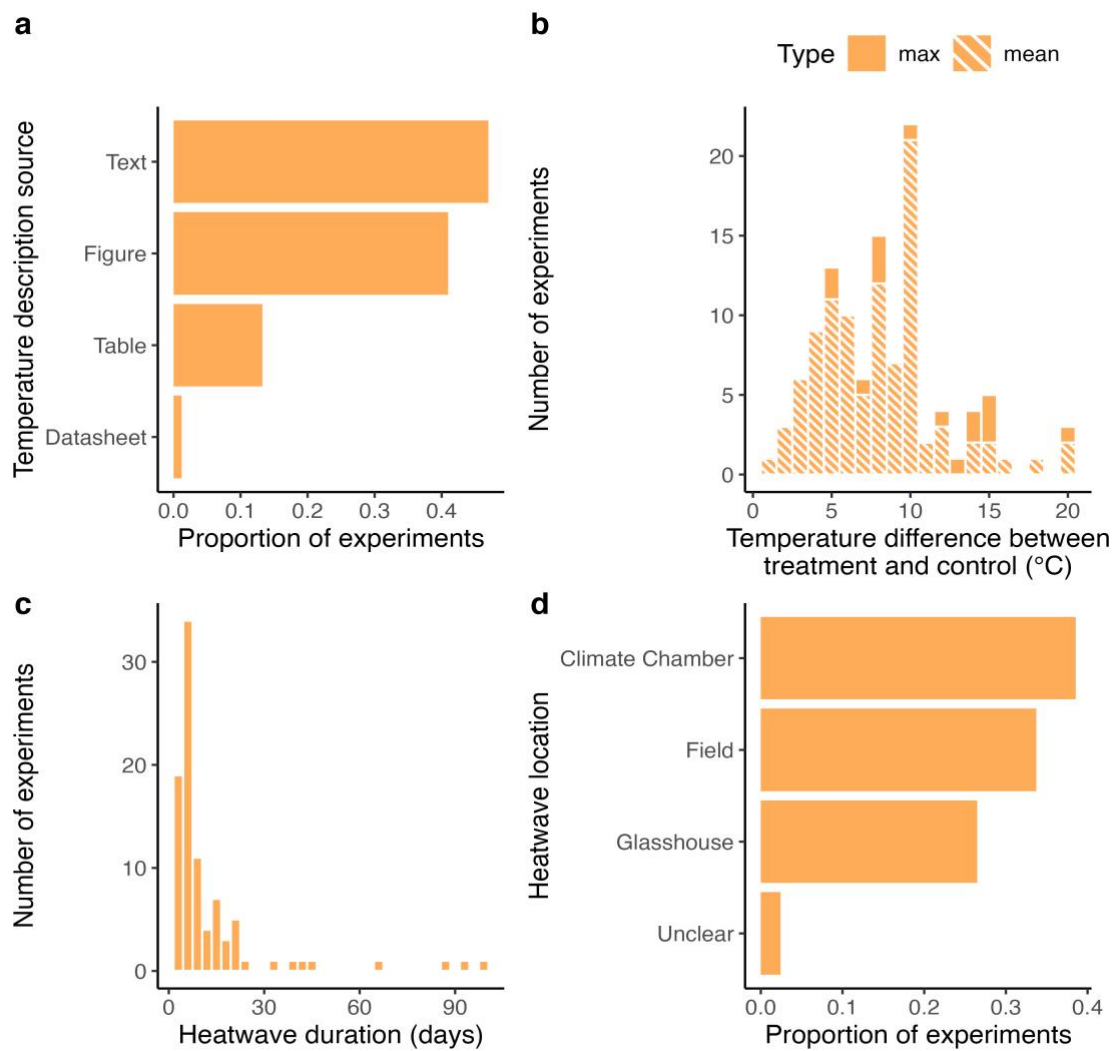262   laboratory conditions to complex, real-world field scenarios (Fig. 3d).

Figure 3. Study setup patterns: source of heatwave simulation description (a); heatwave intensity (b); heatwave duration (c); heatwave simulation location (d).

3.4. Plant type

Studies on heatwave effects have most frequently focused on woody growth forms (55 out of 84 studies, 65.5%; Fig. 4a). However, more herbaceous species have been studied overall (139 out of 269 species, 51.7%; Fig. 4a), likely because herbaceous plants dominate outside of the tropical regions (Taylor *et al.*, 2023)—where all heatwave research has been conducted—and are often represented by multiple species within individual studies.

273   More than half of the studies we included in our systematic review (49 out of 84 studies, 58.3%)

274   focused on early developmental stages, particularly seedlings (38 studies, 45.2%; i.e. the

275   earliest juvenile stage after germination, bearing cotyledons and still partly reliant on seed

276   reserves while establishing independent photosynthesis.) and saplings (11 studies, 13.1%; i.e.

277   well-established juvenile plant that is fully photoautotrophic but not yet reproductively mature;

278   Fig. 4b). This is likely due to the prevalence of woody plants in heatwave research, whose long-

279   life cycles and large size pose challenges for well-controlled experiments on mature individuals,

280   often requiring field settings and sophisticated equipment. Additionally, there is a common

281   assumption that seedlings are more susceptible to extreme climatic events than mature plants

282   (Lenoir *et al.*, 2009; Lloret *et al.*, 2009; Jagadish *et al.*, 2021). Thus, only nine studies (10.7%)

283   of studies in our systematic review applied heatwave treatments to adult plants prior to

284   flowering. Surprisingly, the effects of heatwaves on seeds have been scarcely explored (three

285   studies, 3.6%), and only one study has examined plant reproductive stages (Tushabe *et al.*,

286   2023), despite their notably higher sensitivity to temperature (Hedhly, 2011; Wang *et al.*, 2016;

287   Lohani *et al.*, 2020). Unexpectedly, almost a quarter of the studies (23 out of 84, 27.4%) did

288   not clearly specify the life stage of the plants used in heatwave experiments. In some cases,

289   developmental stage can be roughly inferred from the experimental timeline, yet ambiguous

290   inference may hinder accurate assessments of plant fitness and comparability of results across

291   studies, so we categorised these as unclear.

292
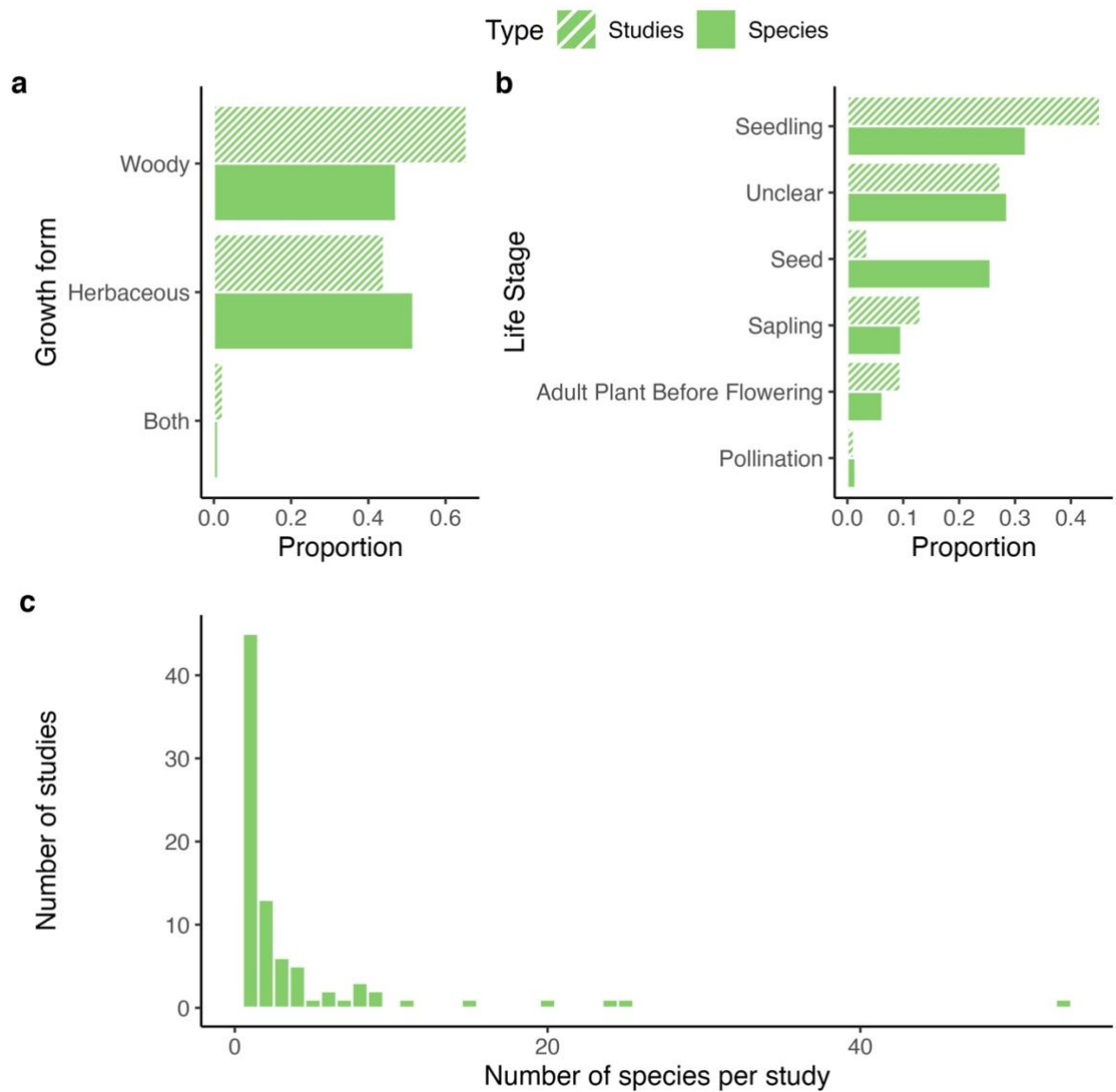
Figure 4. Proportion of studies and species by plant growth form (a) and life stage (b) at the time of heatwave exposure, and number of species included per study (c).

296

3.5. Plant traits

When exposed to high temperatures during heatwaves, plants activate signal-transduction and gene-regulation pathways that drive metabolic shifts and physiological adjustments, often

300 ultimately manifesting as visible morphological changes (Zhao *et al.*, 2020). Physiological

301 measurements were by far the most common approach among the studies included in our

302 systematic review, used by 77 out of 84 studies (91.7%) and covering 265 out of 269 species

303 examined (98.5%) (Fig. 5b). Conversely, morphological assessments represented 47 studies

304 (56%) of traits reported in studies examining heatwave effects on plants, such as structural

305 shifts or biomass allocation. Heat-shock protein expression and changes in biochemical

306 composition were reported in 28 studies (33.3%). Only 16 studies (19%) made all types of

307 measurements (i.e., molecular, physiological, and morphological) together (Fig. 5a),

308 highlighting a gap in multi-scale trait integration that limits our ability to trace causal chains

309 from gene regulation through whole-plant function under stress.

310 When these trait categories are divided into functional sub-categories (e.g., carbon flux, water

311 relations, growth, damage, thermal responses, reproduction, and biochemical processes; Fig.

312 5d), distinct patterns emerge between the study focus and species examined. At the study level,

313 researchers have generally distributed their attention relatively evenly across functional

314 processes, with the exception of reproduction, which has received comparatively little focus.

315 Thus, overall, only one study has covered all six sub-categories (Fig. 5c). In contrast, trait

316 measurements at the species level concentrated on direct indicators of heat injury (114 out of

317 269 species, 42.4%), such as visual damage scores, chlorophyll fluorescence (Fv/Fm), and

318 thermal response traits (e.g., leaf temperature, critical thermal maxima). This pattern suggests

319 that multi-species studies may prioritise indicators of stress impact that are easily comparable

320 across species, rather than regulatory mechanisms. Although five studies measured more than

321 20 traits, the majority focused on fewer than 15 (Fig. 5e). It is worth noting that approximately

322 34 out of 84 studies (40.5%) evaluated biochemical processes, including molecular assays (e.g.,

323 targeting reactive oxygen species [ROS]) and elemental composition, representing a broader

scope than molecular measurements alone (28 studies, 33.3%). This reflects a moderate focus on the biochemical mechanisms underpinning physiological resilience. These patterns collectively show that the impacts of and responses to heatwaves that occur during different points of development need further study to link molecular markers with physiological and morphological traits, and ultimately reproductive fitness.
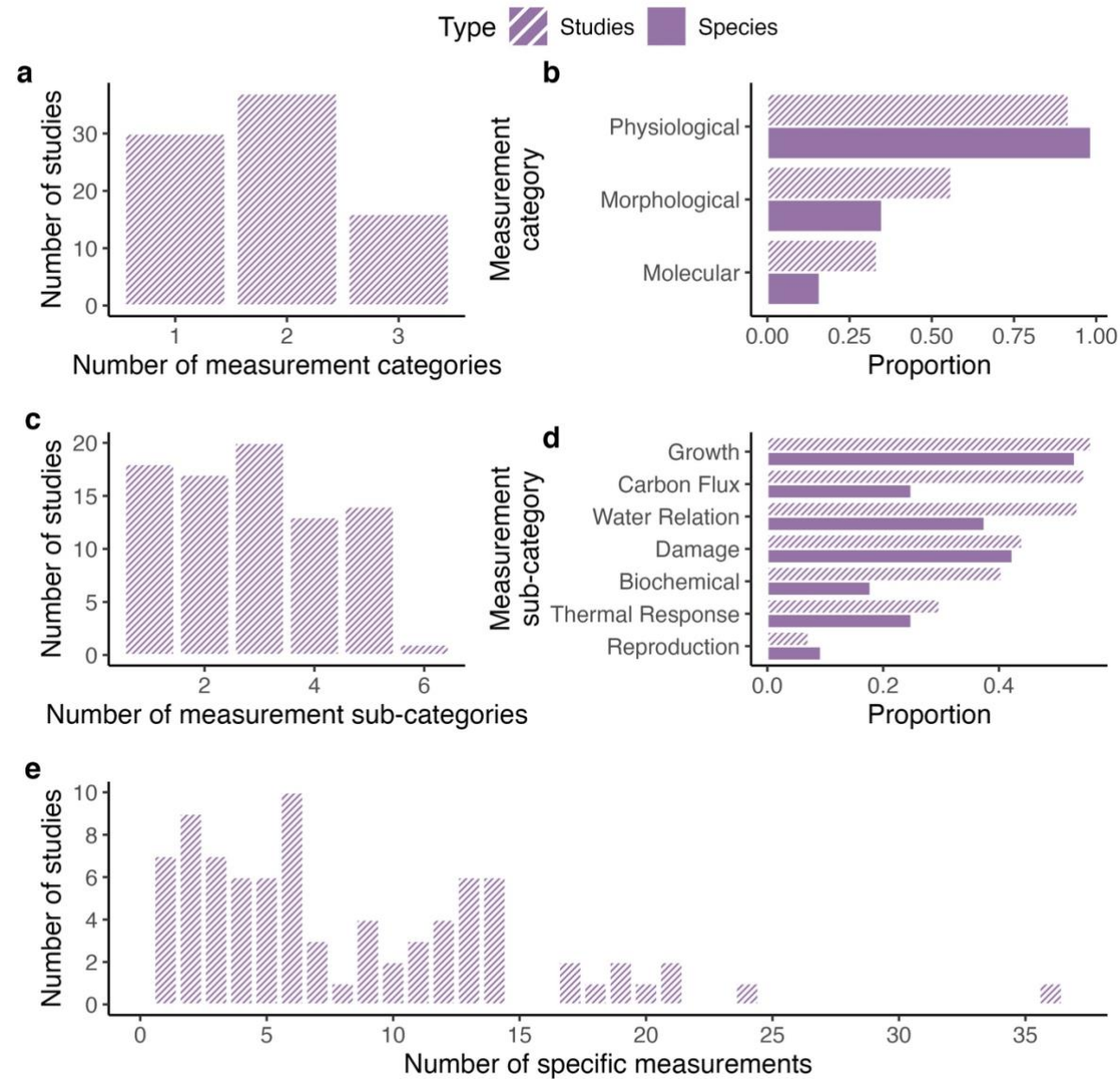

Figure 5. Overview of the coverage across studies and species regarding measurement categories (a, b), measurement sub-categories (c, d), and specific measurements (e).

3.6. Multifactorial Environmental Interaction

Given that climate change and human activities increasingly alter environmental conditions, heatwaves seldom occur in isolation. Instead, heatwaves coincide with multiple abiotic and biotic stressors, possibly producing interactive effects on plants. For example, ongoing warming not only increases baseline growth temperatures but also accelerates soil moisture loss (Mukherjee & Mishra, 2021), which may intensify heat-introduced damage on plants (Marchin *et al.*, 2022) or, in some cases, trigger early tolerance acclimation and increased tolerance (Notarnicola *et al.*, 2021). Additional pressures, such as soil salinity, insect herbivory, and grazing, can further modulate plant responses by triggering distinct defence strategies (Lamalakshmi Devi *et al.*, 2017). Among the 84 studies conducting heatwave experiments on plants we reviewed, more than half of them (53 studies, 63.1%) incorporated at least one additional environmental treatment (Fig. 6). Yet, most studies among them (35 out of 53 studies, 66%) focused exclusively on climatic co-stressors. Drought was by far the most common climatic co-stressor (23 out of 84 studies, 27.4%), likely due to its frequent co-occurrence with heatwaves in both field observations and climate projections (Mukherjee & Mishra, 2021). Other climatic factors, such as elevated CO_2 (eight studies, 9.5%) and pre-heatwave warming temperatures (four studies, 4.8%), received relatively less attention. Non-climatic factors such as biotic interactions, soil chemistry or microbiology, and land-management practices (e.g., irrigation regime, fertilisation, mowing) appeared in only a handful of studies (1–3 per category), which limits the broader applicability of their findings (Fig. 6). For example, just two studies (2.4%) have examined herbivory under heat stress, both focusing on insects and overlooking vertebrate grazers, which may drive plant damage in certain regions (Morgan, 2021). The diversity of stress combinations helps explain the variability in plant performance reported across heatwave studies. To improve our ability to predict plant persistence and

356 ecosystem function under complex, changing climates, future research should embrace

357 multifactorial designs and expand the range of interactive factors examined to include locally

358 and globally relevant variables that co-occur with heatwaves.
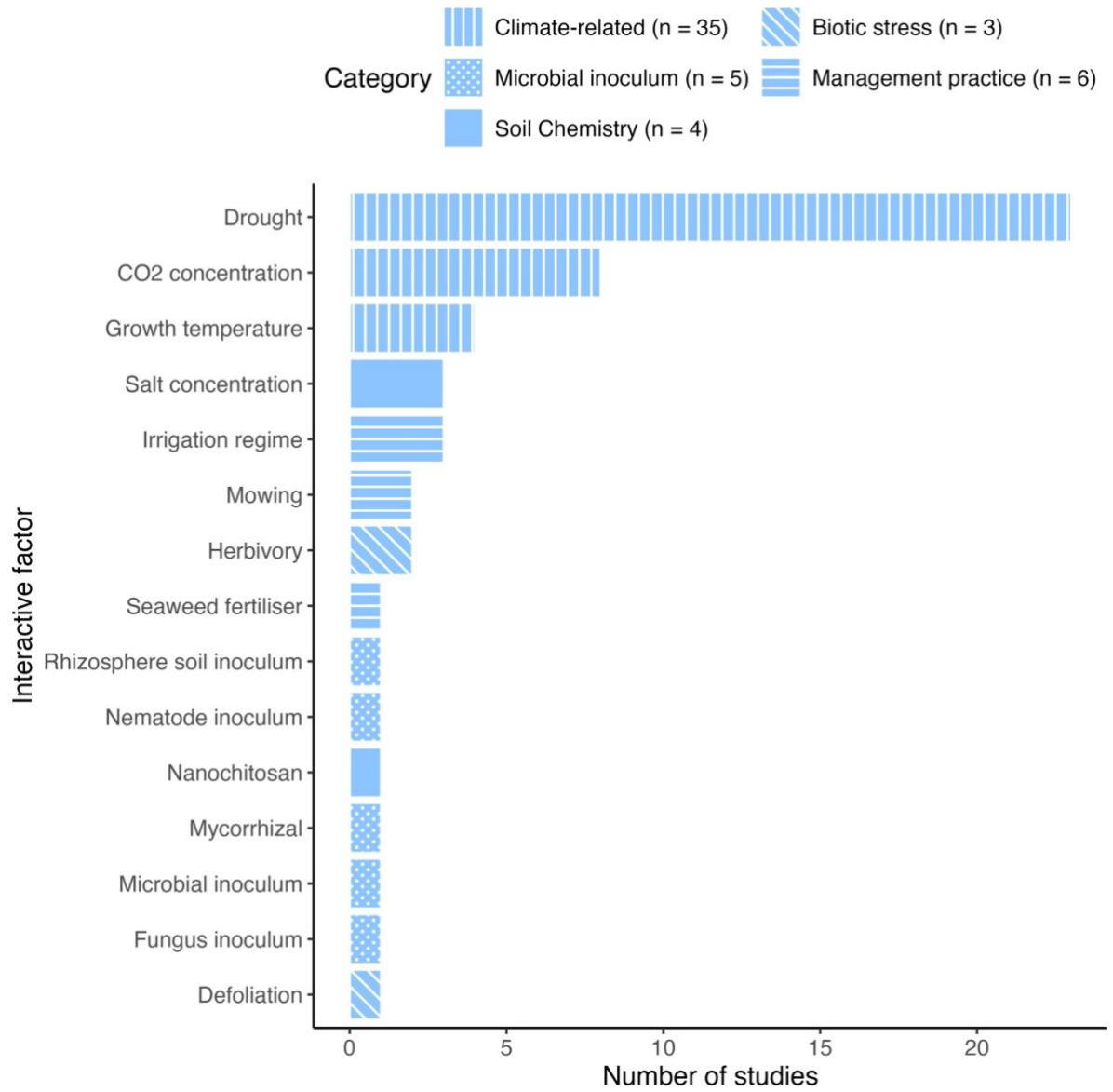

359

360 Figure 6. Number of studies including specific interactive factors.

4. Future directions and research agenda

4. 1. Heatwave simulation: diversity, dilemmas, and development

The diversity of heatwave types, along with variation in experimental environments and research objectives, has led to diverse approaches for simulating heatwaves. While such variety has fostered experimental flexibility and robustness, it also presents challenges for researchers and conservation practitioners in selecting an appropriate experimental framework that aligns with their specific research objectives. Here, we summarise existing and emerging heatwave study designs to facilitate standardising and generalising effective experimental strategies, which may finally enhance the translation of research findings into practical applications.

4.1.1. Designing and reporting heatwave studies to facilitate synthesis

A critical methodological challenge in plant–heatwave research is the representative simulation of heatwave conditions, which requires defining and controlling key parameters of intensity and duration. These are typically derived from heatwave definitions or historical climate records, and in some studies are combined with climate model projections to construct biologically realistic scenarios (e.g., Drake *et al.*, 2018). Possibly due to the diverse definition of 'heatwave' applied across studies, we observed striking variation in both the simulated intensity (i.e., the temperature increases above control conditions; Fig. 3b) and duration (Fig. 3c). While this variation may capture the growing complexity and regional heterogeneity of heatwave patterns under ongoing climate change, it also reduces the comparability of critical experimental conditions across studies. This, in turn, limits cross-study synthesis and hinders efforts to identify the most susceptible species and ecosystems. A key question in heatwave simulation design, therefore, is whether to adopt standardised protocols or retain flexibility to capture site- or context-specific characteristics when setting core heatwave parameters.

385   To address this challenge, we recommend designing heatwave intensity and duration protocols

386   based on the primary research objective, emphasising either practical conservation or

387   theoretical mechanisms. First, for application-oriented studies (often field-based),

388   experimental parameters should closely reflect local heatwave characteristics and

389   environmental conditions, particularly when targeting ecologically important, endangered, or

390   habitat-sensitive species. This context-specific approach can efficiently yield meaningful

391   insights for conservation planning and local ecosystem management. Accordingly, we suggest

392   reporting detailed contextual information, including biome type, regional climate, soil

393   environment, and the data sources or models possibly used to define heatwave scenarios.

394   Ideally, a brief overview of previous studies on the same species, ecosystem, or biome should

395   also be included, along with an assessment of whether and how well the heatwave simulation

396   aligns with commonly applied definitions. Second, for fundamental research, establishing

397   benchmark ranges for heatwave intensity and duration could significantly enhance

398   comparability across studies (Breshears *et al.*, 2021). We therefore advocate developing

399   standardised heatwave simulation guidelines at national or global scales. Such guidelines could

400   be especially valuable for well-controlled environments, where conditions can be optimised to

401   isolate the effects of heat load and enable effective comparisons of species-specific

402   susceptibility. This standardisation may also be appropriate for studies examining how

403   geographical factors (i.e., latitude, elevation, or provenance) influence species' capacity to deal

404   with heatwaves. Furthermore, for multi-species studies and those involving diverse plant

405   growth forms, employing uniform simulation parameters (e.g., French *et al.*, 2017) can provide

406   a robust platform for cross-species comparisons, facilitating theoretical investigations into

407   plant susceptibility based on inherent functional traits.

In addition to heatwave intensity and duration, frequency is a key but often underdefined parameter. In climatology, heatwave frequency refers to the total number of days meeting specific heat index criteria within a year, rather than the number of repeated events that include consecutive heatwave days (Perkins & Alexander, 2013). Translating this into an experimental study design, frequency is often represented by repeated heatwave events applied over a given period. Currently, implementations of repeated heatwave studies vary widely in the internal structure, including intensity, duration, timing, and intervals between episodes. Some studies consider short breaks of a few hours as "reasonable" interruptions that reflect natural fluctuations within a single heatwave (French *et al.*, 2017), rather than classifying them as separate events (Arnold *et al.*, 2025a). This divergence may blur the distinction between studies focused on heatwave frequency and those addressing duration. Moreover, both the timing and length of intervals between heatwave sessions may influence plant responses by allowing for recovery and/or by introducing legacy effects that alter subsequent stress responses. Beyond frequency, seasonal timing of heatwaves is another critical yet underexplored factor. Seasonal context matters (e.g., earlier in spring or later in autumn) because plant susceptibility varies across developmental stages (Grubb, 1977; Dreesen *et al.*, 2015; Cope *et al.*, 2023). Heatwaves that occur "out of season" during sensitive phenological phases (e.g., early in spring during leaf-out or bud formation) can adversely affect growth and reproduction, which jeopardises species fitness and can disrupt community-level synchrony (Dreesen *et al.*, 2015; Trotta *et al.*, 2023).

Advancing our understanding of plant resilience, acclimation, and recovery under repeated or atypically timed heat stress requires targeted heatwave simulations and benchmark ranges for key variables to enhance experimental consistency, possibly informed by global historical

431   patterns. The ecological impacts of heatwave regimes, shaped by intensity, duration, frequency,

432   and timing, remain a critical research frontier.

433   Realistic simulation of heatwaves requires not only specifying key parameters but also

434   manipulating the thermal dynamics throughout the event. Daily temperature variation (e.g.,

435   day–night shifts, ramping rates, random fluctuations) has been implemented in diverse ways

436   (Fig. 1). While such configurations may be tailored to specific research objectives, temperature

437   fluctuations are often difficult to control in settings with variable ambient conditions or limited

438   technical capabilities. In these cases, it is essential to record and report the targeted and realised

439   temperature profiles, along with any unintended temperature deviations, to facilitate

440   interpretation of results. Directly comparing results from studies that employ very different

441   dynamic temperature regimes can be difficult at best and misleading at worst. For example,

442   even with equal peak temperatures and overall durations, heatwave simulations that use

443   different regimes, such as constant heating, diurnal shifts, or pulsed exposures (Fig. 1), impose

444   different cumulative heat loads on plants and potentially elicit markedly different physiological

445   responses. Recent evidence suggests that cumulative heat load may be a stronger predictor of

446   plant responses than peak temperature alone (Cook *et al.*, 2024), such that explicitly

447   incorporating exposure duration potentially offers greater biological relevance (Bauweraerts *et*

448   *al.*, 2013). Continuous temperature monitoring throughout simulated heatwave events enables

449   the calculation of real-time cumulative heat load imposed on plants, providing an informative

450   metric for comparing heatwave severity across studies. Nevertheless, this metric should be

451   applied carefully within a heatwave-specific framework; otherwise, it risks conflating

452   heatwave effects with other warming scenarios (i.e., gradual warming or acute heat shocks)

453   (Jagadish *et al.*, 2021). Furthermore, we emphasise the importance of incorporating night-time

454   temperatures in heatwave simulations (Arnold *et al.*, 2025a). Although nighttime temperatures

455 are generally lower than daytime temperatures in absolute terms, they can increase

456 disproportionately under heatwave conditions (Vose *et al.*, 2005; Davy *et al.*, 2017; Wu *et al.*,

457 2023). Elevated nighttime temperatures may hinder the repair of daytime heat damage and lead

458 to increased respiration, water loss, and energy expenditure, potentially compounding the

459 physiological stress imposed by high daytime temperatures in subsequent days (Kundu et al.,

460 2024).

461

462 4.1.2. Empirical heatwave simulations

463 Compared to the volume of research on general warming effects on plant ecophysiology,

464 empirical studies specifically addressing heatwaves remain remarkably limited. Given

465 mounting evidence of severe heatwave impacts on ecological communities, this gap is a source

466 of critical uncertainty for predicting and mitigating species loss and community shifts,

467 especially among sensitive species and communities, and within vulnerable ecosystems (Chen

468 & Lewis, 2023). Despite the urgent need for such studies, heatwave experiments often present

469 technical, financial, and logistical challenges (Ettinger *et al.*, 2019; Arnold *et al.*, 2025a), which

470 may discourage broader research engagement. Nevertheless, the great effort of researchers and

471 practitioners over the past decades has contributed to a variety of feasible approaches. These

472 methodological developments provide valuable technical support and resource-efficient

473 solutions that fundamentally enable the expansion of heatwave-related research across diverse

474 ecological contexts and research conditions.

475 Field experiments, including common garden studies, typically involve plants exposed to

476 natural environmental conditions and rooted in relatively open soil, whether *in situ*, relocated,

477 or grown in mesocosms (see Table S2 for examples). The core challenge of simulating

478 heatwaves in such settings is maintaining elevated temperatures consistently while minimising

479 confounding effects from other environmental factors. Achieving this goal requires careful

480 consideration of site-specific variables, such as diurnal temperature ranges, as well as

481 precipitation, light availability, and soil moisture. Evaluation of these factors informs

482 equipment selection and maintenance demands. Due to the high-intensity warming needed for

483 simulating heatwaves, passive warming methods (e.g., open- or closed-top chambers) are

484 generally insufficient to achieve sustained high temperatures without active heating (Speights

485 *et al.*, 2018; Ettinger *et al.*, 2019; Arnold *et al.*, 2025a). Instead, active systems such as infrared

486 lamps or air heaters are often necessary, either alone or in combination (Fig. 1). Consequently,

487 these experiments generally demand robust infrastructure, reliable power sources, continuous

488 monitoring tools, and substantial logistical support (Arnold *et al.*, 2025a).

489 Despite the challenges, field heatwave simulations share the general advantages of *in situ* plant

490 studies. They preserve natural environmental heterogeneity (e.g., light, wind, humidity), plant-

491 soil interactions, and community-level dynamics (including herbivory), thereby enabling more

492 ecologically realistic predictions of plant responses to heatwaves. Soil moisture dynamics play

493 a critical role in mediating heatwave effects (De Boeck *et al.*, 2016). Because the dynamics of

494 root water uptake and progressive soil drying during a heatwave are difficult to replicate in

495 controlled pot experiments, field settings remain essential for capturing these critical processes.

496 Field-based heatwave experiments have been successfully implemented across a range of

497 extreme thermal environments, including Arctic (Marchand *et al.*, 2005; Graae *et al.*, 2009;

498 Gemal *et al.*, 2022) and alpine regions (De Boeck *et al.*, 2016; Arnold *et al.*, 2025a), and are

499 increasingly applied to cover plant communities (Dreesen *et al.*, 2012; Arnold *et al.*, 2025a)

500 and even large, mature trees (Drake *et al.*, 2018). Such innovative designs continue to broaden

501 the scope and potential of field heatwave simulations. It is also important to note that empirical

502 and observational studies conducted during naturally occurring heatwaves—though outside the

503   scope of this review—provide rare and valuable, real-world insights that can both validate and

504   extend findings from controlled simulations, particularly in terms of post-heatwave plant

505   responses and recovery (Breshears *et al.*, 2021).

506   Climate chambers and glasshouses provide controlled environments to study plant

507   responses to heatwaves, allowing precise and repeatable manipulation of temperature and other

508   parameters. Yet, artificial conditions—such as limited light, short experimental periods, and

509   reliance on pots—can alter morphology and physiology, reducing relevance to field-grown

510   plants (Poorter *et al.*, 2016). Phenotypic discrepancies are evident even among outdoor gardens,

511   greenhouses, and climate chambers, which differ in control intensity (Karitter *et al.*, 2023). To

512   ensure robust results, such experiments must account for deviations from field conditions,

513   including setup (facility, medium, pot size), sample size, key growth factors (light, CO_2,

514   nutrients, humidity, water, temperature, salinity), and issues under abiotic stress (Poorter *et al.*,

515   2012).

516

517   *4.2. Susceptible plant candidates*

518   One of the primary objectives of plant–heatwave research is to identify the plants most at risk

519   from extreme heat events. Among the *ca.* 374,000 known plant species (Christenhusz & Byng,

520   2016), distinguishing those most susceptible to heat-induced mortality remains a significant

521   challenge. This difficulty stems in part from species having distinct thermoregulation and

522   thermal tolerance limits (Feeley *et al.*, 2020), meaning their vulnerability cannot be reliably

523   inferred from projected climate extremes alone—especially since heatwaves vary substantially

524   across regions (Reddy *et al.*, 2021). This task is urgent, as escalating climate extremes may

525   drive rapid and irreversible biodiversity loss, with cascading consequences for ecological

526   functions and services. Drawing on previous research into plant capacities and adaptive

527 strategies in response to thermal stressors, researchers typically narrow down the pool of

528 vulnerable species by considering the following key factors.

529

530 <u>4.2.1. Plant functional traits</u>

531 Plants have evolved a diverse array of traits that underpin their life-history strategies and enable

532 them to adapt to the environments they inhabit (Reich *et al.*, 2003). In the context of a rapidly

533 warming climate, certain thermoregulatory traits (e.g., leaf colour, size, and shape) may serve

534 as useful indicators of plant vulnerability to heatwaves due to their influence on heat absorption

535 and dissipation (Leigh *et al.*, 2017). Some traits are directly linked to plant's physical properties;

536 for instance, leaf size and thickness influence the thickness of the boundary layer surrounding

537 the leaf—a buffer zone between the leaf surface and the surrounding air that governs the rate

538 of heat convection (Monteith, 1990; Schuepp, 1993). Such traits may also indirectly affect

539 physiological processes related to temperature regulation, such as the rate of evaporative

540 cooling (Buckley *et al.*, 2017; Arnold *et al.*, 2025b). With the rapid expansion of plant trait

541 collection and the increasing availability of open-access databases (e.g., TRY; Kattge *et al.*,

542 2020, and AusTraits; Falster *et al.*, 2021), morphological trait-based approaches have been

543 broadly applied to explore plant responses to environmental stressors (Soudzilovskaia *et al.*,

544 2013; Anderegg *et al.*, 2019). However, this approach remains underexplored in heatwave-

545 specific research. Individual experiments often involve only a limited number of species due

546 to specific constraints, and meta-analyses that synthesise findings across studies are still

547 relatively rare, highlighting a key gap for future synthesis. Additionally, it is important to

548 consider that plants can undergo rapid phenotypic acclimation during heatwaves. For example,

549 changes in leaf orientation, curling, or shedding may occur to reduce water loss and limit

550 thermal stress. These dynamic and reversible morphological responses may play a critical role

551   in coping with acute heat stress and should be incorporated into trait-based assessments to

552   better estimate plant resilience to heatwaves. In this context, large-scale trait datasets may offer

553   a coarse yet efficient approach for identifying species most susceptible to extreme heat,

554   particularly when detailed physiological data are lacking.

555

556   4.2.2. Plant life stage

557   Plants exhibit differing sensitivities to environmental stressors across life stages (Grubb, 1977)

558   making it essential to consider their developmental phase at the time of heatwave exposure

559   (Wahid *et al.*, 2007). Although there is ongoing debate regarding which stage is most affected

560   by extreme heat, current research has disproportionately focused on established seedlings, with

561   far less attention to other potentially sensitive phases. In particular, the immediate post-

562   germination phase is likely to be the most vulnerable period of the life cycle to temperature

563   extremes, yet it remains especially difficult to study. Other critical stages, such as seeds and

564   reproduction, are likewise underrepresented despite their central role in species persistence (Fig.

565   4b). Reproductive success and fitness—especially in annual species—are fundamental to

566   species persistence. This imbalance hinders our ability to identify the most heat-sensitive

567   periods and limits the potential to assess plant risk. Furthermore, it remains uncertain whether

568   seedling performance under heat stress can reliably represent whole-life-cycle resilience, or to

569   what extent it may serve as a meaningful proxy.

570   Compared to the vegetative stage, heatwave experiments targeting the seed and

571   reproductive stages may require additional considerations in both simulation design and

572   performance assessment. For example, seeds in the soil seed bank are primarily heated through

573   the conduction of atmospheric heat and the absorption of solar radiation into the soil. In bare

574   soil conditions, substrate temperatures may exceed surrounding air temperatures during

575 heatwaves, while shallow soil layers can experience rapid declines in moisture content and

576 increased porosity (García-García *et al.*, 2023). These changes may expose seeds to abnormally

577 high temperatures or even direct sunlight. For seeds that are sensitive to temperature, humidity,

578 and light, such conditions may substantially reduce germination rates and seed vigour (Ooi,

579 2012). Given the substantial variability in dormancy-breaking and germination requirements

580 among species, one common approach to assessing post-heatwave plant recruitment is through

581 regular field observations. Alternatively, in controlled experiments, it is essential to investigate

582 the effects of heat after other required environment cues for germination initiation are met (e.g.,

583 high humidity, smoke exposure, or specific light cues).

584   In contrast, heatwaves during the reproductive stage challenge how plants allocate

585 resources between self-maintenance and reproduction, potentially involving both trade-offs

586 and synergies (Lovett Doust, 1989). For some short-lived species, reproductive output may

587 largely depend on lifespan (Notarnicola *et al.*, 2021). Warming can promote earlier flowering

588 (Notarnicola *et al.*, 2021) and increase flower production (Frei *et al.*, 2014), but excessive heat

589 often reduces reproductive success by impairing pollen viability, disrupting pollination, and

590 hindering seed formation—ultimately leading to infertility and yield loss (Qian *et al.*, 2025).

591 For perennial species such as trees and shrubs, heatwaves may disrupt the energy allocation

592 trade-offs among growth, reproduction, and seed viability, potentially affecting long-term

593 community dynamics (Macias & Redmond, 2025). Furthermore, transgenerational effects—

594 including maternal or paternal influences—may confer enhanced heat tolerance to offspring

595 more rapidly than slower evolutionary processes, potentially improving survival under future

596 extreme climatic conditions (Zhou *et al.*, 2022). However, empirical evidence for these

597 responses and their long-term consequences under heatwave scenarios remains limited.

598 Compared to wild species, model plants and crops have been more extensively studied in this

599　context, potentially providing useful but underutilised information to address this knowledge

600　gap (Resentini *et al.*, 2023; Qian *et al.*, 2025).

601　　　　Although plant phenology has been systematically documented across many regions,

602　phenological shifts under climate warming, such as earlier germination following premature

603　snowmelt (Hassan *et al.*, 2023), may expose early life stages to climatic extremes. Concurrently,

604　the seasonal timing of heatwaves is becoming more unpredictable and may impose cumulative

605　physiological stress following recurrent heatwaves or drive acclimation responses across life

606　stages (Perkins-Kirkpatrick & Lewis, 2020). These dynamics underscore the need for

607　experimental frameworks that simulate heatwave exposure at multiple developmental stages,

608　both independently and sequentially, while monitoring legacy and transgenerational effects.

609

610　4.2.3. Thermal tolerance

611　A quantitative approach to estimating plant susceptibility to extreme temperatures is the

612　measurement of critical temperature thresholds, i.e. temperatures beyond which substantial

613　thermal stress occurs. For example, regarding photosynthetic thermal tolerance, T_{50} refers to

614　the temperature at which F_v/F_m declines by 50%, while T_{crit} denotes the onset of rapid decline

615　of F_v/F_m (Perez & Feeley, 2020). In addition to these species-specific thresholds, various

616　physiological indicators (e.g., electrolyte leakage, F_v/F_m), and molecular responses (e.g., heat

617　shock protein expression) serve as markers of stress or thermal tolerance (Geange *et al.*, 2021).

618　With over half a century of methodological development, these approaches have been widely

619　applied to predict the vulnerability of both wild and cultivated species under extreme heat (see

620　(Geange *et al.*, 2021), for a global systematic review).

621　　　　Despite being a valuable indicator of potential tolerance, thermal tolerance metrics

622　should not be used to predict plant performance or survival under extreme conditions, such as

623   heatwaves, if these were not tested directly. For instance, critical thermal thresholds are often

624   determined under conditions less extreme than actual heatwaves. Such measurements may

625   overlook plant acclimation during heatwaves—which can increase thermal tolerance (Andrew

626   *et al.*, 2022; Harris *et al.*, 2024) as well as the development of stress memory following repeated

627   exposures. Therefore, interpreting these metrics requires careful consideration of the

628   environmental context (Andrew *et al.*, 2022) and prior stress history (Harris *et al.*, 2024) to

629   assess their ecological relevance. Moreover, some plants can maintain efficient transpiration

630   during heatwaves, effectively decoupling tissue temperature from ambient air (Arnold *et al.*,

631   2025b; Cox *et al.*, 2025). Consequently, even species with relatively low thermal thresholds

632   may not face elevated risk under such conditions. Nonetheless, incorporating thermal tolerance

633   metrics into heatwave studies can enhance cross-species comparisons of sensitivity. When

634   combined with measurements of leaf temperature regulation and other physiological traits,

635   these metrics offer a more integrated understanding of plant vulnerability to future heat

636   extremes.

637

638   4.2.4. Spatial patterns

639   At broad terrestrial scales, many studies have assessed the resistance of plant systems to climate

640   change by examining spatial patterns in distribution and susceptibility (Evans *et al.*, 2025). For

641   instance, researchers investigated thermal limits across environmental gradients, such as

642   latitude (O'Sullivan *et al.*, 2017; Sklenář *et al.*, 2023), elevation (mountain, alpine,

643   tundra)(Notarnicola *et al.*, 2021; Danzey *et al.*, 2024) and biome (Zhu *et al.*, 2018; Andrew *et*

644   *al.*, 2022; Harris *et al.*, 2024). Other studies have investigated plant migration rates toward

645   cooler regions and higher elevations as a response to warming (Steinbauer *et al.*, 2018; Auld

646   *et al.*, 2022). Notably, vulnerability cannot necessarily be defined by the absolute breadth of

647 tolerance; instead, a more decisive factor may be the gap between local warming patterns and

648 the species' upper thermal limits (Sentinella *et al.*, 2020; Doughty *et al.*, 2023). These large-

649 scale assessments can help refine the areas at high-risk under increased temperatures that

650 should be prioritised for follow-up empirical heatwave experiments.

651 With the increasing application of thermography technology in plant thermal

652 monitoring, researchers can detect plant overheating and death during natural heatwaves

653 rapidly and efficiently (Still *et al.*, 2019). Combined with the broad measurement of plant

654 thermal tolerance, this robust evidence could refine the evaluation of plant vulnerability.

655 Recent advancement in thermal imaging resolution and analytical methods makes it possible

656 to monitor specific, vulnerable plant species in conservation efforts (Jones, 2004). This

657 approach can also be used in controlled heatwave experiments to monitor plant thermal

658 regulation and dynamics at finer spatial scales—for example, capturing temperature variations

659 within individual leaves (Craparo *et al.*, 2017; Iseki & Olaleye, 2020).

660

661 **5. Conclusion**

662 We found substantial variation in existing experimental heatwave studies. These include bias

663 in geographic distribution, plant types (growth forms and life stages), heatwave characteristics

664 (e.g., intensity, duration, frequency), simulation methods and technologies, indicators of plant

665 stress at morphological, physiological, and molecular levels, as well as the types of co-

666 occurring stressors. We have therefore proposed a set of recommendations and potential

667 approaches to improve cross-study comparability and enhance the interpretability of

668 experimental outcomes, thereby facilitating future meta-analyses and fostering a more

669 consistent understanding across ecosystems and species. We aim for these recommendations

670 to serve as a practical framework for designing future experimental studies on heatwaves. By

promoting greater consistency in experimental approaches, they can help advance our understanding of species vulnerability and improve forecasts of ecosystem responses under intensifying climate extremes.

6. Data and code availability

All data and code used in this study are available at: XXX.

7. Author contributions

Conceptualisation: all authors; methodology: all authors; software: XM, PP; validation: PP; formal analysis: XM, PP; investigation: XM, PAA, RFN, PP; data curation: XM, PP; writing – original draft: XM; writing – review & editing: all authors; visualisation: XM, PP, WKC; supervision: PP, WKC; project administration: XM, PP; funding acquisition: WKC.

8. Competing interests

We declare no competing interests.

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10. References

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