Systematic review of heatwave experiments on plant health and survival

Xuemeng Mu[1,*] (ORCID ID: 0009-0000-0331-8573), Rocco F. Notarnicola[2] (ORCID ID: 0000-0001-9860-6497), Pieter A. Arnold[3] (ORCID ID: 0000-0002-6158-7752), Pietro Pollo[1,4‡] (ORCID ID: 0000-0001-6555-5400), Will K. Cornwell[1‡] (ORCID ID: 0000-0003-4080-4073)

[1] Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, The University of New South Wales, Sydney, New South Wales, Australia

[2] Evolutionary Biology Group, Faculty of Biology, Adam Mickiewicz University, Poznan, Poland

[3] Division of Ecology and Evolution, Research School of Biology, The Australian National University, Canberra, ACT, Australia

[4] School of Environmental and Life Sciences, University of Newcastle, Newcastle, Australia

[‡] These authors share senior authorship.

[*] Corresponding author: muxuemeng@hotmail.com

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

Running title: Experimental Insights on Plant Heatwaves

Abstract

Background: Heatwaves, which are becoming more intense and more frequent due to global warming, are a major threat to the stability of plant populations and ecosystems. Safeguarding ecosystem function requires a clear understanding of vulnerability to these extreme events. Yet vulnerability cannot be reliably inferred from experiments that manipulate only mean temperatures or from standard thermal tolerance assays. These limitations have spurred a growing body of research specifically simulating heatwaves and studying their effect on plants.

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

Results: Regional biases are pronounced, reflecting the logistical and financial challenges of conducting these costly experiments. Likely for similar reasons, studies have largely been restricted to seedlings, with little attention to adult plants and wild species in the reproductive stage. Experimental approaches are also highly diverse, particularly in how heatwaves are simulated, creating major hurdles for cross-study comparison. More than half of the studies (53/84) incorporated at least one interacting factor—most commonly drought (23/84)—yet other ecologically important interactions, such as grazing and microbial associations, remain underexplored.

Implications: This review offers a comprehensive resource to guide the next generation of heatwave experiments, highlighting underrepresented plant groups and geographic regions, and underscores the pressing need for greater standardisation in experimental approaches to facilitate a synthetic understanding of heatwave effects globally. Such coordination will improve our ability to identify heatwave-sensitive species and better predict ecological responses to climate extremes.

Keywords: heat resilience; heat resistance; high temperature; research bias; comparative synthesis.

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.

2.2. Screening process and inclusion criteria

Our screening criteria are summarised in Table 1 and in Figure S1 (slightly different from our pre-registration; see Mu *et al.*, 2024). We used Rayyan QCRI (Ouzzani *et al.*, 2016) for both the initial and the full-text screenings. P.A., P.P., R.N. and X.M. conducted the initial screening, i.e. assessed the title, abstract, and keywords of retrieved studies. The full-text content of studies that passed the initial screening was then assessed by two people: X.M. (100%) and either P.A., P.P. or R.N. (33%, 34%, 33% of the cases, respectively). In both initial and full-text screening, authors resolved conflicts through discussion until consensus was reached. Full-text screening decisions are shown in Supporting Information SI2.

Table 1. Scope of our systematic review on topics related to the impact of heatwaves on plants, according to the population, intervention/exposure, comparator, outcome, and study-design (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

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.

X.M. recorded the country where each study was conducted based primarily on the described experimental location. If no specific location was provided, X.M. used the country of the first author's institutional affiliation. For plant measurements, X.M. extracted the measurement names from figures, tables, or datasets provided by authors. X.M. categorised these measurements as multilevel traits—spanning morphological, physiological, and molecular categories—and further subcategorised them according to their relevance to key metabolic processes and core plant functions (as shown in Fig. 1). Although some measurements are associated with multiple metabolic pathways, X.M. assigned each to the category most critical to plant health and survival. For example, although stomatal conductance is linked to both water relation and carbon flux, X.M. classified stomatal conductance as water relation because transpiration may be more vital than photosynthesis for plant survival under heatwave conditions.

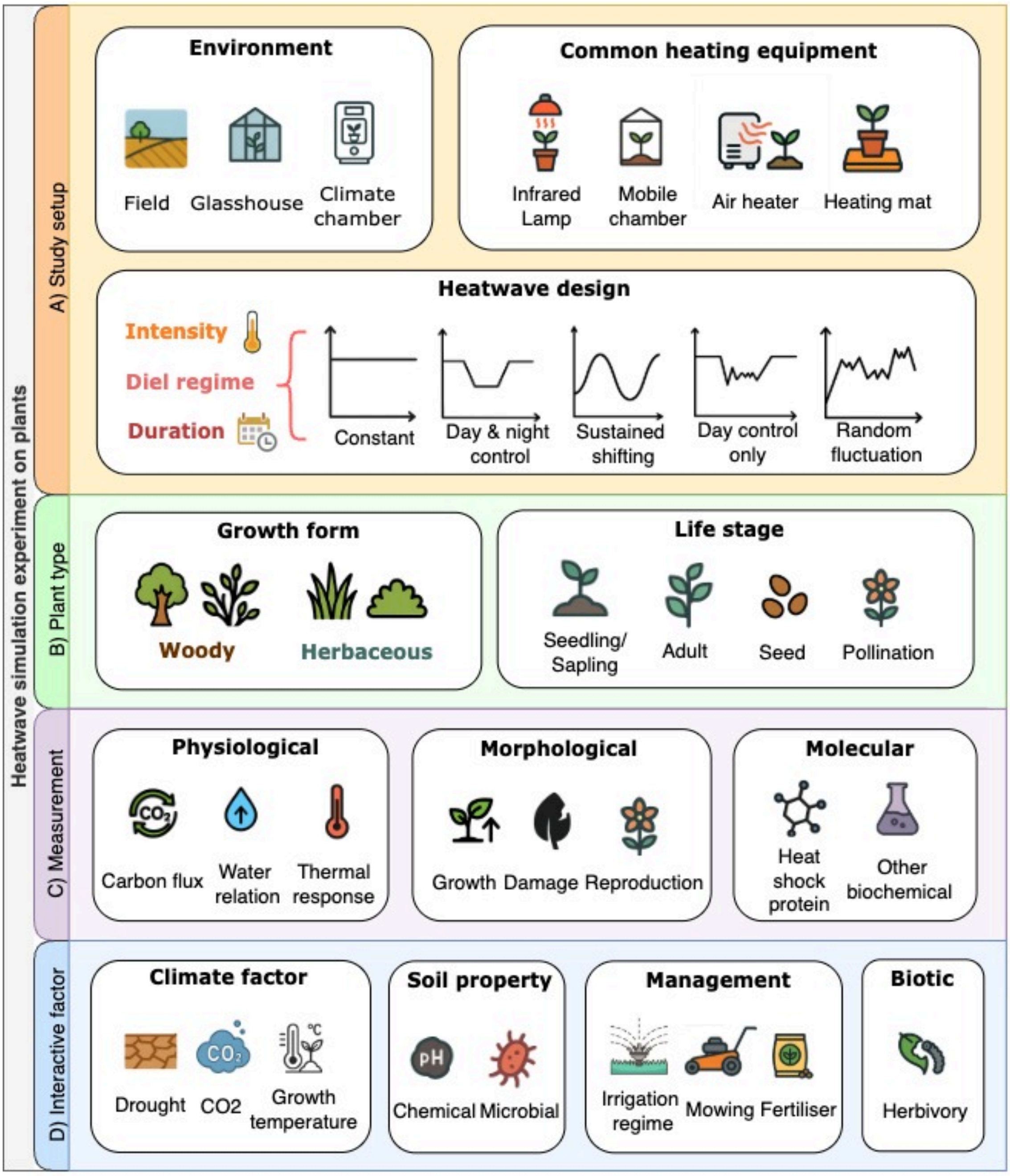


Fig. 1 Conceptual diagram illustrating the categories used in this study as meaningful proxies for sources of variation in heatwave experimental designs. Variation may arise from: (A) Study setup (yellow section), including aspects of the study environment, heating equipment, and temperature control; (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.

In total, this process resulted in the inclusion of 84 eligible studies in the systematic review (see the list of studies in Appendix 2 and details in Supporting Information SI3). The first study on the effects of a simulated heatwave on plants was published in 2004.

3.2. Geographic spread

Although the 84 studies in our systematic review reported experiments globally, the majority were conducted in only a few countries (Fig. 2). The uneven distribution we found regarding heatwave experiments is probably due to institutional bias (Zvereva & Kozlov, 2021), the availability of research funding (Luukkonen *et al.*, 1992), and research attention driven by the impacts of historical extreme climate events (Steffen *et al.*, 2014). Notably, three studies were conducted in tundra regions within polar zones, demonstrating the feasibility of simulating heat events even under extremely low temperatures. In contrast, tropical regions (including large parts of Africa and South America) remain severely understudied, despite their high levels of plant diversity (Raven *et al.*, 2020). While this distribution pattern is consistent with studies measuring thermal tolerance in wild plant species (Geange *et al.*, 2021), current empirical research on the effects of heatwaves on plants remains notably restricted in geographical scope.

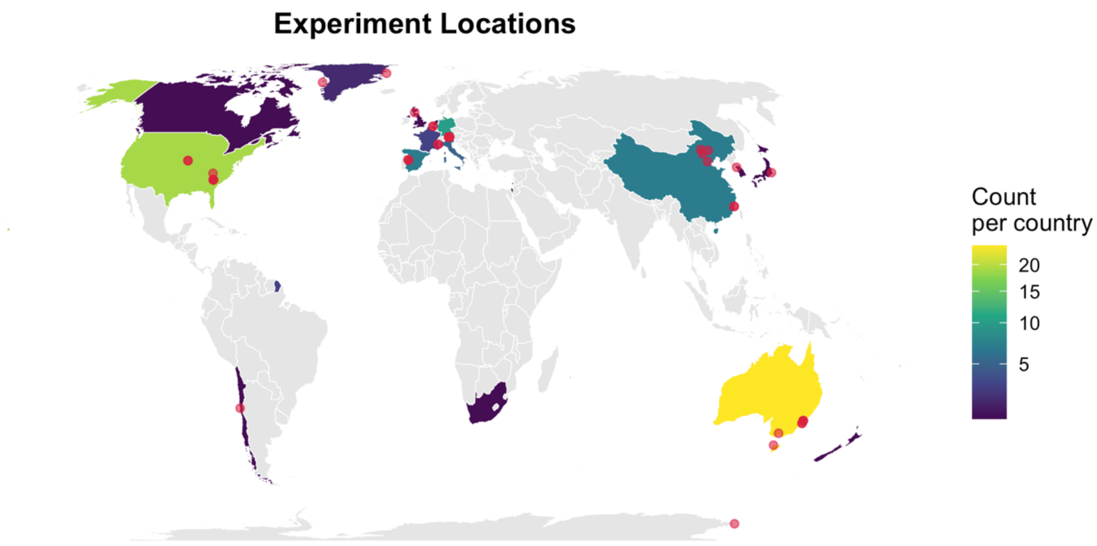


Fig. 2 Global distribution of 84 heatwave studies (field and laboratory). Red dots mark the specific experiment locations where such information was available. Detailed information is provided in Supporting Information SI3.

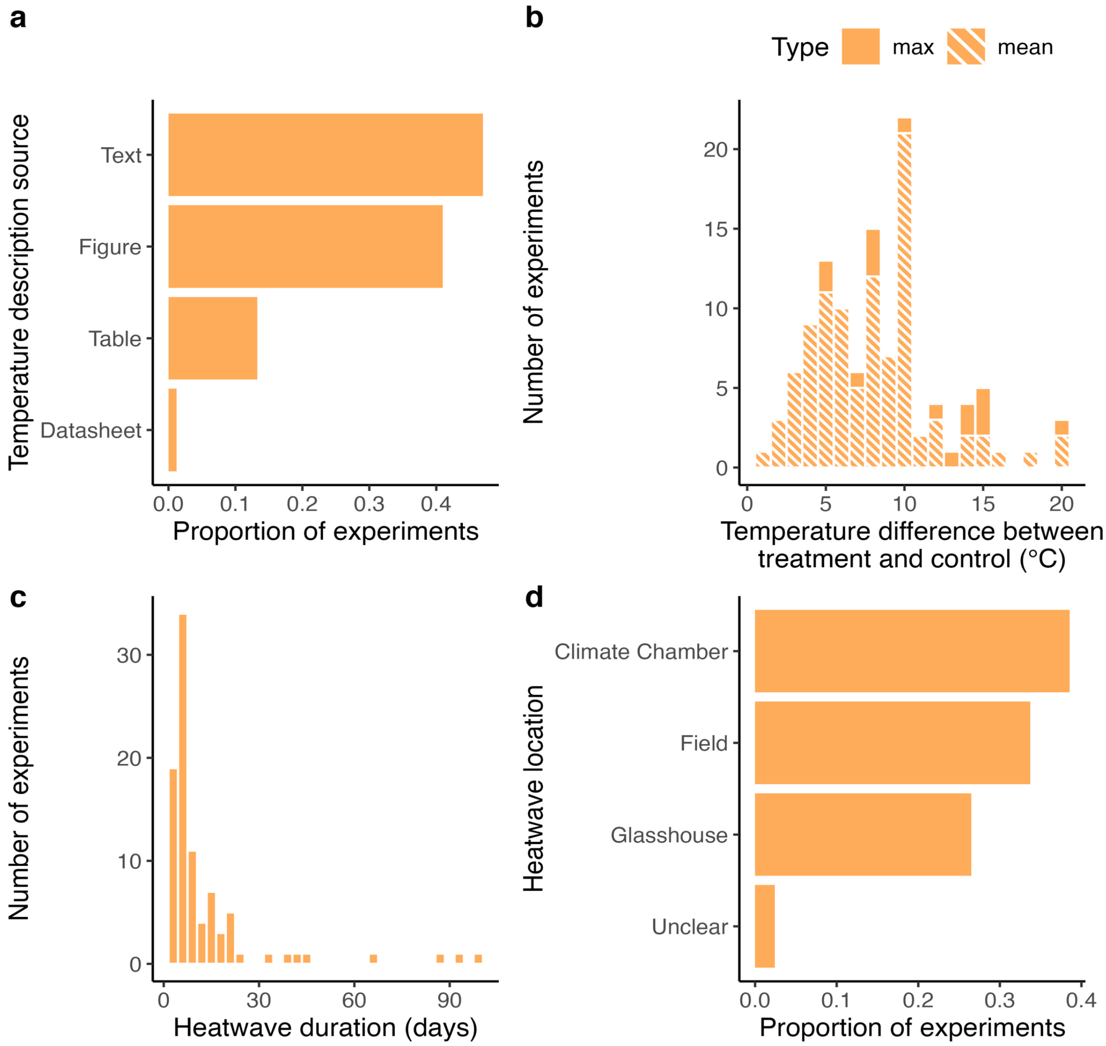
3.3. Heatwave design

Transparent reporting of temperature regimes is essential as thermal settings and their interaction with ambient conditions may critically influence plant responses. Yet approximately 39 out of 84 studies (46.4%) described the heatwave regime only in the text. Some of these studies reported only a mean or maximum temperature, obscuring diurnal shifts and the true heat load experienced by plants (Fig. 3a). In contrast, 34 studies (40.5%) included graphical representations (raw data traces or schematic diagrams), which more effectively convey temporal fluctuations. Only 11 studies (13.1%) showed the temperature information in a table and one study in a datasheet (1.2%).

Studies included in our systematic review varied considerably both in the number and characteristics of the simulated heatwaves they conducted. Most studies applied a single heatwave treatment, typically characterized by a specific temperature pattern maintained over a continuous period. However, a subset of studies included multiple heatwave events, either by varying key characteristics such as intensity and duration, or by repeating heatwaves over intervals spanning days (French *et al.*, 2019; Birami *et al.*, 2021), weeks (Ahrens *et al.*, 2021; Liu *et al.*, 2023), months (Yu *et al.*, 2023), or even up to a year (Qu *et al.*, 2020; Li *et al.*, 2021). Heatwave intensity (i.e. temperature difference between heatwave and control groups) ranged widely across studies, from 1°C to over 20°C, with the majority of studies applying increases of 10°C or less (Fig. 3b). Although we only included studies applying at least 4°C increase in maximum temperature under heatwave conditions compared to a control condition in our systematic review, peak temperatures (i.e., maximum values) may only be sustained briefly due to ramping protocols or temperature fluctuations (Fig. 1) and we thus focused on mean temperature differences (see section 2.3).

The duration of the heatwaves simulated by studies ranged from three days (minimum required for inclusion in this review) to as long as 99 days, with most experiments clustering around one week in length (Fig. 3c). This heatwave duration is consistent with the natural heatwaves observed in both historical records and current climate conditions (Perkins-Kirkpatrick & Lewis, 2020; Trancoso *et al.*, 2020). As heatwaves are projected to become increasingly prolonged under future climate scenarios, studies simulating durations longer than one week are particularly relevant for assessing plant persistence under extreme conditions in coming decades (Trancoso *et al.*, 2020). Notably, six studies imposed heatwave treatments lasting more than three weeks, perhaps exceeding the length of recommended heatwaves by experimental guidelines proposed by Breshears *et al.*, 2021. However, these long heatwaves may be plausible under certain regional projections, high-emission scenarios, or late-century timeframes (Trancoso *et al.*, 2020). Given that extended heat exposure can increase the risk of cumulative stress or trigger acclimation responses in plant (Marchand *et al.*, 2005), these studies may yield distinct physiological or ecological outcomes and should therefore be interpreted with caution when comparing results across studies.

Regarding the location of the experimental simulation of heatwaves, studies were mostly conducted in climate chambers, greenhouses, and field settings (natural sites and common gardens). These markedly differ in their temperature-control capacity (from precise regulation to fully dynamic fluctuations), ambient conditions (e.g., light intensity, humidity), plant growth context (*ex situ* vs *in situ*), and experimental scale (e.g., number of plants, species diversity, interacting factors). The choice by researchers reflects trade-offs among their objectives, priorities, and logistical constraints. Interestingly, we found that simulated heatwaves were applied relatively evenly across the three experimental locations, from tightly controlled laboratory conditions to complex, real-world field scenarios (Fig. 3d).



263

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

266

267 *3.4. Plant type*

268 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.

More than half of the studies we included in our systematic review (49 out of 84 studies, 58.3%) focused on early developmental stages, particularly seedlings (38 studies, 45.2%; i.e. the earliest juvenile stage after germination, bearing cotyledons and still partly reliant on seed reserves while establishing independent photosynthesis.) and saplings (11 studies, 13.1%; i.e. well-established juvenile plant that is fully photoautotrophic but not yet reproductively mature; Fig. 4b). This is likely due to the prevalence of woody plants in heatwave research, whose long-life cycles and large size pose challenges for well-controlled experiments on mature individuals, often requiring field settings and sophisticated equipment. Additionally, there is a common assumption that seedlings are more susceptible to extreme climatic events than mature plants (Lenoir *et al.*, 2009; Lloret *et al.*, 2009; Jagadish *et al.*, 2021). Thus, only nine studies (10.7%) of studies in our systematic review applied heatwave treatments to adult plants prior to flowering. Surprisingly, the effects of heatwaves on seeds have been scarcely explored (three studies, 3.6%), and only one study has examined plant reproductive stages (Tushabe *et al.*, 2023), despite their notably higher sensitivity to temperature (Hedhly, 2011; Wang *et al.*, 2016; Lohani *et al.*, 2020). Unexpectedly, almost a quarter of the studies (23 out of 84, 27.4%) did not clearly specify the life stage of the plants used in heatwave experiments. In some cases, developmental stage can be roughly inferred from the experimental timeline, yet ambiguous inference may hinder accurate assessments of plant fitness and comparability of results across studies, so we categorised these as unclear.

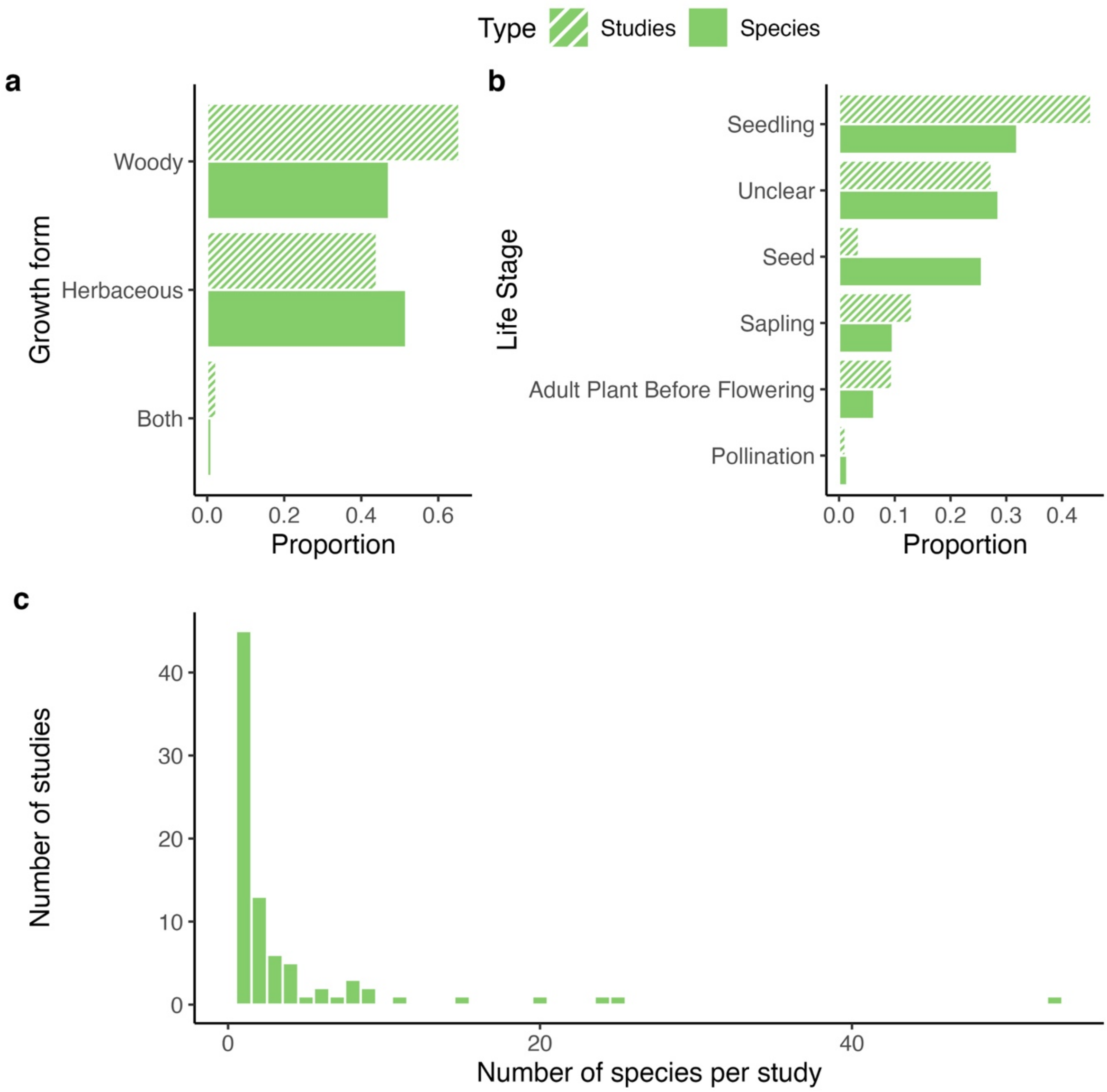


Figure 4. Proportion of studies and species by plant growth form (a) and life stage (b) at the time of heatwave exposure, and number of species included per study (c).

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 ultimately manifesting as visible morphological changes (Zhao *et al.*, 2020). Physiological measurements were by far the most common approach among the studies included in our systematic review, used by 77 out of 84 studies (91.7%) and covering 265 out of 269 species examined (98.5%) (Fig. 5b). Conversely, morphological assessments represented 47 studies (56%) of traits reported in studies examining heatwave effects on plants, such as structural shifts or biomass allocation. Heat-shock protein expression and changes in biochemical composition were reported in 28 studies (33.3%). Only 16 studies (19%) made all types of measurements (i.e., molecular, physiological, and morphological) together (Fig. 5a), highlighting a gap in multi-scale trait integration that limits our ability to trace causal chains from gene regulation through whole-plant function under stress.

When these trait categories are divided into functional sub-categories (e.g., carbon flux, water relations, growth, damage, thermal responses, reproduction, and biochemical processes; Fig. 5d), distinct patterns emerge between the study focus and species examined. At the study level, researchers have generally distributed their attention relatively evenly across functional processes, with the exception of reproduction, which has received comparatively little focus. Thus, overall, only one study has covered all six sub-categories (Fig. 5c). In contrast, trait measurements at the species level concentrated on direct indicators of heat injury (114 out of 269 species, 42.4%), such as visual damage scores, chlorophyll fluorescence (Fv/Fm), and thermal response traits (e.g., leaf temperature, critical thermal maxima). This pattern suggests that multi-species studies may prioritise indicators of stress impact that are easily comparable across species, rather than regulatory mechanisms. Although five studies measured more than 20 traits, the majority focused on fewer than 15 (Fig. 5e). It is worth noting that approximately 34 out of 84 studies (40.5%) evaluated biochemical processes, including molecular assays (e.g., 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.

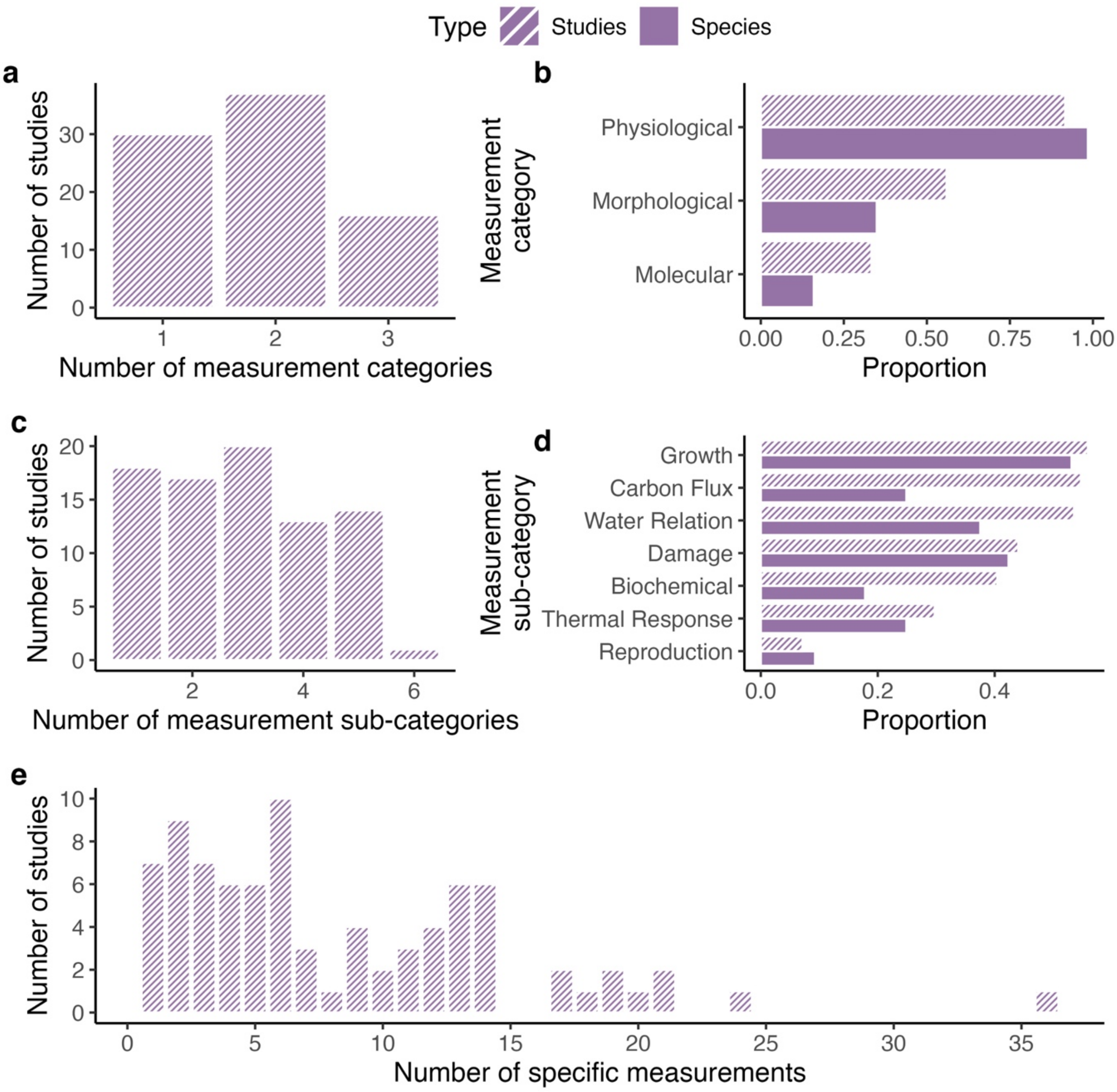


Figure 5. Overview of the coverage across studies and species regarding measurement categories (a, b), measurement sub-categories (c, d), and specific measurements (e).

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 ecosystem function under complex, changing climates, future research should embrace multifactorial designs and expand the range of interactive factors examined to include locally and globally relevant variables that co-occur with heatwaves.

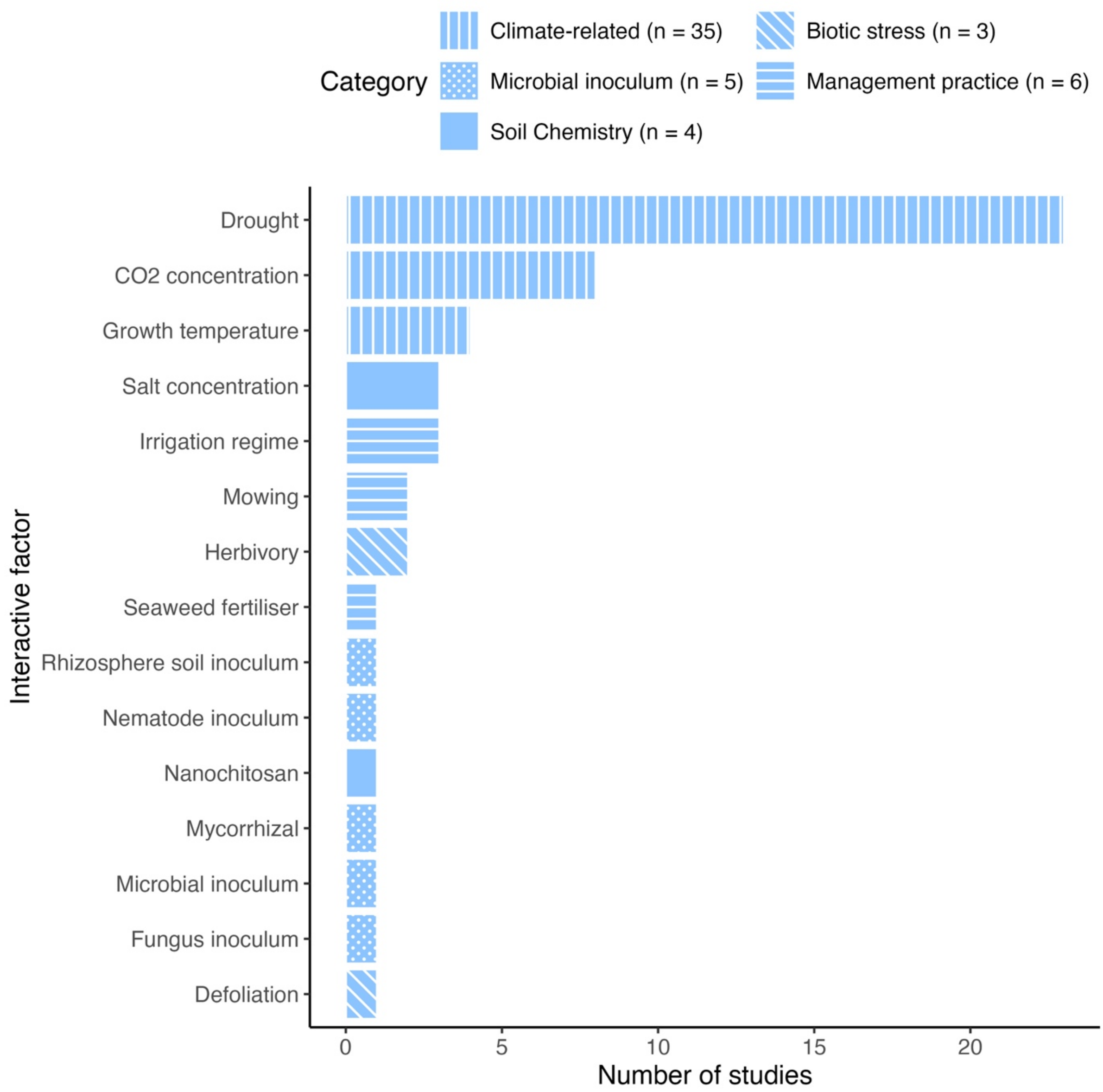


Figure 6. Number of studies including specific interactive factors.

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.

<u>4.1.1. Designing and reporting heatwave studies to facilitate synthesis</u>

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.

To address this challenge, we recommend designing heatwave intensity and duration protocols based on the primary research objective, emphasising either practical conservation or theoretical mechanisms. First, for application-oriented studies (often field-based), experimental parameters should closely reflect local heatwave characteristics and environmental conditions, particularly when targeting ecologically important, endangered, or habitat-sensitive species. This context-specific approach can efficiently yield meaningful insights for conservation planning and local ecosystem management. Accordingly, we suggest reporting detailed contextual information, including biome type, regional climate, soil environment, and the data sources or models possibly used to define heatwave scenarios. Ideally, a brief overview of previous studies on the same species, ecosystem, or biome should also be included, along with an assessment of whether and how well the heatwave simulation aligns with commonly applied definitions. Second, for fundamental research, establishing benchmark ranges for heatwave intensity and duration could significantly enhance comparability across studies (Breshears *et al.*, 2021). We therefore advocate developing standardised heatwave simulation guidelines at national or global scales. Such guidelines could be especially valuable for well-controlled environments, where conditions can be optimised to isolate the effects of heat load and enable effective comparisons of species-specific susceptibility. This standardisation may also be appropriate for studies examining how geographical factors (i.e., latitude, elevation, or provenance) influence species' capacity to deal with heatwaves. Furthermore, for multi-species studies and those involving diverse plant growth forms, employing uniform simulation parameters (e.g., French *et al.*, 2017) can provide a robust platform for cross-species comparisons, facilitating theoretical investigations into 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 patterns. The ecological impacts of heatwave regimes, shaped by intensity, duration, frequency, and timing, remain a critical research frontier.

Realistic simulation of heatwaves requires not only specifying key parameters but also manipulating the thermal dynamics throughout the event. Daily temperature variation (e.g., day–night shifts, ramping rates, random fluctuations) has been implemented in diverse ways (Fig. 1). While such configurations may be tailored to specific research objectives, temperature fluctuations are often difficult to control in settings with variable ambient conditions or limited technical capabilities. In these cases, it is essential to record and report the targeted and realised temperature profiles, along with any unintended temperature deviations, to facilitate interpretation of results. Directly comparing results from studies that employ very different dynamic temperature regimes can be difficult at best and misleading at worst. For example, even with equal peak temperatures and overall durations, heatwave simulations that use different regimes, such as constant heating, diurnal shifts, or pulsed exposures (Fig. 1), impose different cumulative heat loads on plants and potentially elicit markedly different physiological responses. Recent evidence suggests that cumulative heat load may be a stronger predictor of plant responses than peak temperature alone (Cook *et al.*, 2024), such that explicitly incorporating exposure duration potentially offers greater biological relevance (Bauweraerts *et al.*, 2013). Continuous temperature monitoring throughout simulated heatwave events enables the calculation of real-time cumulative heat load imposed on plants, providing an informative metric for comparing heatwave severity across studies. Nevertheless, this metric should be applied carefully within a heatwave-specific framework; otherwise, it risks conflating heatwave effects with other warming scenarios (i.e., gradual warming or acute heat shocks) (Jagadish *et al.*, 2021). Furthermore, we emphasise the importance of incorporating night-time temperatures in heatwave simulations (Arnold *et al.*, 2025a). Although nighttime temperatures are generally lower than daytime temperatures in absolute terms, they can increase disproportionately under heatwave conditions (Vose *et al.*, 2005; Davy *et al.*, 2017; Wu *et al.*, 2023). Elevated nighttime temperatures may hinder the repair of daytime heat damage and lead to increased respiration, water loss, and energy expenditure, potentially compounding the physiological stress imposed by high daytime temperatures in subsequent days (Kundu et al., 2024).

4.1.2. Empirical heatwave simulations

Compared to the volume of research on general warming effects on plant ecophysiology, empirical studies specifically addressing heatwaves remain remarkably limited. Given mounting evidence of severe heatwave impacts on ecological communities, this gap is a source of critical uncertainty for predicting and mitigating species loss and community shifts, especially among sensitive species and communities, and within vulnerable ecosystems (Chen & Lewis, 2023). Despite the urgent need for such studies, heatwave experiments often present technical, financial, and logistical challenges (Ettinger *et al.*, 2019; Arnold *et al.*, 2025a), which may discourage broader research engagement. Nevertheless, the great effort of researchers and practitioners over the past decades has contributed to a variety of feasible approaches. These methodological developments provide valuable technical support and resource-efficient solutions that fundamentally enable the expansion of heatwave-related research across diverse ecological contexts and research conditions.

Field experiments, including common garden studies, typically involve plants exposed to natural environmental conditions and rooted in relatively open soil, whether *in situ*, relocated, or grown in mesocosms (see Table S2 for examples). The core challenge of simulating heatwaves in such settings is maintaining elevated temperatures consistently while minimising confounding effects from other environmental factors. Achieving this goal requires careful consideration of site-specific variables, such as diurnal temperature ranges, as well as precipitation, light availability, and soil moisture. Evaluation of these factors informs equipment selection and maintenance demands. Due to the high-intensity warming needed for simulating heatwaves, passive warming methods (e.g., open- or closed-top chambers) are generally insufficient to achieve sustained high temperatures without active heating (Speights *et al.*, 2018; Ettinger *et al.*, 2019; Arnold *et al.*, 2025a). Instead, active systems such as infrared lamps or air heaters are often necessary, either alone or in combination (Fig. 1). Consequently, these experiments generally demand robust infrastructure, reliable power sources, continuous monitoring tools, and substantial logistical support (Arnold *et al.*, 2025a).

Despite the challenges, field heatwave simulations share the general advantages of *in situ* plant studies. They preserve natural environmental heterogeneity (e.g., light, wind, humidity), plant-soil interactions, and community-level dynamics (including herbivory), thereby enabling more ecologically realistic predictions of plant responses to heatwaves. Soil moisture dynamics play a critical role in mediating heatwave effects (De Boeck *et al.*, 2016). Because the dynamics of root water uptake and progressive soil drying during a heatwave are difficult to replicate in controlled pot experiments, field settings remain essential for capturing these critical processes. Field-based heatwave experiments have been successfully implemented across a range of extreme thermal environments, including Arctic (Marchand *et al.*, 2005; Graae *et al.*, 2009; Gemal *et al.*, 2022) and alpine regions (De Boeck *et al.*, 2016; Arnold *et al.*, 2025a), and are increasingly applied to cover plant communities (Dreesen *et al.*, 2012; Arnold *et al.*, 2025a) and even large, mature trees (Drake *et al.*, 2018). Such innovative designs continue to broaden the scope and potential of field heatwave simulations. It is also important to note that empirical and observational studies conducted during naturally occurring heatwaves—though outside the scope of this review—provide rare and valuable, real-world insights that can both validate and extend findings from controlled simulations, particularly in terms of post-heatwave plant responses and recovery (Breshears *et al.*, 2021).

Climate chambers and glasshouses provide controlled environments to study plant responses to heatwaves, allowing precise and repeatable manipulation of temperature and other parameters. Yet, artificial conditions—such as limited light, short experimental periods, and reliance on pots—can alter morphology and physiology, reducing relevance to field-grown plants (Poorter *et al.*, 2016). Phenotypic discrepancies are evident even among outdoor gardens, greenhouses, and climate chambers, which differ in control intensity (Karitter *et al.*, 2023). To ensure robust results, such experiments must account for deviations from field conditions, including setup (facility, medium, pot size), sample size, key growth factors (light, CO_2, nutrients, humidity, water, temperature, salinity), and issues under abiotic stress (Poorter *et al.*, 2012).

4.2. Susceptible plant candidates

One of the primary objectives of plant–heatwave research is to identify the plants most at risk from extreme heat events. Among the *ca.* 374,000 known plant species (Christenhusz & Byng, 2016), distinguishing those most susceptible to heat-induced mortality remains a significant challenge. This difficulty stems in part from species having distinct thermoregulation and thermal tolerance limits (Feeley *et al.*, 2020), meaning their vulnerability cannot be reliably inferred from projected climate extremes alone—especially since heatwaves vary substantially across regions (Reddy *et al.*, 2021). This task is urgent, as escalating climate extremes may drive rapid and irreversible biodiversity loss, with cascading consequences for ecological functions and services. Drawing on previous research into plant capacities and adaptive strategies in response to thermal stressors, researchers typically narrow down the pool of vulnerable species by considering the following key factors.

4.2.1. Plant functional traits

Plants have evolved a diverse array of traits that underpin their life-history strategies and enable them to adapt to the environments they inhabit (Reich *et al.*, 2003). In the context of a rapidly warming climate, certain thermoregulatory traits (e.g., leaf colour, size, and shape) may serve as useful indicators of plant vulnerability to heatwaves due to their influence on heat absorption and dissipation (Leigh *et al.*, 2017). Some traits are directly linked to plant's physical properties; for instance, leaf size and thickness influence the thickness of the boundary layer surrounding the leaf—a buffer zone between the leaf surface and the surrounding air that governs the rate of heat convection (Monteith, 1990; Schuepp, 1993). Such traits may also indirectly affect physiological processes related to temperature regulation, such as the rate of evaporative cooling (Buckley *et al.*, 2017; Arnold *et al.*, 2025b). With the rapid expansion of plant trait collection and the increasing availability of open-access databases (e.g., TRY; Kattge *et al.*, 2020, and AusTraits; Falster *et al.*, 2021), morphological trait-based approaches have been broadly applied to explore plant responses to environmental stressors (Soudzilovskaia *et al.*, 2013; Anderegg *et al.*, 2019). However, this approach remains underexplored in heatwave-specific research. Individual experiments often involve only a limited number of species due to specific constraints, and meta-analyses that synthesise findings across studies are still relatively rare, highlighting a key gap for future synthesis. Additionally, it is important to consider that plants can undergo rapid phenotypic acclimation during heatwaves. For example, changes in leaf orientation, curling, or shedding may occur to reduce water loss and limit thermal stress. These dynamic and reversible morphological responses may play a critical role in coping with acute heat stress and should be incorporated into trait-based assessments to better estimate plant resilience to heatwaves. In this context, large-scale trait datasets may offer a coarse yet efficient approach for identifying species most susceptible to extreme heat, particularly when detailed physiological data are lacking.

4.2.2. Plant life stage

Plants exhibit differing sensitivities to environmental stressors across life stages (Grubb, 1977) making it essential to consider their developmental phase at the time of heatwave exposure (Wahid *et al.*, 2007). Although there is ongoing debate regarding which stage is most affected by extreme heat, current research has disproportionately focused on established seedlings, with far less attention to other potentially sensitive phases. In particular, the immediate post-germination phase is likely to be the most vulnerable period of the life cycle to temperature extremes, yet it remains especially difficult to study. Other critical stages, such as seeds and reproduction, are likewise underrepresented despite their central role in species persistence (Fig. 4b). Reproductive success and fitness—especially in annual species—are fundamental to species persistence. This imbalance hinders our ability to identify the most heat-sensitive periods and limits the potential to assess plant risk. Furthermore, it remains uncertain whether seedling performance under heat stress can reliably represent whole-life-cycle resilience, or to what extent it may serve as a meaningful proxy.

Compared to the vegetative stage, heatwave experiments targeting the seed and reproductive stages may require additional considerations in both simulation design and performance assessment. For example, seeds in the soil seed bank are primarily heated through the conduction of atmospheric heat and the absorption of solar radiation into the soil. In bare soil conditions, substrate temperatures may exceed surrounding air temperatures during heatwaves, while shallow soil layers can experience rapid declines in moisture content and increased porosity (García-García *et al.*, 2023). These changes may expose seeds to abnormally high temperatures or even direct sunlight. For seeds that are sensitive to temperature, humidity, and light, such conditions may substantially reduce germination rates and seed vigour (Ooi, 2012). Given the substantial variability in dormancy-breaking and germination requirements among species, one common approach to assessing post-heatwave plant recruitment is through regular field observations. Alternatively, in controlled experiments, it is essential to investigate the effects of heat after other required environment cues for germination initiation are met (e.g., high humidity, smoke exposure, or specific light cues).

In contrast, heatwaves during the reproductive stage challenge how plants allocate resources between self-maintenance and reproduction, potentially involving both trade-offs and synergies (Lovett Doust, 1989). For some short-lived species, reproductive output may largely depend on lifespan (Notarnicola *et al.*, 2021). Warming can promote earlier flowering (Notarnicola *et al.*, 2021) and increase flower production (Frei *et al.*, 2014), but excessive heat often reduces reproductive success by impairing pollen viability, disrupting pollination, and hindering seed formation—ultimately leading to infertility and yield loss (Qian *et al.*, 2025). For perennial species such as trees and shrubs, heatwaves may disrupt the energy allocation trade-offs among growth, reproduction, and seed viability, potentially affecting long-term community dynamics (Macias & Redmond, 2025). Furthermore, transgenerational effects—including maternal or paternal influences—may confer enhanced heat tolerance to offspring more rapidly than slower evolutionary processes, potentially improving survival under future extreme climatic conditions (Zhou *et al.*, 2022). However, empirical evidence for these responses and their long-term consequences under heatwave scenarios remains limited. Compared to wild species, model plants and crops have been more extensively studied in this context, potentially providing useful but underutilised information to address this knowledge gap (Resentini *et al.*, 2023; Qian *et al.*, 2025).

Although plant phenology has been systematically documented across many regions, phenological shifts under climate warming, such as earlier germination following premature snowmelt (Hassan *et al.*, 2023), may expose early life stages to climatic extremes. Concurrently, the seasonal timing of heatwaves is becoming more unpredictable and may impose cumulative physiological stress following recurrent heatwaves or drive acclimation responses across life stages (Perkins-Kirkpatrick & Lewis, 2020). These dynamics underscore the need for experimental frameworks that simulate heatwave exposure at multiple developmental stages, both independently and sequentially, while monitoring legacy and transgenerational effects.

4.2.3. Thermal tolerance

A quantitative approach to estimating plant susceptibility to extreme temperatures is the measurement of critical temperature thresholds, i.e. temperatures beyond which substantial thermal stress occurs. For example, regarding photosynthetic thermal tolerance, T_{50} refers to the temperature at which F_v/F_m declines by 50%, while T_{crit} denotes the onset of rapid decline of F_v/F_m (Perez & Feeley, 2020). In addition to these species-specific thresholds, various physiological indicators (e.g., electrolyte leakage, F_v/F_m), and molecular responses (e.g., heat shock protein expression) serve as markers of stress or thermal tolerance (Geange *et al.*, 2021). With over half a century of methodological development, these approaches have been widely applied to predict the vulnerability of both wild and cultivated species under extreme heat (see (Geange *et al.*, 2021), for a global systematic review).

Despite being a valuable indicator of potential tolerance, thermal tolerance metrics should not be used to predict plant performance or survival under extreme conditions, such as heatwaves, if these were not tested directly. For instance, critical thermal thresholds are often determined under conditions less extreme than actual heatwaves. Such measurements may overlook plant acclimation during heatwaves—which can increase thermal tolerance (Andrew *et al.*, 2022; Harris *et al.*, 2024) as well as the development of stress memory following repeated exposures. Therefore, interpreting these metrics requires careful consideration of the environmental context (Andrew *et al.*, 2022) and prior stress history (Harris *et al.*, 2024) to assess their ecological relevance. Moreover, some plants can maintain efficient transpiration during heatwaves, effectively decoupling tissue temperature from ambient air (Arnold *et al.*, 2025b; Cox *et al.*, 2025). Consequently, even species with relatively low thermal thresholds may not face elevated risk under such conditions. Nonetheless, incorporating thermal tolerance metrics into heatwave studies can enhance cross-species comparisons of sensitivity. When combined with measurements of leaf temperature regulation and other physiological traits, these metrics offer a more integrated understanding of plant vulnerability to future heat extremes.

4.2.4. Spatial patterns

At broad terrestrial scales, many studies have assessed the resistance of plant systems to climate change by examining spatial patterns in distribution and susceptibility (Evans *et al.*, 2025). For instance, researchers investigated thermal limits across environmental gradients, such as latitude (O'Sullivan *et al.*, 2017; Sklenář *et al.*, 2023), elevation (mountain, alpine, tundra)(Notarnicola *et al.*, 2021; Danzey *et al.*, 2024) and biome (Zhu *et al.*, 2018; Andrew *et al.*, 2022; Harris *et al.*, 2024). Other studies have investigated plant migration rates toward cooler regions and higher elevations as a response to warming (Steinbauer *et al.*, 2018; Auld *et al.*, 2022). Notably, vulnerability cannot necessarily be defined by the absolute breadth of tolerance; instead, a more decisive factor may be the gap between local warming patterns and the species' upper thermal limits (Sentinella *et al.*, 2020; Doughty *et al.*, 2023). These large-scale assessments can help refine the areas at high-risk under increased temperatures that should be prioritised for follow-up empirical heatwave experiments.

With the increasing application of thermography technology in plant thermal monitoring, researchers can detect plant overheating and death during natural heatwaves rapidly and efficiently (Still *et al.*, 2019). Combined with the broad measurement of plant thermal tolerance, this robust evidence could refine the evaluation of plant vulnerability. Recent advancement in thermal imaging resolution and analytical methods makes it possible to monitor specific, vulnerable plant species in conservation efforts (Jones, 2004). This approach can also be used in controlled heatwave experiments to monitor plant thermal regulation and dynamics at finer spatial scales—for example, capturing temperature variations within individual leaves (Craparo *et al.*, 2017; Iseki & Olaleye, 2020).

5. Conclusion

We found substantial variation in existing experimental heatwave studies. These include bias in geographic distribution, plant types (growth forms and life stages), heatwave characteristics (e.g., intensity, duration, frequency), simulation methods and technologies, indicators of plant stress at morphological, physiological, and molecular levels, as well as the types of co-occurring stressors. We have therefore proposed a set of recommendations and potential approaches to improve cross-study comparability and enhance the interpretability of experimental outcomes, thereby facilitating future meta-analyses and fostering a more consistent understanding across ecosystems and species. We aim for these recommendations 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: 10.5281/zenodo.17083241.

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.

9. Funding

XM was supported by the China Scholarship Council (CSC). RFN was supported by the Narodowe Centrum Nauki (Grant/Award Number: 2019/34/A/NZ8/00231). PAA was supported by an Australian Research Council Discovery Project DP240100177.

10. References

Ahrens, C.W., Challis, A., Byrne, M., Leigh, A., Nicotra, A.B., Tissue, D. & Rymer, P. (2021) Repeated extreme heatwaves result in higher leaf thermal tolerances and greater safety margins. *New Phytologist*, **232**, 1212–1225.

Anderegg, W.R.L., Trugman, A.T., Bowling, D.R., Salvucci, G. & Tuttle, S.E. (2019) Plant functional traits and climate influence drought intensification and land–atmosphere feedbacks. *Proceedings of the National Academy of Sciences*, **116**, 14071–14076.

Andrew, S.C., Arnold, P.A., Simonsen, A.K. & Briceño, V.F. (2022) Consistently high heat tolerance acclimation in response to a simulated heatwave across species from the broadly distributed Acacia genus. *Functional Plant Biology*, **50**, 71–83.

Arnold, P., Brown, F., Brown, Z., Aitken, S., Danzey, L., Hanley, T., King, J., Mu, X., Osmolovsky, I., Sumner, E., Williamson, V., Xirocostas, Z., Leigh, A., Moles, A., Venn, S. & Nicotra, A. (2025a) Effective heating chamber design to simulate acute heatwaves and night-time warming for ecological communities under natural field conditions. *Methods in Ecology and Evolution*, n/a-n/a.

Arnold, P.A., White, M.J., Cook, A.M., Leigh, A., Briceño, V.F. & Nicotra, A.B. (2025b) Plants originating from more extreme biomes have improved leaf thermoregulation. *Annals of Botany*, mcaf080.

Auld, J., Everingham, S.E., Hemmings, F.A. & Moles, A.T. (2022) Alpine plants are on the move: Quantifying distribution shifts of Australian alpine plants through time. *Diversity and Distributions*, **28**, 943–955.

Backes, D. (2022) The biogeography of plant heat tolerance and vulnerability to heatwaves.

Bauweraerts, I., Wertin, T.M., Ameye, M., McGuire, M.A., Teskey, R.O. & Steppe, K. (2013) The effect of heat waves, elevated [CO_2] and low soil water availability on northern red oak (*Quercus rubra* L.) seedlings. *Global Change Biology*, **19**, 517–528.

Bernacchi, C.J., Ruiz-Vera, U.M., Siebers, M.H., DeLucia, N.J. & Ort, D.R. (2023) Short- and long-term warming events on photosynthetic physiology, growth, and yields of field grown crops. *Biochemical Journal*, **480**, 999–1014.

Birami, B., Bamberger, I., Ghirardo, A., Grote, R., Arneth, A., Gaona-Colmán, E., Nadal-Sala, D. & Ruehr, N.K. (2021) Heatwave frequency and seedling death alter stress-specific emissions of volatile organic compounds in Aleppo pine. *Oecologia*, **197**, 939–956.

Breshears, D.D., Fontaine, J.B., Ruthrof, K.X., Field, J.P., Feng, X., Burger, J.R., Law, D.J., Kala, J. & Hardy, G.E.St.J. (2021) Underappreciated plant vulnerabilities to heat waves. *New Phytologist*, **231**, 32–39.

Buckley, T.N., John, G.P., Scoffoni, C. & Sack, L. (2017) The Sites of Evaporation within Leaves. *Plant Physiology*, **173**, 1763–1782.

Chen, J. & Lewis, O.T. (2023) Experimental heatwaves facilitate invasion and alter species interactions and composition in a tropical host-parasitoid community. *Global Change Biology*, **29**, 6261–6275.

Christenhusz, M. & Byng, J. (2016) The number of known plant species in the world and its annual increase. *Phytotaxa*, **261**, 201–217.

Cook, A.M., Rezende, E.L., Petrou, K. & Leigh, A. (2024) Beyond a single temperature threshold: Applying a cumulative thermal stress framework to plant heat tolerance. *Ecology Letters*, **27**, e14416.

Cope, O.L., Zehr, L.N., Agrawal, A.A. & Wetzel, W.C. (2023) The timing of heat waves has multiyear effects on milkweed and its insect community. *Ecology*, **104**, e3988.

Cox, D., Marchin, R.M., Ellsworth, D.S., Wujeska-Klause, A., Ossola, A., Crous, K.Y., Leishman, M.R., Rymer, P.D. & Tjoelker, M.G. (2025) Thermal Safety Margins and Peak Leaf Temperatures Predict Vulnerability of Diverse Plant Species to an Experimental Heatwave. *Plant, Cell & Environment*, **n/a**.

Craparo, A., Steppe, K., Van Asten, P.J.A., Laderach, P., Jassogne, L. & Grab, S. (2017) Application of thermography for monitoring stomatal conductance of *Coffea arabica* under different shading systems. *Science of The Total Environment*, **609**, 755–763.

Danzey, L.M., Briceño, V.F., Cook, A.M., Nicotra, A.B., Peyre, G., Rossetto, M., Yap, J.-Y.S. & Leigh, A. (2024) Environmental and Biogeographic Drivers behind Alpine Plant Thermal Tolerance and Genetic Variation. *Plants*, **13**, 1271.

Davies, M., Ecroyd, H., Robinson, S.A. & French, K. (2018) Stress in native grasses under ecologically relevant heat waves. *PLOS ONE*, **13**, e0204906.

Davy, R., Esau, I., Chernokulsky, A., Outten, S. & Zilitinkevich, S. (2017) Diurnal asymmetry to the observed global warming. *International Journal of Climatology*, **37**, 79–93.

De Boeck, H.J., Bassin, S., Verlinden, M., Zeiter, M. & Hiltbrunner, E. (2016) Simulated heat waves affected alpine grassland only in combination with drought. *New Phytologist*, **209**, 531–541.

De Boeck, H.J., Dreesen, F.E., Janssens, I.A. & Nijs, I. (2010) Climatic characteristics of heat waves and their simulation in plant experiments. *Global Change Biology*, **16**, 1992–2000.

Doughty, C.E., Keany, J.M., Wiebe, B.C., Rey-Sanchez, C., Carter, K.R., Middleby, K.B., Cheesman, A.W., Goulden, M.L., da Rocha, H.R., Miller, S.D., Malhi, Y., Fauset, S., Gloor, E., Slot, M., Oliveras Menor, I., Crous, K.Y., Goldsmith, G.R. & Fisher, J.B. (2023) Tropical forests are approaching critical temperature thresholds. *Nature*, **621**, 105–111.

Drake, J.E., Tjoelker, M.G., Vårhammar, A., Medlyn, B.E., Reich, P.B., Leigh, A., Pfautsch, S., Blackman, C.J., López, R., Aspinwall, M.J., Crous, K.Y., Duursma, R.A., Kumarathunge, D., De Kauwe, M.G., Jiang, M., Nicotra, A.B., Tissue, D.T., Choat, B., Atkin, O.K. & Barton, C.V.M. (2018) Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. *Global Change Biology*, **24**, 2390–2402.

Dreesen, F.E., De Boeck, H.J., Horemans, J.A., Janssens, I.A. & Nijs, I. (2015) Recovery dynamics and invasibility of herbaceous plant communities after exposure to experimental climate extremes. *Basic and Applied Ecology*, **16**, 583–591.

Dreesen, F.E., De Boeck, H.J., Janssens, I.A. & Nijs, I. (2012) Summer heat and drought extremes trigger unexpected changes in productivity of a temperate annual/biannual plant community. *Environmental and Experimental Botany*, **79**, 21–30.

Ettinger, A.K., Chuine, I., Cook, B.I., Dukes, J.S., Ellison, A.M., Johnston, M.R., Panetta, A.M., Rollinson, C.R., Vitasse, Y. & Wolkovich, E.M. (2019) How do climate change experiments alter plot-scale climate? *Ecology Letters*, **22**, 748–763.

Evans, M.E.K., Hu, J. & Michaletz, S.T. (2025) Scaling plant responses to heat: From molecules to the biosphere. *Science*, **388**, 1167–1173.

Falster, D., Gallagher, R., Wenk, E.H., Wright, I.J., Indiarto, D., Andrew, S.C., Baxter, C., Lawson, J., Allen, S., Fuchs, A., Monro, A., Kar, F., Adams, M.A., Ahrens, C.W., Alfonzetti, M., Angevin, T., Apgaua, D.M.G., Arndt, S., Atkin, O.K., Atkinson, J., Auld, T., Baker, A., von Balthazar, M., Bean, A., Blackman, C.J., Bloomfield, K., Bowman, D.M.J.S., Bragg, J., Brodribb, T.J., Buckton, G., Burrows, G., Caldwell, E., Camac, J., Carpenter, R., Catford, J.A., Cawthray, G.R., Cernusak, L.A., Chandler, G., Chapman, A.R., Cheal, D., Cheesman, A.W., Chen, S.-C., Choat, B., Clinton, B., Clode, P.L., Coleman, H., Cornwell, W.K., Cosgrove, M., Crisp, M., Cross, E., Crous, K.Y., Cunningham, S., Curran, T., Curtis, E., Daws, M.I., DeGabriel, J.L., Denton, M.D., Dong, N., Du, P., Duan, H., Duncan, D.H., Duncan, R.P., Duretto, M., Dwyer, J.M., Edwards, C., Esperon-Rodriguez, M., Evans, J.R., Everingham, S.E., Farrell, C., Firn, J., Fonseca, C.R., French, B.J., Frood, D., Funk, J.L., Geange, S.R., Ghannoum, O., Gleason, S.M., Gosper, C.R., Gray, E., Groom, P.K., Grootemaat, S., Gross, C., Guerin, G., Guja, L., Hahs, A.K., Harrison, M.T., Hayes, P.E., Henery, M., Hochuli, D., Howell, J., Huang, G., Hughes, L., Huisman, J., Ilic, J., Jagdish, A., Jin, D., Jordan, G., Jurado, E., Kanowski, J., Kasel, S., Kellermann, J., Kenny, B., Kohout, M., Kooyman, R.M., Kotowska, M.M., Lai, H.R., Laliberté, E., Lambers, H., Lamont, B.B., Lanfear, R., van Langevelde, F., Laughlin, D.C., Laugier-Kitchener, B.-A., Laurance, S., Lehmann, C.E.R., Leigh, A., Leishman, M.R., Lenz, T., Lepschi, B., Lewis, J.D., Lim, F., Liu, U., Lord, J., Lusk, C.H., Macinnis-Ng, C., McPherson, H., Magallón, S., Manea, A., López-Martinez, A., Mayfield, M., McCarthy, J.K., Meers, T., van der Merwe, M., Metcalfe, D.J., Milberg, P., Mokany, K., Moles, A.T., Moore, B.D., Moore, N., Morgan, J.W., Morris, W., Muir, A., Munroe, S., Nicholson, Á., Nicolle, D., Nicotra, A.B., Niinemets, Ü., North, T., O'Reilly-Nugent, A., O'Sullivan, O.S., Oberle, B., Onoda, Y., Ooi, M.K.J., Osborne, C.P., Paczkowska, G., Pekin, B., Guilherme Pereira, C., Pickering, C., Pickup, M., Pollock, L.J., Poot, P., Powell, J.R., Power, S.A., Prentice, I.C., Prior, L., Prober, S.M., Read, J., Reynolds, V., Richards, A.E., Richardson, B., Roderick, M.L., Rosell, J.A., Rossetto, M., Rye, B., Rymer, P.D., Sams, M.A., Sanson, G., Sauquet, H., Schmidt, S., Schönenberger, J., Schulze, E.-D., Sendall, K., Sinclair, S., Smith, B., Smith, R., Soper, F., Sparrow, B., Standish, R.J., Staples, T.L., Stephens, R., Szota, C., Taseski, G., Tasker, E., Thomas, F., Tissue, D.T., Tjoelker, M.G., Tng, D.Y.P., de Tombeur, F., Tomlinson, K., Turner, N.C., Veneklaas, E.J., Venn, S., Vesk, P., Vlasveld, C., Vorontsova, M.S., Warren, C.A., Warwick, N., Weerasinghe, L.K., Wells, J., Westoby, M., White, M., Williams, N.S.G., Wills, J., Wilson, P.G., Yates, C., Zanne, A.E., Zemunik, G. & Ziemińska, K. (2021) AusTraits, a curated plant trait database for the Australian flora. *Scientific Data*, **8**, 254.

Feeley, K., Martinez-Villa, J., Perez, T., Silva Duque, A., Triviño Gonzalez, D. & Duque, A. (2020) The Thermal Tolerances, Distributions, and Performances of Tropical Montane Tree Species. *Frontiers in Forests and Global Change*, **3**, 25.

Foo, Y.Z., O'Dea, R.E., Koricheva, J., Nakagawa, S. & Lagisz, M. (2021) A practical guide to question formation, systematic searching and study screening for literature reviews in ecology and evolution. *Methods in Ecology and Evolution*, **12**, 1705–1720.

Frei, E.R., Ghazoul, J., Matter, P., Heggli, M. & Pluess, A.R. (2014) Plant population differentiation and climate change: responses of grassland species along an elevational gradient. *Global Change Biology*, **20**, 441–455.

French, K., Jansens, I.B., Ashcroft, M.B., Ecroyd, H. & Robinson, S.A. (2019) High tolerance of repeated heatwaves in Australian native plants. *Austral Ecology*, **44**, 597–608.

French, K., Robinson, S.A. & Lia, J. (2017) Thermotolerance capacities of native and exotic coastal plants will lead to changes in species composition under increased heat waves. *Conservation Physiology*, **5**.

García-García, A., Cuesta-Valero, F.J., Miralles, D.G., Mahecha, M.D., Quaas, J., Reichstein, M., Zscheischler, J. & Peng, J. (2023) Soil heat extremes can outpace air temperature extremes. *Nature Climate Change*, **13**, 1237–1241.

Geange, S.R., Arnold, P.A., Catling, A.A., Coast, O., Cook, A.M., Gowland, K.M., Leigh, A., Notarnicola, R.F., Posch, B.C., Venn, S.E., Zhu, L. & Nicotra, A.B. (2021) The thermal tolerance of photosynthetic tissues: a global systematic review and agenda for future research. *New Phytologist*, **229**, 2497–2513.

Gemal, E.L., Green, T.G.A., Cary, S.C. & Colesie, C. (2022) High Resilience and Fast Acclimation Processes Allow the Antarctic Moss *Bryum argenteum* to Increase Its Carbon Gain in Warmer Growing Conditions. *Biology*, **11**, 1773.

Graae, B.J., Ejrnæs, R., Marchand, F.L., Milbau, A., Shevtsova, A., Beyens, L. & Nijs, I. (2009) The effect of an early-season short-term heat pulse on plant recruitment in the Arctic. *Polar Biology*, **32**, 1117–1126.

Grubb, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.

Harris, R.J., Alvarez, P.R., Bryant, C., Briceño, V.F., Cook, A.M., Leigh, A. & Nicotra, A.B. (2024) Acclimation of thermal tolerance in juvenile plants from three biomes is suppressed when extremes co-occur. *Conservation Physiology*, **12**, coae027.

Hassan, T., Gulzar, R., Hamid, M., Ahmad, R., Waza, S.A. & Khuroo, A.A. (2023) Plant phenology shifts under climate warming: a systematic review of recent scientific literature. *Environmental Monitoring and Assessment*, **196**, 36.

Hedhly, A. (2011) Sensitivity of flowering plant gametophytes to temperature fluctuations. *Environmental and Experimental Botany*, **74**, 9–16.

Iseki, K. & Olaleye, O. (2020) A new indicator of leaf stomatal conductance based on thermal imaging for field grown cowpea. *Plant Production Science*, **23**, 136–147.

Jagadish, S.V.K., Way, D.A. & Sharkey, T.D. (2021) Plant heat stress: Concepts directing future research. *Plant, Cell & Environment*, **44**, 1992–2005.

Jones, H.G. (2004) *Application of Thermal Imaging and Infrared Sensing in Plant Physiology and Ecophysiology*. *Advances in Botanical Research* Incorporating Advances in Plant Pathology., pp. 107–163. Academic Press.

Karitter, March Salas, M., Ensslin, A., Rauschkolb, R., Godefroid, S., Poorter, H. & Scheepens, J.F. (2023) *Garden, greenhouse or climate chamber? Experimental conditions influence whether genetic differences are phenotypically expressed*,.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., Alcázar C, C., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M.M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D.M.G., Ashman, T.-L., Asmara, D.H., Asner, G.P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W.J., Bakker, J.P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D.R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M.L., Berenguer, E., Bergamin, R., Bergmann, J., Bergmann Carlucci, M., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A.D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K.T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C.C.F., Bordin, K., Boughton, E.H., Boukili, V., Bowman, D.M.J.S., Bravo, S., Brendel, M.R., Broadley, M.R., Brown, K.A., Bruelheide, H., Brumnich, F., Bruun, H.H., Bruy, D., Buchanan, S.W., Bucher, S.F., Buchmann, N., Buitenwerf, R., Bunker, D.E., Bürger, J., Burrascano, S., Burslem, D.F.R.P., Butterfield, B.J., Byun, C., Marques, M., Scalon, M.C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J.J., Campany, C., Campetella, G., Campos, J.A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J.A., Cavender-Bares, J., Cerabolini, B.E.L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F.S., Chelli, S., Chen, S.-C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.-S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C.G., Conti, L., Coomes, D., Cornelissen, J.H.C., Cornwell, W.K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J.P.G.M., Csecserits, A., Cufar, K., Cuntz, M., da Silva, A.C., Dahlin, K.M., Dainese, M., Dalke, I., Dalle Fratte, M., Dang-Le, A.T., Danihelka, J., Dannoura, M., Dawson, S., de Beer, A.J., De Frutos, A., De Long, J.R., Dechant, B., Delagrange, S., Delpierre, N., Derroire, G., Dias, A.S., Diaz-Toribio, M.H., Dimitrakopoulos, P.G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R.L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M.B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T.F., Fagan, W.F., Fagúndez, J., Falster, D.S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T.J., Flynn, D.F.B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, M., Frank, D., Frenette-Dussault, C., Freschet, G.T., Fry, E.L., Fyllas, N.M., Mazzochini, G.G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J.L., de Gasper, A.L., Gea-Izquierdo, G., Gibson, D., Gillison, A.N., Giroldo, A., Glasenhardt, M.-C., Gleason, S., Gliesch, M., Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J.L., González-Melo, A., González-Robles, A., Graae, B.J., Granda, E., Graves, S., Green, W.A., Gregor, T., Gross, N., Guerin, G.R., Günther, A., Gutiérrez, A.G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S.P., Hattingh, W., Hawes, J.E., He, T., He, P., Heberling, J.M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A.-M., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A.L., Hirons, A., Hock, M., Hogan, J.A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K.A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C.M., Izquierdo, J., Jackson, R.B., Jackson, B., Jactel, H., Jagodzinski, A.M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J.R.P., Jiang, G.-F., Johansen, J.L., Johnson, D., Jokela, E.J., Joly, C.A., Jordan, G.J., Joseph, G.S., Junaedi, D., Junker, R.R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M.I., Kinlock, N.L., Kissling, W.D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J.M.H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N.J.B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.-P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D.J., Laughlin, D., Le Bagousse-Pinguet, Y., le Maire, G., le Roux, P.C., le Roux, E., Lee, T., Lens, F., Lewis, S.L., Lhotsky, B., Li, Y., Li, X., Lichstein, J.W., Liebergesell, M., Lim, J.Y., Lin, Y.-S., Linares, J.C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., López-García, Á., Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B.A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Maciel Rabelo Pereira, C., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A.C.M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T.J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M.L., McCulloh, K., McFadden, I.R., McGill, B.J., McPartland, M.Y., Medeiros, J.S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F.P.L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S.T., Michelaki, C., Migalina, S., Milla, R., Miller, J.E.D., Minden, V., Ming, R., Mokany, K., Moles, A.T., Molnár V, A., Molofsky, J., Molz, M., Montgomery, R.A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A.S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C.D., Müller, S.C., Munoz, F., Myers-Smith, I.H., Myster, R.W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, A.S., Neuschulz, E.L., Ni, J., Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Network, T.N., Nystuen, K.O., O’Grady, A., O’Hara, K., O’Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M.E., Onipchenko, V., Onoda, Y., Onstein, R.E., Ordonez, J.C., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G.E., Ozinga, W.A., Pahl, A.T., Paine, C.E.T., Pakeman, R.J., Papageorgiou, A.C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J.G., Peco, B., Penuelas, J., Perea, A., Peri, P.L., Petisco-Souza, A.C., Petraglia, A., Petritan, A.M., Phillips, O.L., Pierce, S., Pillar, V.D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A.S., Power, S.A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C.A., Reich, P.B., Reichstein, M., Reid, D.E.B., Réjou-Méchain, M., de Dios, V.R., Ribeiro, S., Richardson, S., Riibak, K., Rillig, M.C., Riviera, F., Robert, E.M.R., Roberts, S., Robroek, B., Roddy, A., Rodrigues, A.V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J.A., Rosenfield, M.F., Rossi, C., Roy, D.B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S.B., Rusch, G.M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A.C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J.V., Schowanek, S.D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Selaya Garvizu, G., Semchenko, M., Seymour, C., Sfair, J.C., Sharpe, J.M., Sheppard, C.S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T.A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N.G., Sodhi, D., Soltis, P., Soltis, D., Somers, B., Sonnier, G., Sørensen, M.V., Sosinski Jr, E.E., Soudzilovskaia, N.A., Souza, A.F., Spasojevic, M., Sperandii, M.G., Stan, A.B., Stegen, J., Steinbauer, K., Stephan, J.G., Sterck, F., Stojanovic, D.B., Strydom, T., Suarez, M.L., Svenning, J.-C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., te Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P.E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M.G., Tng, D.Y.P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J.M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J.L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., van Bodegom, P.M., van Breugel, M., Van Cleemput, E., van de Weg, M., van der Merwe, S., van der Plas, F., van der Sande, M.T., van Kleunen, M., Van Meerbeek, K., Vanderwel, M., Vanselow, K.A., Vårhammar, A., Varone, L., Vasquez Valderrama, M.Y., Vassilev, K., Vellend, M., Veneklaas, E.J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A.P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, J., Weber, U., Weedon, J.T., Wei, L., Weigelt, P., Weiher, E., Wells, A.W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P.J., Whitten, M., Williams, M., Winkler, D.E., Winter, K., Womack, C., Wright, I.J., Wright, S.J., Wright, J., Pinho, B.X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K.J., Zanne, A.E., Zelený, D., Zhao, Y.-P., Zheng, J., Zheng, J., Ziemińska, K., Zirbel, C.R., Zizka, G., Zo-Bi, I.C., Zotz, G. & Wirth, C. (2020) TRY plant trait database – enhanced coverage and open access. *Global Change Biology*, **26**, 119–188.

Lamalakshmi Devi, E., Kumar, S., Basanta Singh, T., Sharma, S.K., Beemrote, A., Devi, C.P., Chongtham, S.K., Singh, C.H., Yumlembam, R.A., Haribhushan, A., Prakash, N. & Wani, S.H. (2017) *Adaptation Strategies and Defence Mechanisms of Plants During Environmental Stress*. *Medicinal Plants and Environmental Challenges*, pp. 359–413. Springer, Cham.

Leigh, A., Sevanto, S., Close, J.D. & Nicotra, A.B. (2017) The influence of leaf size and shape on leaf thermal dynamics: does theory hold up under natural conditions?: Leaf size, shape and temperature. *Plant, Cell & Environment*, **40**, 237–248.

Lenoir, J., Gégout, J.-C., Pierrat, J.-C., Bontemps, J.-D. & Dhôte, J.-F. (2009) Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). *Ecography*, **32**, 765–777.

Li, L., Zheng, Z., Biederman, J.A., Qian, R., Ran, Q., Zhang, B., Xu, C., Wang, F., Zhou, S., Che, R., Dong, J., Xu, Z., Cui, X., Hao, Y. & Wang, Y. (2021) Drought and heat wave impacts on grassland carbon cycling across hierarchical levels. *Plant, Cell & Environment*, **44**, 2402–2413.

Liu, N., Qu, L., Tang, X., Yu, H., Zhang, Z., Wang, H., Shao, C. & Dong, G. (2023) Effects of Water Conditions and Heat Wave Frequency on the Photosynthetic Characteristics and Growth Rate of *Schima superba* Seedlings. *Linye Kexue/Scientia Silvae Sinicae*, **59**, 104–114.

Lloret, F., Peñuelas, J., Prieto, P., Llorens, L. & Estiarte, M. (2009) Plant community changes induced by experimental climate change: Seedling and adult species composition. *Perspectives in Plant Ecology, Evolution and Systematics*, **11**, 53–63.

Lohani, N., Singh, M.B. & Bhalla, P.L. (2020) High temperature susceptibility of sexual reproduction in crop plants. *Journal of Experimental Botany*, **71**, 555–568.

Lovett Doust, J. (1989) Plant reproductive strategies and resource allocation. *Trends in Ecology & Evolution*, **4**, 230–234.

Luukkonen, T., Persson, O. & Sivertsen, G. (1992) Understanding Patterns of International Scientific Collaboration. *Science Technology & Human Values*, **17**, 101–126.

Macias, D.S. & Redmond, M.D. (2025) Climate-warming alters resource allocation in unpredictable ways. *Trends in Ecology & Evolution*, **40**, 428–430.

Marchand, F.L., Mertens, S., Kockelbergh, F., Beyens, L. & Nijs, I. (2005) Performance of High Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biology*, **11**, 2078–2089.

Marchin, R.M., Backes, D., Ossola, A., Leishman, M.R., Tjoelker, M.G. & Ellsworth, D.S. (2022) Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species. *Global Change Biology*, **28**, 1133–1146.

McNutt, M.K., Bradford, M., Drazen, J.M., Hanson, B., Howard, B., Jamieson, K.H., Kiermer, V., Marcus, E., Pope, B.K., Schekman, R., Swaminathan, S., Stang, P.J. & Verma, I.M. (2018) Transparency in authors' contributions and responsibilities to promote integrity in scientific publication. *Proceedings of the National Academy of Sciences*, **115**, 2557–2560.

Monteith, J.L. (1990) *Principles of environmental physics*, 2nd ed / J.L. Monteith and M.H. Unsworth.. Edward Arnold, London.

Morgan, J.W. (2021) Overabundant native herbivore impacts on native plant communities in south-eastern Australia. *Ecological Management & Restoration*, **22**, 9–15.

Mu, X., Notarnicola, R., Arnold, P., Pollo, P. & Cornwell, W. (2024) Heatwave meta-analysis pre-registration. (https://doi.org/10.17605/OSF.IO/T95BJ).

Mukherjee, S. & Mishra, A.K. (2021) Increase in Compound Drought and Heatwaves in a Warming World. *Geophysical Research Letters*, **48**, e2020GL090617.

Nakagawa, S., Ivimey-Cook, E.R., Grainger, M.J., O'Dea, R.E., Burke, S., Drobniak, S.M., Gould, E., Macartney, E.L., Martinig, A.R., Morrison, K., Paquet, M., Pick, J.L., Pottier, P., Ricolfi, L., Wilkinson, D.P., Willcox, A., Williams, C., Wilson, L.A.B., Windecker, S.M., Yang, Y. & Lagisz, M. (2023) Method Reporting with Initials for Transparency (MeRIT) promotes more granularity and accountability for author contributions. *Nature Communications*, **14**, 1788.

Notarnicola, R.F., Nicotra, A.B., Kruuk, L.E.B. & Arnold, P.A. (2021) Tolerance of Warmer Temperatures Does Not Confer Resilience to Heatwaves in an Alpine Herb. *Frontiers in Ecology and Evolution*, **9**, 615119.

O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H., Gurevitch, J., Page, M.J., Stewart, G., Moher, D. & Nakagawa, S. (2021) Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biological Reviews*, **96**, 1695–1722.

Ooi, M.K.J. (2012) Seed bank persistence and climate change. *Seed Science Research*, **22**, S53–S60.

O'Sullivan, O.S., Heskel, M.A., Reich, P.B., Tjoelker, M.G., Weerasinghe, L.K., Penillard, A., Zhu, L., Egerton, J.J.G., Bloomfield, K.J., Creek, D., Bahar, N.H.A., Griffin, K.L., Hurry, V., Meir, P., Turnbull, M.H. & Atkin, O.K. (2017) Thermal limits of leaf metabolism across biomes. *Global Change Biolog*, **23**, 209–223.

Ouzzani, M., Hammady, H., Fedorowicz, Z. & Elmagarmid, A. (2016) Rayyan—a web and mobile app for systematic reviews. *Systematic Reviews*, **5**, 210.

Perez, T.M. & Feeley, K.J. (2020) Photosynthetic heat tolerances and extreme leaf temperatures. *Functional Ecology*, **34**, 2236–2245.

Perkins, S.E. & Alexander, L.V. (2013) On the Measurement of Heat Waves. *Journal of Climate*, **26**, 4500–4517.

Perkins-Kirkpatrick, S. & Lewis, S.C. (2020) Increasing trends in regional heatwaves. *Nature Communications*, **11**, 3357.

Poorter, H., Fiorani, F., Pieruschka, R., Wojciechowski, T., van der Putten, W.H., Kleyer, M., Schurr, U. & Postma, J. (2016) Pampered inside, pestered outside? Differences and similarities between plants growing in controlled conditions and in the field. *New Phytologist*, **212**, 838–855.

Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P. & Mommer, L. (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control: Tansley review. *New Phytologist*, **193**, 30–50.

Qian, D., Wang, M., Niu, Y., Yang, Y. & Xiang, Y. (2025) Sexual reproduction in plants under high temperature and drought stress. *Cell Reports*, **44**, 115390.

Qu, L., Dong, G., De Boeck, H.J., Tian, L., Chen, J., Tang, H., Xin, X., Chen, J., Hu, Y. & Shao, C. (2020) Joint forcing by heat waves and mowing poses a threat to grassland ecosystems: Evidence from a manipulative experiment. *Land Degradation & Development*, **31**, 785–800.

Raven, P.H., Gereau, R.E., Phillipson, P.B., Chatelain, C., Jenkins, C.N. & Ulloa Ulloa, C. (2020) The distribution of biodiversity richness in the tropics. *Science Advances*, **6**, eabc6228.

Reddy, P., Perkins-Kirkpatrick, S. & Sharples, J. (2021) Intensifying Australian Heatwave Trends and Their Sensitivity to Observational Data. *Earth's Future*, **9**.

Reich, P.B., Wright, I.J., Cavender-Bares, J., Craine, J.M., Oleksyn, J., Westoby, M. & Walters, M.B. (2003) The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies. *International Journal of Plant Sciences*, **164**, S143–S164.

Resentini, F., Orozco-Arroyo, G., Cucinotta, M. & Mendes, M.A. (2023) The impact of heat stress in plant reproduction. *Frontiers in Plant Science*, **14**.

Richardson, W.S., Wilson, M.C., Nishikawa, J. & Hayward, R.S.A. (1995) The well-built clinical question: a key to evidence-based decisions. *ACP Journal Club*, **123**, A12.

Schuepp, P.H. (1993) Tansley Review No. 59 Leaf boundary layers. *New Phytologist*, **125**, 477–507.

Sentinella, A.T., Warton, D.I., Sherwin, W.B., Offord, C.A. & Moles, A.T. (2020) Tropical plants do not have narrower temperature tolerances, but are more at risk from warming because they are close to their upper thermal limits. *Global Ecology and Biogeography*, **29**, 1387–1398.

Sklenář, P., Jaramillo, R., Wojtasiak, S.S., Meneses, R.I., Muriel, P. & Klimeš, A. (2023) Thermal tolerance of tropical and temperate alpine plants suggests that 'mountain passes are not higher in the tropics.' *Global Ecology and Biogeography*, **32**, 1073–1086.

Soudzilovskaia, N.A., Elumeeva, T.G., Onipchenko, V.G., Shidakov, I.I., Salpagarova, F.S., Khubiev, A.B., Tekeev, D.K. & Cornelissen, J.H.C. (2013) Functional traits predict relationship between plant abundance dynamic and long-term climate warming. *Proceedings of the National Academy of Sciences*, **110**, 18180–18184.

Speights, C.J., Wolff, C.L., Barton, M.E. & Barton, B.T. (2018) Why and How to Create Nighttime Warming Treatments for Ecological Field Experiments. *The Yale Journal of Biology and Medicine*, **91**, 471–480.

Steffen, W.L., Hughes, L. & Perkins, S. (2014) *Heatwaves: hotter, longer, more often*, Climate Council, Canberra.

Steinbauer, M.J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A.D., Breiner, F.T., Burg, S., Czortek, P., Dawes, M.A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V.A., Fernández-Arberas, O., Fossheim, K.F., Gómez-García, D., Georges, D., Grindrud, E.T., Haider, S., Haugum, S.V., Henriksen, H., Herreros, M.J., Jaroszewicz, B., Jaroszynska, F., Kanka, R., Kapfer, J., Klanderud, K., Kühn, I., Lamprecht, A., Matteodo, M., di Cella, U.M., Normand, S., Odland, A., Olsen, S.L., Palacio, S., Petey, M., Piscová, V., Sedlakova, B., Steinbauer, K., Stöckli, V., Svenning, J.-C., Teppa, G., Theurillat, J.-P., Vittoz, P., Woodin, S.J., Zimmermann, N.E. & Wipf, S. (2018) Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, **556**, 231–234.

Still, C., Powell, R., Aubrecht, D., Kim, Y., Helliker, B., Roberts, D., Richardson, A.D. & Goulden, M. (2019) Thermal imaging in plant and ecosystem ecology: applications and challenges. *Ecosphere*, **10**.

Taseski, G., Beloe, C., Gallagher, R., Chan, J., Dalrymple, R. & Cornwell, W. (2019) A global growth-form database for 143,616 vascular plant species. *Ecology*, **100**.

Taylor, A., Weigelt, P., Denelle, P., Cai, L. & Kreft, H. (2023) The contribution of plant life and growth forms to global gradients of vascular plant diversity. *New Phytologist*, **240**, 1548–1560.

Thakur, M.P., Risch, A.C. & van der Putten, W.H. (2022) Biotic responses to climate extremes in terrestrial ecosystems. *iScience*, **25**, 104559.

Trancoso, R., Syktus, J., Toombs, N., Ahrens, D., Wong, K.K.-H. & Pozza, R.D. (2020) Heatwaves intensification in Australia: A consistent trajectory across past, present and future. *Science of The Total Environment*, **742**, 140521.

Trivedi, P., Batista, B.D., Bazany, K.E. & Singh, B.K. (2022) Plant–microbiome interactions under a changing world: responses, consequences and perspectives. *New Phytologist*, **234**, 1951–1959.

Trotta, G., Vuerich, M., Petrussa, E., Hay, F.R., Assolari, S. & Boscutti, F. (2023) Germination performance of alien and native species could shape community assembly of temperate grasslands under different temperature scenarios. *Plant Ecology*, **224**, 1097–1111.

Tushabe, D., Altmann, F., Koehler, E., Woods, S. & Rosbakh, S. (2023) Negative effects of high-temperature stress on gametophyte performance and their consequences for seed reproduction in wild plants. *Environmental and Experimental Botany*, **216**.

Ummenhofer, C.C. & Meehl, G.A. (2017) Extreme weather and climate events with ecological relevance: a review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **372**, 20160135.

Urban, M.C. (2015) Accelerating extinction risk from climate change. *Science*, **348**, 571–573.

Vose, R.S., Easterling, D.R. & Gleason, B. (2005) Maximum and minimum temperature trends for the globe: An update through 2004. *Geophysical Research Letters*, **32**, L23822.

Wahid, A., Gelani, S., Ashraf, M. & Foolad, M. (2007) Heat tolerance in plants: An overview. *Environmental and Experimental Botany*, **61**, 199–223.

Wang, D., Heckathorn, S.A., Mainali, K. & Tripathee, R. (2016) Timing Effects of Heat-Stress on Plant Ecophysiological Characteristics and Growth. *Frontiers in Plant Science*, **7**, 1629.

Wu, S., Luo, M., Zhao, R., Li, J., Sun, P., Liu, Z., Wang, X., Wang, P. & Zhang, H. (2023) Local mechanisms for global daytime, nighttime, and compound heatwaves. *npj Climate and Atmospheric Science*, **6**, 36.

Yu, H., Tang, X., Liu, N., Wang, H., Zhang, Z., Shao, C., Dong, G. & Qu, L. (2023) Influences of multiple successive heat waves combined with water control and supplement on photosynthetic characteristics and growth rate of *Phoebe bournei* seedlings. *Shengtai Xuebao*, **43**, 3224–3235.

Zhao, J., Lu, Z., Wang, L. & Jin, B. (2020) Plant Responses to Heat Stress: Physiology, Transcription, Noncoding RNAs, and Epigenetics. *International Journal of Molecular Sciences*, **22**, 117.

Zhou, X.-H., Li, J.-J., Gao, Y.-Y., Peng, P.-H. & He, W.-M. (2022) Maternal effects of climate warming and nitrogen deposition vary with home and introduced ranges. *Functional Ecology*, **36**, 751–762.

Zhu, L. (2017) Thermal plasticity of leaf energy metabolism: ecological, physiological and biochemical linkages.

Zhu, L., Bloomfield, K.J., Hocart, C.H., Egerton, J.J.G., O'Sullivan, O.S., Penillard, A., Weerasinghe, L.K. & Atkin, O.K. (2018) Plasticity of photosynthetic heat tolerance in plants adapted to thermally contrasting biomes. *Plant, Cell & Environment*, **41**, 1251–1262.

Zhu, L., Scafaro, A.P., Vierling, E., Ball, M.C., Posch, B.C., Stock, F. & Atkin, O.K. (2024) Heat tolerance of a tropical–subtropical rainforest tree species *Polyscias elegans*: time-dependent dynamic responses of physiological thermostability and biochemistry. *New Phytologist*, **241**, 715–731.

Zvereva, E.L. & Kozlov, M.V. (2021) Biases in ecological research: attitudes of scientists and ways of control. *Scientific Reports*, **11**, 226.

Supplementary figures

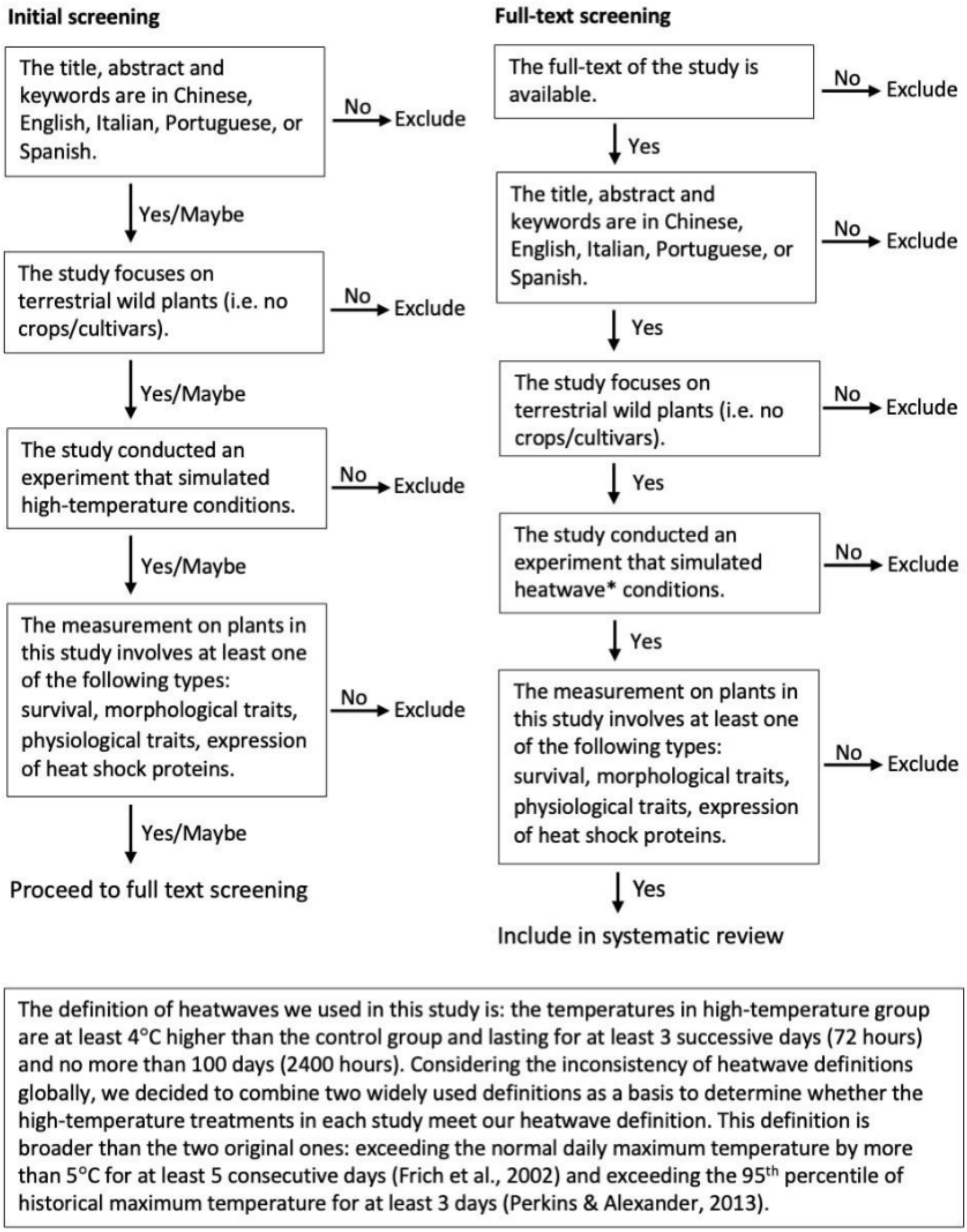


Figure S1. Decision tree used for literature screening. The initial screening was based on the title, abstract, and keywords of retrieved studies, while the full-text screening was based on the full content of studies that had passed the initial screening.

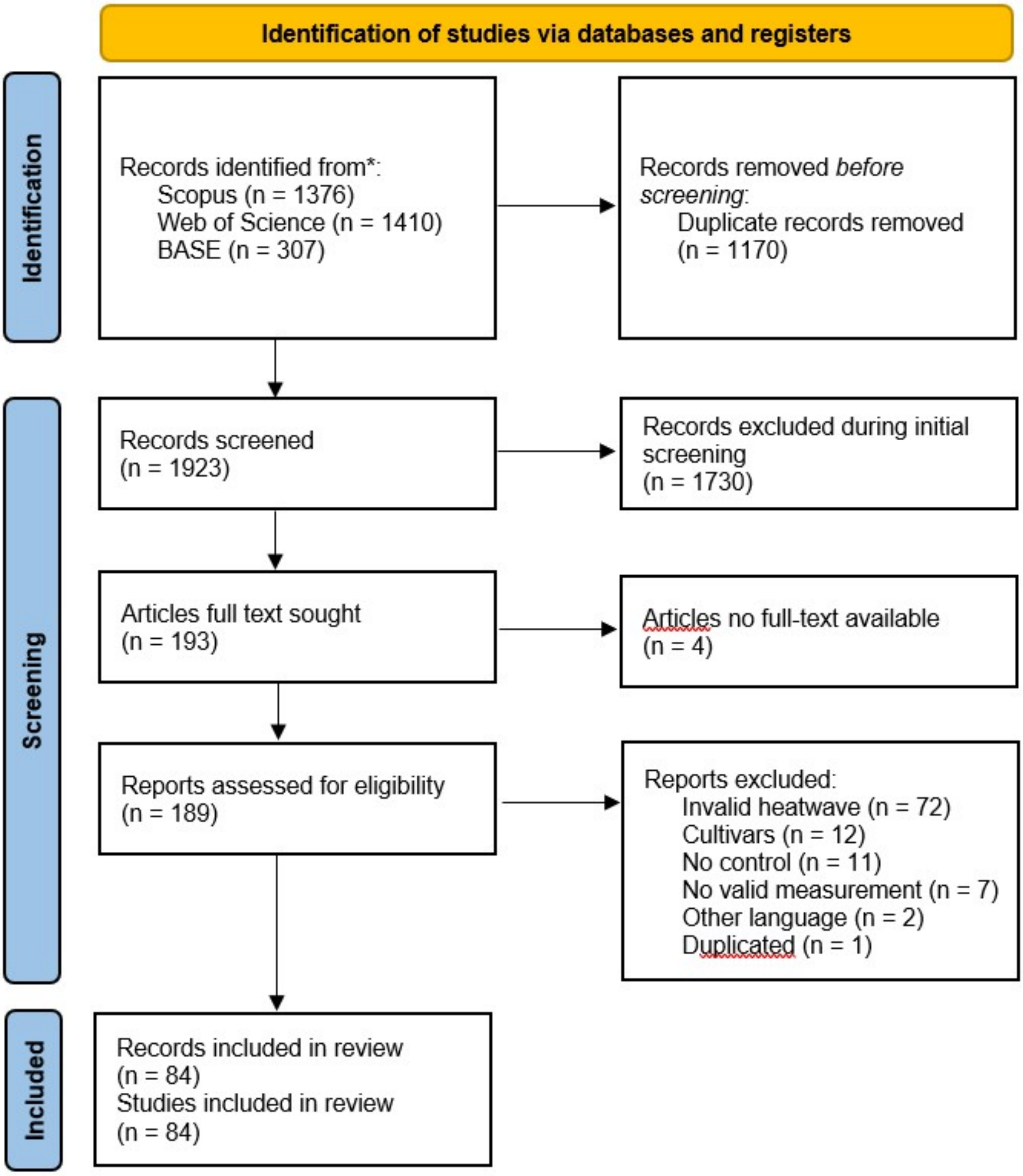


Figure S2. PRISMA flow diagram of the screening process.

Supplementary tables

Table S1. Strings used to search the literature.

Source	Search strings
Scopus	(heatwave* OR (heat w/1 wave*)) AND (tree* OR shrub* OR grass* OR herb* OR forb* OR vein* OR graminoid* OR monocot* OR veget* OR plant* OR sapling* OR seed*) AND (*physiolog* OR *morpholog* OR function* OR “shock protein*” OR “HSP*” OR fluorescence OR “Fv/Fm” OR senesc* OR product* OR phytomass OR biomass OR height* OR (stomata* AND conductance) OR defen* OR weight OR size OR growth OR hydraulic* OR photosynt* OR “photosystem II” OR “PSII” OR transpira* OR evapora* OR evapotranspira* OR surviv* OR mortal*) AND NOT (crop* OR “phylogenetic tree*” OR marine OR kelp OR seagrass OR "power plant*")
Web of Science (Core collection)	(heatwave* OR (heat NEAR/1 wave*)) AND (tree* OR shrub* OR grass* OR herb* OR forb* OR vein* OR graminoid* OR monocot* OR veget* OR plant* OR sapling* OR seed*) AND

	(*physiolog* OR *morpholog* OR function* OR “shock protein*” OR “HSP*” OR fluorescence OR “Fv/Fm” OR senesc* OR product* OR phytomass OR biomass OR height* OR (stomata* AND conductance) OR defen* OR weight OR size OR growth OR hydraulic* OR photosynt* OR “photosystem II” OR “PSII” OR transpira* OR evapora* OR evapotranspira* surviv* OR mortal*) NOT (crop* OR (phylogenetic NEAR/0 tree) OR marine OR kelp OR seagrass OR "power plant*")
BASE	(“heat wave” OR “heat waves” OR heatwave*) AND (tree* OR shrub* OR *grass* OR herb* OR forb* OR vein* OR graminoid* OR monocot* OR veget* OR plant* OR sapling* OR seed*) AND (*physiolog* OR *morpholog* OR function* OR “shock protein” OR “shock proteins” OR HSP* OR fluorescence OR “Fv/Fm” OR senesc* OR product* OR phytomass OR biomass OR height* OR “stomatal conductance” OR defen* OR weight OR size OR growth OR hydraulic* OR photosynt* OR “photosystem II” OR “PSII” OR transpira* OR evapora* OR evapotranspira* OR surviv* OR mortal*) NOT (“phylogenetic tree” OR “phylogenetic trees” OR crop* OR marine OR kelp OR seagrass OR “power plant” OR “power plants”) doctype:18*

Google Scholar	**English** (“heat wave” OR “heat waves” OR heatwave) AND (tree OR shrub OR grass OR herb OR plant OR sapling OR seed) AND (physiology OR physiological OR morphology OR morphological OR function OR “shock protein” OR “shock proteins” OR fluorescence OR senescence OR product OR phytomass OR biomass OR height OR “stomatal conductance” OR defense OR defence OR weight OR size OR growth OR hydraulic OR photosynthesis OR photosynthetic OR “photosystem II” OR transpiration OR evaporation OR evapotranspiration OR surviv* OR mortal*) NOT (“phylogenetic tree” OR “phylogenetic trees” OR crop OR marine OR kelp OR seagrass OR “power plant” OR “power plants”)
	Italian (“ondata di caldo” OR “ondate di caldo” OR “onda di calore” OR “onde di calore”) AND (albero OR alberi OR arbusto OR arbusti OR cespuglio OR cespugli OR macchia OR erba OR erbe OR pianta OR piante OR alberello OR virgulto OR piantina OR piantine OR germoglio OR germogli OR pianticella OR pianticelle)

AND

(fisiologia OR fisiologico OR morfologia OR morfologico OR funzione OR “proteina da shock” OR “proteine da shock” OR fluorescenza OR senescenza OR prodotto OR fitomassa OR biomassa OR altezza OR “conduttività stomatica” OR difesa OR peso OR massa OR dimensione OR altezza OR crescita OR idraulico OR fotosintesi OR fotosintetico OR “fotosistema II” OR traspirazione OR evaporazione OR evapotraspirazione OR sopravvivenza OR mortalità)

NOT

(“albero filogenetico” OR “alberi filogenetici” OR coltura OR coltivazione OR marino OR marine OR marini OR alga OR alghe OR “centrale elettrica” OR “centrali elettriche” OR “gruppo elettrogeno” OR “gruppi elettrogeni”

Portuguese

(“onda de calor” OR “ondas de calor”)

AND

(árvore OR arbusto OR grama OR erva OR planta OR muda OR semente)

AND

(fisiologia OR fisiológico OR fisiológica OR morfologia OR morfológico OR morfológica OR função OR “proteína de choque” OU “proteínas de choque” OU fluorescência OU senescência OU produto OU fitomassa OU biomassa OU altura OU “condutância estomática” OR defesa OR peso OR tamanho OR crescimento OR hidráulico OR fotossíntese OR

	fotossintético OR “fotossistema II” OR transpiração OR evaporação OR evapotranspiração) NOT (“árvore filogenética” OU “árvores filogenéticas” OU marinho OU alga OU “usina de energia” OU “usinas de energia”)
	<u>Simplified and Traditional Chinese</u> (热浪 OR 熱浪) AND (树 OR 樹 OR 木 OR 灌木 OR 草 OR 植物 OR 苗 OR 芽) AND (生理 OR 生理的 OR 形态 OR 形態 OR 形态的 OR 形態的 OR 功能 OR 休克蛋白 OR 荧光 OR 螢光 OR 衰老 OR 生产 OR 生產 OR 产物 OR 產物 OR 植物量 OR 生物量 OR 高度 OR 气孔导度 OR 氣孔導度 OR 防御 OR 防禦 OR 重量 OR 尺寸 OR 大小 OR 生长 OR 生長 OR 液压 OR 液壓 OR 光合作用 OR 光系统 II OR 光系統 II OR 光系統 II OR 蒸腾作用 OR 蒸騰作用 OR 蒸发 OR 蒸發 OR 蒸散量 OR 生存率 OR 存活率 OR 死亡率) NOT (系统发育树 OR 系統發育樹 OR 庄稼 OR 莊稼 OR 作物 OR 海洋 OR 海藻 OR 海草 OR 发电厂 OR 發電廠)

Table S2. Overview of heatwave simulation approaches in field experiments. NA indicates that no relevant device/factors were involved in the study.

Active heater	Passive heater	Growth form	Interactive factor	Working environment	Literature
air heater	open top chamber (OTC)	woody	drought	subtropical	Liu et al., 2023
	open	woody	NA	subtropical	Qu et al., 2020a
	open	herbaceous	mowing	semiarid	Qu et al., 2020b
	open	herbaceous	NA	oak-savannah glacial sand ecosystem	Wang et al., 2008
	open	woody	NA	subtropical	Yu, 2023
	open	herbaceous	NA	mesic tall-grass prairies	Mainali et al., 2014
	closed top chamber (closed)	woody	CO2; drought	whitehall Forest	Bauweraerts et al., 2014a
	closed	woody	CO2	whitehall Forest	Ameye et al., 2012; Bauweraerts et al., 2014b, 2013
	NA	herbaceous	irrigation frequency	managed pasture	Langworthy et al., 2020
irradiation lamp	closed	herbaceous	drought	tallgrass prairie; mid-continent	Hoover et al., 2014
	closed	herbaceous; woody	NA	Arctic tundra	Marchand et al., 2005b
	NA	herbaceous	drought	temperate	Dreesen et al., 2012
	NA	herbaceous	heated rhizosphere soil	restored service road	Rubin et al., 2018
	NA	herbaceous	drought	tallgrass prairie ecosystem	Hoffman et al., 2018
	NA	woody	drought; heavy rainfall	experimental tree nursery	Noh et al., 2021;
	NA	herbaceous	drought; heavy rainfall	temperate	Dreesen et al., 2015b
	NA	woody	NA	European grasslands	Van Peer et al., 2004
	NA	woody	drought	semiarid steppe	Li et al., 2021b

	NA	herbaceous	mowing	subalpine grassland	Benot et al., 2014
	NA	herbaceous	NA	arctic tundra	Graae et al., 2009b
	NA	herbaceous	Mowing	subalpine grasslands	Benot et al., 2013
Others	closed	woody	NA	woodland	Drake et al., 2018
	closed	woody	growth temperature	woodland	Dhami et al., 2020
	closed	herbaceous	NA	Antarctica; coastline	Gemal et al., 2022
	open	herbaceous	herbivory	recently tilled old field	Cope et al., 2023

Appendix 1 – Changes from pre-registration

- We initially planned to conduct a meta-analysis using the studies reviewed, but we decided to perform only qualitative analyses (i.e. systematic review only).
- We initially defined heatwaves as periods when temperatures in the high-temperature group were at least 5 °C higher than the control group, lasting for at least three consecutive days (72 hours) and no more than fifteen days (360 hours) to screen papers. However, we later adopted a broader definition, requiring temperatures in the high-temperature group to be at least 4 °C higher than the control group, lasting for at least three consecutive days (72 hours) and up to 100 days (2400 hours).
- We initially planned to classify plants into detailed growth forms (i.e. tree, shrub, herb/forb, graminoid, liana, vine, succulent, moss, liverwort, other), but later adopted broader categories (woody and herbaceous) using the R package *growthform*.
- We initially planned to record the plant organ from which measurements were taken, but later decided not to include this variable.
- We initially planned to categorize *temperature_transition_type* into two levels (‘ramping transition’ and ‘transient transition’), but later expanded it into five levels: ‘Constant’, ‘Day & night control’, ‘Sustained shifting’, ‘Day control only’, and ‘Random fluctuation’.
- Because we decided to conduct only a systematic review, variables initially planned for the meta-analysis were excluded from data collection (e.g., variables that would have required extraction from figures).

Appendix 2 – List of studies included in the review. Studies marked in red were excluded in R, with reasons provided in Supporting Information SI2 (full-text screening decisions)

1. Duarte et al. (2016). Immediate and potential long-term effects of consecutive heat waves on the photosynthetic performance and water balance in Douglas-fir. Journal of Plant Physiology. 10.1016/j.jplph.2016.08.012

2. Lopez-Hidalgo et al. (2023). Untargeted metabolomics revealed essential biochemical rearrangements towards combined heat and drought stress acclimatization in *Pinus pinaster*. Environmental and Experimental Botany. 10.1016/j.envexpbot.2023.105261

3. Resco de Dios et al. (2018). Effects of a Heat Wave on Nocturnal Stomatal Conductance in *Eucalyptus camaldulensis*. Forests. 10.3390/f9060319

4. Anita Wesolowski (2017). The effects of drought, heat and elevated atmospheric CO2 on physiology and growth of *Eucalyptus* – Does climate-of-origin matter?. PhD thesis, Western Sydney University, Sydney

5. Liu et al. (2023). Effects of water conditions and heat wave frequency on the photosynthetic characteristics and growth rate of *Schima superba* seedlings. Scientia Silvae Sinicae. 10.11707/j.1001-7488.LYKX20210944

6. Dakhiya et al. (2023). The importance of the circadian system for adaptation to heat wave stress in wild barley (*Hordeum spontaneum*). Environmental and Experimental Botany. 10.1016/j.envexpbot.2022.105152

7. Mainali et al. (2014). Impact of a short-term heat event on C and N relations in shoots vs. roots of the stress-tolerant C4 grass, *Andropogon gerardii*. Journal of Plant Physiology. 10.1016/j.jplph.2014.04.006

8. R. Lalor et al. (2023). Mortality thresholds of juvenile trees to drought and heatwaves: implications for forest regeneration across a landscape gradient. Frontiers in Forests and Global Change. 10.3389/ffgc.2023.1198156

9. Andrew et al. (2024). Expression–environment associations in transcriptomic heat stress responses for a global plant lineage. Molecular Ecology. 10.1111/mec.17473

10. Marchin et al. (2020). A Simple Method for Simulating Drought Effects on Plants. Frontiers in Plant Science. 10.3389/fpls.2019.01715

11. Birami et al. (2018). Heat Waves Alter Carbon Allocation and Increase Mortality of Aleppo Pine Under Dry Conditions. Frontiers in Forests and Global Change. 10.3389/ffgc.2018.00008

12. Harris et al. (2024). Acclimation of thermal tolerance in juvenile plants from three biomes is suppressed when extremes co-occur. Conservation Physiology. 10.1093/conphys/coae027

13. Loik et al. (2017). Relationships between climate of origin and photosynthetic responses to an episodic heatwave depend on growth CO_2 concentration for *Eucalyptus camaldulensis* var. *camaldulensis*. Functional Plant Biology. https://doi.org/10.1071/FP17077

14. Rehschuh et al. (2021). Diverging responses of water and carbon relations during and after heat and hot drought stress in *Pinus sylvestris*. Tree Physiology. https://doi.org/10.1093/treephys/tpab141

15. Dreesen et al. (2012). Summer heat and drought extremes trigger unexpected changes in productivity of a temperate annual/biannual plant community. Environmental and Experimental Botany. 10.1016/j.envexpbot.2012.01.005

16. O'Connell et al. (2023). Heatwaves do not limit recovery following defoliation but alter leaf drought tolerance traits. Plant, Cell & Environment. 10.1111/pce.14750

17. Qu et al. (2018). Joint forcing by heat waves and mowing poses a threat to grassland ecosystems: Evidence from a manipulative experiment. Land Degradation & Development. 10.1002/ldr.3483

18. Aspinwall (2018). Range size and growth temperature influence *Eucalyptus* species responses to an experimental heatwave. Global Change Biology. 10.1111/gcb.14590

19. Dhami et al. (2020). An extreme heatwave enhanced the xanthophyll de-epoxidation state in leaves of *Eucalyptus* trees grown in the field. Physiology and Molecular Biology of Plants. 10.1007/s12298-019-00729-6

20. Young et al. (2022). Heatwave implications for the future of longleaf pine savanna understory restoration. Plant Ecology. 10.1007/s11258-021-01212-7

21. Birami et al. (2021). Heatwave frequency and seedling death alter stress-specific emissions of volatile organic compounds in Aleppo pine. Oecologia. 10.1007/s00442-021-04905-y

22. Langworthy et al. (2020). Can irrigating more frequently mitigate detrimental heat wave effects on perennial ryegrass growth and persistence?. Agricultural and Forest Meteorology. doi.org/10.1016/j.agrformet.2020.108074

23. Guha et al. (2018). Differential ecophysiological responses and resilience to heat wave events in four co-occurring temperate tree species. Environmental Research Letters. doi.org/10.1088/1748-9326/aabcd8

24. French et al. (2019). High tolerance of repeated heatwaves in Australian native plants. Austral Ecology. 10.1111/aec.12700

25. Jansen et al. (2014). Douglas-Fir Seedlings Exhibit Metabolic Responses to Increased Temperature and Atmospheric Drought. PLOS One. 10.1371/journal.pone.0114165

26. Dorado et al. (2023). Heat stress and recovery effects on the physiology and biochemistry of *Castanea sativa* Mill. Frontiers in Forests and Global Change. 10.3389/ffgc.2022.1072661

27. Gemal et al. (2022). High Resilience and Fast Acclimation Processes Allow the Antarctic Moss *Bryum argenteum* to Increase Its Carbon Gain in Warmer Growing Conditions. Biology. 10.3390/biology11121773

28. Rubin et al. (2018). Developing climate-smart restoration: can plant microbiomes be hardened against heat waves?. Ecological Applications. 10.1002/eap.1763

29. Qu et al. (2020). Diverging Responses of Two Subtropical Tree Species (*Schima superba* and *Cunninghamia lanceolata*) to Heat Waves. Forests. 10.3390/f11050513

30. Hoffman et al. (2018). Codominant grasses differ in gene expression under experimental climate extremes in native tallgrass prairie. PeerJ. 10.7717/peerj.4394

31. Zhu et al. (2023). Heat tolerance of a tropical–subtropical rainforest tree species *Polyscias elegans*: time-dependent dynamic responses of physiological thermostability and biochemistry. New Phytologist. 10.1111/nph.19356

32. Field et al. (2024). Soil amendment mitigates mortality from drought and heat waves in dryland tree juveniles. Frontiers in Forests and Global Change. 10.3389/gc.2024.1215051

33. Tushabe et al. (2023). Negative effects of high-temperature stress on gametophyte performance and their consequences for seed reproduction in wild plants. Environmental and Experimental Botany. 10.1016/j.envexpbot.2023.105532

34. Hoover et al. (2014). Contrasting sensitivities of two dominant C4 grasses to heat waves and drought. Plant Ecology. 10.1007/s11258-014-0345-8

35. Alvarez et al. (2023). Impact of extreme heatwaves and life-history traits on seed germination responses in Cumberland Plain Woodland native plant species. Australian Journal of Botany. 10.1071/BT22117

36. Noh et al. (2021). Early Growth Responses of *Larix kaempferi* (Lamb.) Carr. Seedling to Short-Term Extreme Climate Events in Summer. Forests. 10.3390/f12111595

37. Dreesen et al. (2015). Recovery dynamics and invasibility of herbaceous plant communities after exposure to experimental climate extremes. Basic and Applied Ecology. 10.1016/j.baae.2015.05.002

38. Wang et al. (2008). Effects of N on Plant Response to Heat-wave: A Field Study with Prairie Vegetation. Journal of Integrative Plant Biology. 10.1111/j.1744-7909.2008.00748.x

39. Tian et al. (2022). Heat wave event facilitates defensive responses in invasive C3 plant *Ambrosia artemisiifolia* L. under elevated CO2 concentration to the detriment of *Ophraella communa*. Frontiers in Plant Science. 10.3389/fpls.2022.907764

40. Gerdol et al. (2011). Response to heat stress of populations of two *Sphagnum* species from alpine bogs at different altitudes. Environmental and Experimental Botany. 10.1016/j.envexpbot.2011.04.010

41. Ameye et al. (2012). The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO2 atmospheres. New Phytologist. 10.1111/j.1469-8137.2012.04267.x

42. Lopez-Goldar et al. (2024). Heat waves induce milkweed resistance to a specialist herbivore via increased toxicity and reduced nutrient content. Plant, Cell & Environment. 10.1111/pce.15040

43. Maher et al. (2018). Evidence from the proteome for local adaptation to extreme heat in a widespread tree species. Functional Ecology. 10.1111/1365-2435.13260

44. Van Peer et al. (2004). Species richness and susceptibility to heat and drought extremes in synthesized grassland ecosystems: compositional vs physiological effects. Functional Ecology. 10.1111/j.0269-8463.2004.00901.x

45. Quist et al. (2020). Soil predator loss alters aboveground stoichiometry in a native but not in a related range-expanding plant when exposed to periodic heat waves. Soil Biology and Biochemistry. 10.1016/j.soilbio.2020.107999

46. Rehschuh et al. (2021). Tree allocation dynamics beyond heat and hot drought stress reveal changes in carbon storage, belowground translocation and growth. New Phytologist. 10.1111/nph.17815

47. Bauweraerts et al. (2014). Water availability is the decisive factor for the growth of two tree species in the occurrence of consecutive heat waves. Agricultural and Forest Meteorology. 10.1016/j.agrformet.2014.01.001

48. Dorado et al. (2022). Assessing heat stress tolerance in *Castanea sativa*. Forestry. 10.1093/forestry/cpac021

49. Lingling Zhu (2017). Thermal plasticity of leaf energy metabolism: ecological, physiological and biochemical linkages. PhD thesis, Australian National University, Canberra

50. Anthea Challis (2020). Genetic adaptation and phenotypic plasticity influence trait expression under heatwave and water deficit conditions in the foundation tree, *Corymbia calophylla.* Thesis. PhD thesis, Western Sydney University, Sydney

51. Werner et al. (2020). Heat Waves Change Plant Carbon Allocation Among Primary and Secondary Metabolism Altering CO2 Assimilation, Respiration, and VOC Emissions. Frontiers in Plant Science. 10.3389/fpls.2020.01242

52. Perez-Romero et al. (2018). Impact of short-term extreme temperature events on physiological performance of *Salicornia ramosissima* J. Woods under optimal and sub-optimal saline conditions. Scientific Reports. 10.1038/s41598-018-37346-4

53. Wang et al. (2008). Effects of N on Plant Response to Heat-wave: A Field Study with Prairie Vegetation. Journal of Integrative Plant Biology. 10.1111/j.1744-7909.2008.00748.x

54. Davies et al. (2018). Stress in native grasses under ecologically relevant heat waves. PLOS ONE. 10.1371/journal.pone.0204906

55. Matías et al. (2014). Larger investment in roots in southern range-edge populations of Scots pine is associated with increased growth and seedling resistance to extreme drought in response to simulated climate change. Environmental and Experimental Botany. 10.1016/j.envexpbot.2014.04.003

56. Perez-Romero et al. (2020). *Sarcocornia fruticosa* photosynthetic response to short-term extreme temperature events in combination with optimal and sub-optimal salinity concentrations. Plant Physiology and Biochemistry. 10.1016/j.plaphy.2019.12.026

57. Li et al. (2020). Drought and heat wave impacts on grassland carbon cycling across hierarchical levels. Plant, Cell & Environment. 10.1111/pce.13767

58. Ruehr et al. (2015). Water availability as dominant control of heat stress responses in two contrasting tree species. Tree Physiology. 10.1093/treephys/tpv102

59. Marchand et al. (2005). Performance of High Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. Global Change Biology. 10.1111/j.1365-2486.2005.01046.x

60. French et al. (2017). Thermotolerance capacities of native and exotic coastal plants will lead to changes in species composition under increased heat waves. Conservation Physiology. 10.1093/conphys/cox029

61. Bamberger et al. (2017). Isoprene emission and photosynthesis during heatwaves and drought in black locust. Biogeosciences. 10.5194/bg-14-3649-2017

62. Wujeska-Klause et al. (2015). Responses to heatwaves of gas exchange, chlorophyll fluorescence and antioxidants ascorbic acid and glutathione in congeneric pairs of *Acacia* and *Eucalyptus* species from relatively cooler and warmer climates. Trees. 10.1007/s00468-015-1274-4

63. Andrew et al. (2022). Consistently high heat tolerance acclimation in response to a simulated heatwave across species from the broadly distributed *Acacia* genus. Functional Plant Biology. 10.1016/j.soilbio.2020.107999

64. Marchin et al. (2021). Extreme heat increases stomatal conductance and drought-induced mortality risk in vulnerable plant species. Global Change Biology. 10.1111/gcb.15976

65. Cope et al. (2023). The timing of heat waves has multiyear effects on milkweed and its insect community. Ecology. 10.1002/ecy.3988

66. Gagne et al. (2020). Limited physiological acclimation to recurrent heatwaves in two boreal tree species. Tree Physiology. 10.1093/treephys/tpaa102

67. Cerasoli et al. (2014). Poplar saplings exposed to recurring temperature shifts of different amplitude exhibit differences in leaf gas exchange and growth despite equal mean temperature. AoB Plants. 10.1093/aobpla/plu018

68. Milbau et al. (2005). Ecophysiological and morphological parameters related to survival in grass species exposed to an extreme climatic event. Physiologia Plantarum. 10.1111/j.1399-3054.2005.00586.x

69. Drake et al. (2017). Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. Global Change Biology. 10.1111/gcb.14037

70. Benot et al. (2014). Stronger Short-Term Effects of Mowing Than Extreme Summer Weather on a Subalpine Grassland. Ecosystems. 10.1007/s10021-013-9734-4

71. Padje et al. (2021). Quantifying Nutrient Trade in the Arbuscular Mycorrhizal Symbiosis Under Extreme Weather Events Using Quantum-Dot Tagged Phosphorus. Frontiers in Ecology and Evolution. 10.3389/fevo.2021.613119

72. Genavee Georgeia Rhodes (2024). Physiological responses of three native plants to drought and heatwave. PhD thesis, The University of Auckland, Auckland

73. Dorado et al. (2023). Warming Scenarios and *Phytophthora cinnamomi* Infection in Chestnut (*Castanea sativa* Mill.). Plants. 10.3390/plants12030556

74. Gong et al. (2023). Sand dune shrub species prioritize hydraulic integrity over transpirational cooling during an experimental heatwave. Agricultural and Forest Meteorology. 10.1016/j.agrformet.2023.109483

75. Bauweraerts et al. (2014). Acclimation effects of heat waves and elevated [CO2] on gas exchange and chlorophyll fluorescence of northern red oak (*Quercus rubra* L.) seedlings. Plant Ecology. 10.1007/s11258-014-0352-9

76. Ahrens et al. (2021). Repeated extreme heatwaves result in higher leaf thermal tolerances and greater safety margins. New Phytologist. 10.1111/nph.17640

77. Bauweraerts et al. (2013). The effect of heat waves, elevated [CO2] and low soil water availability on northern red oak (*Quercus rubra* L.) seedlings. Global Change Biology. 10.1111/gcb.12044

78. Diana Backes (2022). The biogeography of plant heat tolerance and vulnerability to heatwaves (Thesis Chapter 4). PhD thesis, Western Sydney University, Sydney

79. Twala et al. (2022). The effects of heat and drought stress on the ecophysiological responses and growth of *Afrocarpus falcatus* and *Podocarpus henkelii* seedlings. South African Journal of Botany. 10.1016/j.sajb.2022.06.011

80. Notarnicola et al. (2021). Tolerance of Warmer Temperatures Does Not Confer Resilience to Heatwaves in an Alpine Herb. Frontiers in Ecology and Evolution. 10.3389/fevo.2021.615119

81. Ostria-Gallardo et al. (2023). Two Congeneric Shrubs from the Atacama Desert Show Different Physiological Strategies That Improve Water Use Efficiency under a Simulated Heat Wave. Plants. 10.3390/plants12132464

82. Okubo et al. (2023). Tolerance and acclimation of the leaves of nine urban tree species to high temperatures. Forests. 10.3390/f14081639

83. Graae et al. (2009). The effect of an early-season short-term heat pulse on plant recruitment in the Arctic. Polar Biology. 10.1007/s00300-009-0608-3

84. Ravn et al. (2022). Phenotypic plasticity enables considerable acclimation to heat and drought in a cold-adapted boreal forest tree species. Frontiers in Forests and Global Change. 10.3389/ffgc.2022.1075787

85. Mateos-Naranjo et al. (2021). Understanding the impact of a complex environmental matrix associated with climate change on the European marshes engineer species *Spartina martima*. Environmental and Experimental Botany. 10.1016/j.envexpbot.2020.104304

86. Haworth et al. (2018). Impaired photosynthesis and increased leaf construction costs may induce floral stress during episodes of global warming over macroevolutionary timescales. Scientific Reports. 10.1038/s41598-018-24459-z

87. Di Iorio et al. (2016). Acclimation of fine root respiration to soil warming involves starch deposition in very fine and fine roots: a case study in *Fagus sylvatica* saplings. Physiologia Plantarum. 10.1111/ppl.12363

88. Marchand et al. (2005). Are heat and cold resistance of arctic species affected by successive extreme temperature events?. New Phytologist. 10.1111/j.1469-8137.2006.01659.x

89. Marchand et al. (2006). Disentangling effects of an experimentally imposed extreme temperature event and naturally associated desiccation on Arctic tundra. Functional Ecology. 10.1111/j.1365-2435.2006.01203.x

90. Orsenigo (2015). Effects of Autumn and Spring Heat Waves on Seed Germination of High Mountain Plants. PLOS One. 10.1371/journal.pone.0133626

91. Trotta et al. (2023). Germination performance of alien and native species could shape community assembly of temperate grasslands under different temperature scenarios. Plant Ecology. 10.1007/s11258-023-01365-7

92. Waring et al. (2017). High growth temperatures and high soil nitrogen do not alter differences in CO2 assimilation between invasive *Phalaris arundinacea* (reed canarygrass) and *Carex stricta* (tussock sedge). American Journal of Botany. 104 (7): 999 – 1007 , 2017

93. Benot et al. (2013). How extreme summer weather may limit control of *Festuca paniculata* by mowing in subalpine grasslands. Plant Ecology & Diversity. 10.1080/17550874.2013.784818

94. Diana Backes (2022). The biogeography of plant heat tolerance and vulnerability to heatwaves (Thesis Chapter 3). PhD thesis, Western Sydney University, Sydney