Title: The incredible vulnerability that reproduction poses for plant species in a warming world

Short title: Plant reproduction under heat

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Abstract

Temperatures are rising globally and threatening the persistence of natural plant populations. Elevated temperatures disrupt gametogenesis, fertilization, and seed filling, often at lower thresholds than those affecting photosynthesis, growth, or survival. While crop scientists have found that key reproductive stages are particularly vulnerable to heat stress across plant systems, ecological and evolutionary studies have largely focused on other fitness metrics to estimate populations' resilience to warming. We advocate for integrating pollen and ovule developmental metrics into ecological and evolutionary studies to improve predictions of plant population dynamics under future climates. Such studies will offer not only a better understanding of how natural populations will respond to increasing temperature stress, but also are likely to reveal novel mechanistic insights that can be utilized to improve crop resilience in a warming world.

Introduction

Anthropogenic climate change is causing elevated temperatures and increasingly severe heat waves, pushing natural populations to their limits (Parmesan, 2006; Parmesan & Hanley, 2015). While ecological and evolutionary biologists have long appreciated the consequences of climate change, the underlying mechanisms of how and why populations will be impacted by heat are still largely unexplored in natural plant populations (Haider et al., 2021).

It is broadly understood that temperatures above a critical threshold lead to irreversible damage for plants (Jagadish, Way, and Sharkey 2021). However, it is often overlooked that even modestly elevated temperatures can lead to reproductive failure. While plants can persist and maintain vegetative growth under heat stress, even for temperatures as high as 60°C in some species, the average optimal temperatures for gametophyte and seed development are approximately 26°C in crops and horticultural plants (Nievola et al., 2017; Tushabe & Rosbakh, 2025). Crop scientists have recognized that the development of plant reproductive tissues - especially pollen, ovules, and seed development - are generally the most vulnerable to rising global temperatures (Chaturvedi et al., 2021; Zinn et al., 2010). Consequently, there has been extensive research to understand the mechanisms underlying reproductive failure in the face of heat stress (Table 1).

In contrast, ecological and evolutionary studies have not distinguished between the effects of heat stress on vegetative growth and reproduction. These studies often focus on proxies of an individual's fitness, using traits such as biomass, survival, and flower or fruit number (Wadgymar et al., 2024). These proxies may not capture the full effects of elevated temperatures on reproduction. Although some recent plant evolutionary ecology studies have recognized heat impacts on plant reproductive development (Heiling & Koski, 2024; Tushabe et al., 2025), important complementary insights from the crop literature remain underappreciated.

Here, we highlight the effects of heat on pollen and seed development and the reproductive consequences of whole plant heat response mechanisms. Our goal is to inspire scientists to incorporate the susceptibility of plant reproduction to heat into future ecological, evolutionary and conservation research. Developing effective strategies to mitigate climate change will require clarifying the underlying mechanisms of extinction due to warmer temperatures. Moreover, future studies of genetic variation in reproductive heat tolerance within natural plant populations are likely to inform crop science by revealing new mechanisms that enhance reproductive resilience to elevated temperatures (Yeaman, 2025).

Plant reproductive development is disrupted by exposure to heat

Sexual reproduction is a complex process that can fail at multiple stages under heat stress (Zinn et al., 2010). Extensive research on food crops and model species has begun to reveal the mechanisms by which heat disrupts reproductive processes (Fig. 1). These research efforts have led to the identification of heat-tolerant crop varieties (Chaudhary et al., 2020) and gene families involved in heat-stress responses (Kan et al., 2023; Tiwari et al., 2022). However, crop-centered research focusing on yield may be missing other indicators of success important to natural systems. Additionally, crop and model systems are not always representative of natural plant populations, particularly for perennials and rare species (Kooyers et al., 2025). Indeed, crop scientists have begun looking to natural systems as an avenue to increase reproductive resilience to heat stress (Phillips et al., 2025). Below we describe some of the key mechanisms of reproductive development identified through crop research.

Pollen development is widely regarded as the most heat-sensitive stage of reproduction (Zinn et al., 2010). Although the exact reasons for this sensitivity are not fully understood, several key patterns are found across plant species. For example, nutritive tapetal tissue within the anther breaks down rapidly when exposed to heat during microsporogenesis, leading to pollen inviability (Chaturvedi et al., 2021). Additionally, heat can interfere with meiosis and proper chromosomal segregation (Bomblies et al., 2015; De Jaeger-Braet & Schnittger, 2024; Khaitova et al., 2024; Lohani et al., 2025), leading to a reduction in viable microspores. These failures are rarely visible in common ecological fitness metrics like plant size and flower number, but they have profound effects on plant fitness.

Ovule development also suffers from heat stress (Jagadish, 2020; Sage et al., 2015). However, fewer studies have explored the effects of heat on the pistil (Resentini et al., 2023; Wang et al., 2021). As such, our understanding of heat-induced ovule dysfunction remains limited and is mostly derived from a small number of studies on crop plants (Wang et al., 2021). These studies found that heat exposure can cause abnormal embryo sac development (Shi et al., 2022), reduced ovule viability (Djanaguiraman et al., 2018) and increased sterility through excessive callose deposition in the ovary (Zhang et al., 2018). Such dysfunction may be masked by apparently normal pistil structures, meaning female reproductive failure may go undetected in common ecological assessments of fitness.

Although most people focus on pollen, fertilization and embryogenesis are also sensitive to heat (Sankaranarayanan et al., 2020). Heat exposure can accelerate embryo development, leading to a mismatch between seed coat and endosperm production and, ultimately, seed abortion (Mácová et al., 2022). Crucially, seed development can remain impaired even under favorable conditions if plants experienced elevated temperatures during earlier reproductive stages (Cope et al., 2023; Kooyers, Genung, et al., 2025; Resentini et al., 2023; Tushabe et al., 2023).

Despite these reproductive sensitivities, the consequences of inviable pollen, dysfunctional ovules, or aborted seeds often go undetected when fitness is assessed using metrics such as flowering time, flowering duration, flower number (Gaudinier & Blackman, 2020) or fecundity measures such as fruit number (Buckley et al., 2021; Tushabe et al., 2025). To better understand how climate change shapes plant performance and evolutionary trajectories, ecological and evolutionary studies should explicitly account for the effects of elevated temperature on pollen, ovule, and seed development.

Whole plant mechanisms affecting reproduction

While heat can directly disrupt gametophyte and seed development (Fig. 1), these processes are also vulnerable to physiological shifts that occur in other parts of the plant in response to elevated temperatures. For example, leaf exposure to elevated temperatures can reduce sucrose and other important metabolites supplied to developing reproductive structures, resulting in the failure of pollen development (Santiago et al., 2021), or an imbalance in hormone signaling molecules can prevent successful fertilization (Ali & Muday, 2024; Sankaranarayanan et al., 2020). Ecological and evolutionary studies have, for the most part, overlooked this whole-plant perspective, but it is critical for understanding how heat affects reproduction. In this section, we briefly highlight some of the whole-plant mechanisms involved in heat stress and their downstream effects on reproductive development (Fig 1).

Heat stress can affect whole plant physiology through oxidative stress and hormonal changes. Heat induces both systemic oxidative stress and localized reactive oxygen species (ROS) accumulation in rapidly developing sink tissues, including floral organs. While moderate increases in ROS throughout the plant can promote stress tolerance (Huang et al., 2019; Mittler et al., 2022), excessive ROS accumulation in the flower causes early tapetum degradation in the anther (Santiago et al. 2021), reduces pollen production and viability (Lohani et al., 2025), suppresses pollen tube growth, and reduces fertilization efficiency (Ali & Muday, 2024; Wang et al., 2021). Hormonal disruption further contributes to reproductive failure. Auxin is essential for anther and pollen development and elevated temperatures reduce auxin (Ozga et al., 2017), leading to reduced pollen viability and sterility even under mild heat stress (Chaturvedi et al., 2021; Jing et al., 2023). Mild heat stress can also induce ethylene production in leaves, which interacts with auxin and ROS pathways (Huang et al., 2023) and affects reproductive development by promoting premature fruit senescence or delaying ripening (Savada et al., 2017).

Beyond these molecular and hormonal effects, heat stress impacts broader physiological processes including carbon assimilation and source-sink dynamics. Photosynthesis is sensitive to elevated temperatures, but stomatal regulation can prevent reductions in carbon assimilation and increases in photorespiration due to decreased Rubisco activity, maintaining photosynthesis (Dusenge et al., 2019; Kan et al., 2023). However, source-sink dynamics are often disrupted at lower temperature thresholds than photosynthesis (Soltani et al., 2019). The allocation of non-structural carbon into sugars and starch is disrupted at lower temperature thresholds than those required to impair photosynthesis, leading to a net carbon deficit despite ongoing photosynthesis (Du et al., 2020; Fatichi et al., 2014). Floral structures act as strong resource sinks (Santiago et al., 2021; Shen et al., 2023) and when source-sink dynamics are perturbed during reproductive development, plants can experience pollen sterility, seed abortion (Liu et al., 2021), and reduced seed production (Miret et al., 2024). Heat exposure has also been shown to reduce seed size, weight, number and overall seed quality due to reallocation of carbon away from maturing fruits during seed filling (Niu et al., 2021; Resentini et al., 2023; Wang et al., 2021).

Disruption of signaling pathways and source-sink mechanisms by elevated temperatures has significant implications for reproduction, yet these dynamics are often overlooked in ecological and evolutionary studies. For example, meta-analyses have found correlations between biomass, warming, and fruit production (e.g. Dobson & Zarnetske, 2025; Younginger et al., 2017), inadvertently encouraging researchers to treat growth traits as useful proxies for fruit production. However, crop studies show that even short-term heat exposure drastically reduces pollen viability and seed set, despite plants producing more flowers or fruits in these conditions (Lohani et al., 2022, 2025). Further, ecological studies that only evaluate the tolerance of already formed pollen grains to heat overlook the role that whole-plant processes play in the success or failure of pollen formation in the first place. As a consequence, ignoring the role of whole-plant responses in reproductive development can lead to overestimates of plant fitness and misleading predictions about persistence under climate change.

Integrating reproductive development into ecological and evolutionary research

For decades, plant ecologists have investigated the effects of elevated temperatures on plant populations, often focusing on shifts in phenology (CaraDonna et al., 2014; Inouye, 2020; Parmesan, 2006; Price & Waser, 1998), altered patterns of selection (Anderson et al., 2025; Colautti & Barrett, 2013; Etterson, 2004; Franks et al., 2018; Santangelo et al., 2022; Vtipil & Sheth, 2020) and phenotypic plasticity (Arnold et al., 2022; Atkin et al., 2006; Chevin et al., 2010; Nicotra et al., 2010). These studies have documented global trends such as shifting flowering times (Parmesan, 2006), altered life-history strategies (Boyko et al., 2023), conferred stress resistance through transgenerational plasticity (Donelson et al., 2018), and the potential for adaptive evolution (Anderson et al., 2025; Kooyers et al., 2025). The detrimental effects of elevated temperatures on pollen development and seed filling in natural populations are generally unknown, yet are likely to play a major role in how those systems will respond to future climates. Now is the time for ecological and evolutionary studies to incorporate our understanding of the most sensitive life-history stages into future research.

First and foremost, it is crucial for ecologists and evolutionary biologists to recognize the critical vulnerability of plant reproduction to elevated temperatures. Many studies have focused on the effects of heat on photosynthesis, while reproduction will be negatively impacted at lower temperatures than photosynthesis (Liu et al., 2021; Soltani et al., 2019). Evaluation of the temperature ranges where populations can and cannot successfully reproduce will be necessary to predict extinction risk with future climate change. One crucial aspect of this research will be the intersection of phenology with reproductive sensitivity. Many natural populations of plants already flower during cooler parts of the season to avoid the negative impacts of high temperatures on reproduction (Luo et al., 2025). Future shifts in phenology through plasticity and evolution are expected and these shifts may protect populations from increasing temperatures. However, changes in phenology may not be sufficient to avoid heat waves and hotter parts of the year. For those populations, selection for higher reproductive resilience will occur, with local reproductive failure and extinction occurring for populations without sufficient standing genetic variation for resilience.

While there is now broad recognition of the deleterious impacts of elevated temperatures on reproduction by crop scientists, the mechanisms by which this failure occurs are still not fully understood. Natural populations present an opportunity to identify the underlying mechanisms, an important goal for both conservation and improvement of crop resilience. In particular, natural systems with short generation times and well-established genetic resources represent a critical opportunity to identify the ultimate causes of reproductive failure in elevated temperatures, along with identifying the genes harboring standing genetic variation for resilience (Kooyers et al., 2025). Studies in those systems could clarify the relative contributions of source-sink relationships, meiosis, tapetal development, and other factors on pollen vulnerability. Further, studies in those systems may uncover why nighttime temperatures are so critical for successful pollen formation and seed filling. Elevated nighttime temperatures have reduced yield in several major crops, including soybean, rice, maize, and wheat (Giménez et al., 2025; Thenveettil et al., 2025) but the consequences of shrinking diurnal temperature ranges remain poorly understood. Studies incorporating nighttime warming and its effects on reproductive development will provide valuable insight for ecological and evolutionary research while also informing crop improvement efforts.

Going forward, studies of warming climate impacts on natural populations should aim to incorporate quantification of the impacts of temperature on reproduction. While fully dissecting the underlying physiological mechanisms may be impractical for the many species in natural plant communities, simpler measurements can be highly informative in documenting the impacts of heat stress on reproduction. Quantification of both pollen viability and seed filling are relatively straightforward and inexpensive measurements that can be made through staining pollen and weighing fruits. These measurements, conducted under controlled temperature manipulations in the field or greenhouse, can then be used to inform our predictions of how natural populations will be impacted by warming. For systems amenable to experimental manipulation, evolutionary biologists should aim to quantify the genetic variation in reproductive tolerance to elevated temperatures, identify the underlying alleles, and model how natural populations will respond evolutionarily through gene flow, genetic drift, and natural selection. Incorporating these approaches will provide a more complete understanding of the impacts of heat on plant populations and inform strategies to preserve biodiversity.

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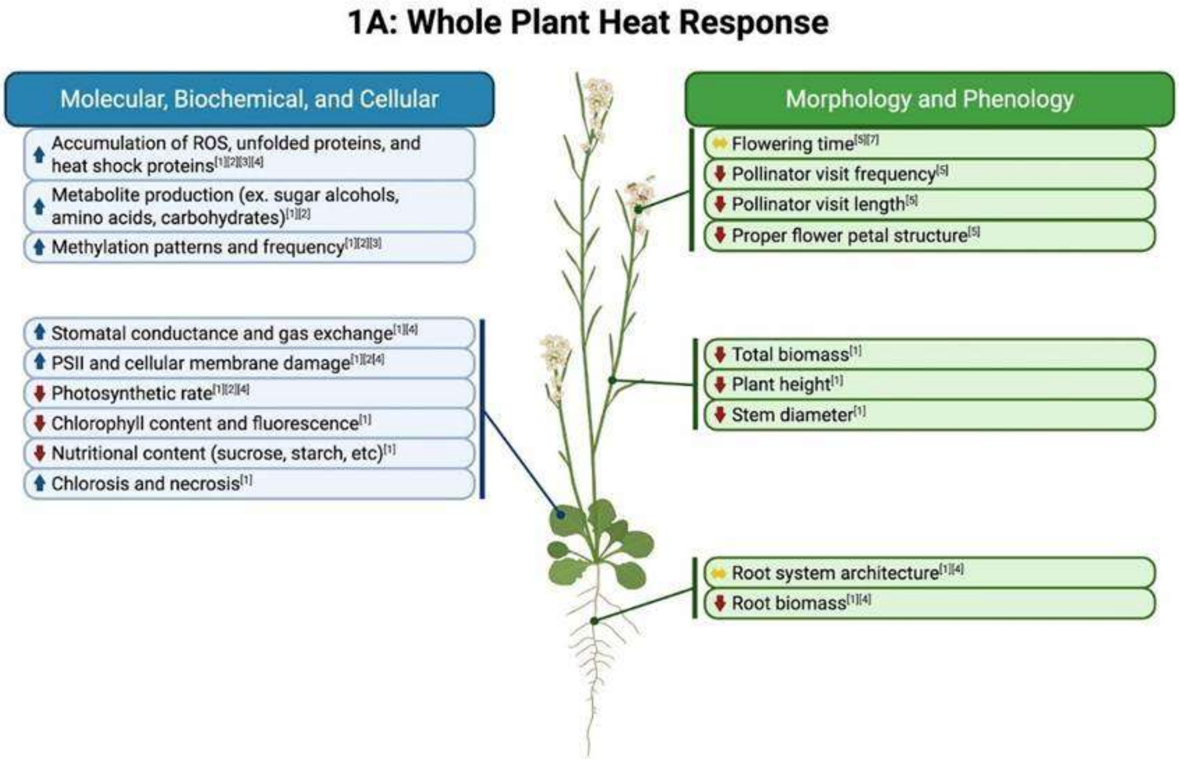
Table 1

Effects of elevated temperature and heat stress on plants. This table contains a non-exhaustive list of recent reviews related to the mechanisms and effects of elevated temperature and heat stress on various stages related to plant reproductive development in crop species.

Structure	**References**
Whole plant	Datta et al., 2024; Haider et al., 2021; Jagadish et al., 2021; Kan et al., 2023; Zhang et al., 2021
Whole flower	Ali & Muday, 2024; Resentini et al., 2023; Sinha et al., 2021; van der Kooi et al., 2019; Walsh et al., 2019, Walters et al., 2022
Pollen	Althiab-Almasaud et al., 2024; Chaturvedi et al., 2021; Liu et al., 2021; Lohani et al., 2025; Mesihovic et al., 2016
Pistil	Y. Wang et al., 2021, Resentini et al., 2023



1A: Whole Plant Heat Response
Molecular, Biochemical, and Cellular
Accumulation of ROS, unfolded proteins, and heat shock proteins[1][2][3][4]
Metabolite production (ex. sugar alcohols, amino acids, carbohydrates)[1][2]
Methylation patterns and frequency[1][2][3]
Stomatal conductance and gas exchange[1][4]
PSII and cellular membrane damage[1][2][4]
Photosynthetic rate[1][2][4]
Chlorophyll content and fluorescence[1]
Nutritional content (sucrose, starch, etc)[1]
Chlorosis and necrosis[1]
Morphology and Phenology
Flowering time[5][7]
Pollinator visit frequency[5]
Pollinator visit length[5]
Proper flower petal structure[5]
Total biomass[1]
Plant height[1]
Stem diameter[1]
Root system architecture[1][4]
Root biomass[1][4]

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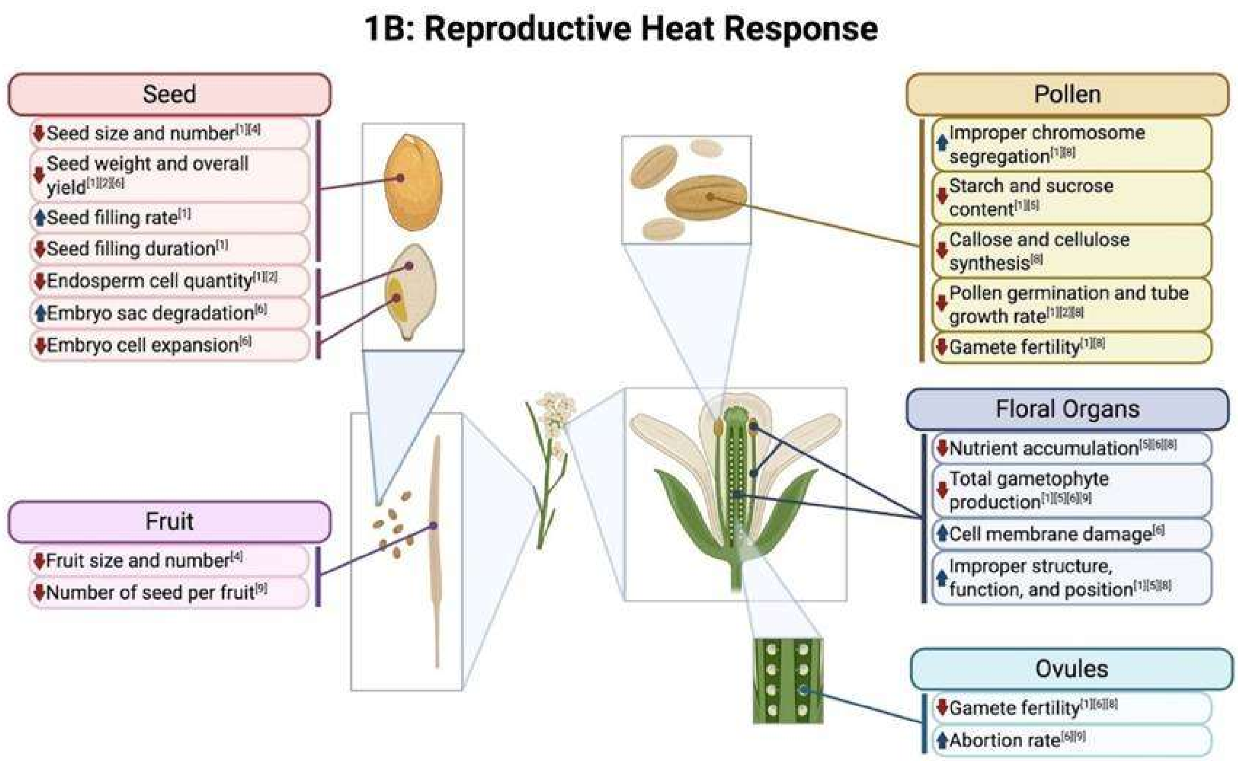

Figure 1

Generalized plant responses to heat stress. A. Heat stress can impose a variety of effects on the whole plant by molecular, cellular or physiological mechanisms. B. Within reproductive tissues, heat stress is generally detrimental to production of gametes, fertilization, and seed production. Phenotypic increases are indicated with blue arrow, decreasing with red arrow, or variable changes with yellow arrow. Superscripts represent references; see references for full citation. [1] Chaudhary et al., 2020 [2] Kan et al., 2023 [3] Haider et al., 2021 [4] Jagadish et al., 2021 [5] Walters et al., 2022 [6] Wang et al., 2021 [7] Sinha et al., 2021 [8] Chaturvedi et al., 2021 [9] Ali & Muday 2024.

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