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Impacts of higher daytime temperatures on viable pollen and fruit production in common Cerrado tree *Byrsonima pachyphylla* (Malpighiaceae)

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Abstract

Already threatened by deforestation, the Brazilian Cerrado—a complex and biodiverse tropical savannah that provides important ecosystem services—could experience climate warming of 1–5°C by 2100. This could negatively impact sexual reproduction (considered particularly sensitive to temperature stress) in native plant species, potentially limiting the production of viable pollen, fruits, and seeds; however, such impacts are largely unstudied in wild tropical species. To investigate the potential effects of higher temperatures on Cerrado species reproduction, developing inflorescences of common and widespread tree *Byrsonima pachyphylla* (Malpighiaceae) were passively heated in situ from an early bud stage (by 3–4°C during the daytime). Viability of pollen samples (analyzed through in vitro pollen germination and differential pollen staining) and fruit set (the proportion of hand-pollinated flowers that developed into mature fruit) were compared between heated and control (ambient temperature) inflorescences, hypothesizing that both would be lower in heated inflorescences. However, higher daytime temperatures had no impact on viable pollen production, suggesting a strong resilience to warming. Nevertheless, fruit set was significantly reduced, which could have serious implications for future species recruitment and potentially Cerrado community structure, insect and animal food chains, and human populations, especially if representative of other Cerrado species. To the best of our knowledge, this experiment is the first manipulative warming of Cerrado vegetation in situ. It provides initial insights into the effects that increasing temperatures could have on future reproductive success and demonstrates the importance of considering reproduction when evaluating the possible impacts of climate change on tropical ecosystems.

Abstract in Portuguese is available with online material.

KEYWORDS
Brazil, climate change impacts, direct heating, fruit set, pollen viability, savannah, tropical tree reproduction

1 | INTRODUCTION

The Cerrado, the second largest biome in South America (originally covering around 2 million km^2; Ratter et al., 1997), extends from the southeastern border of Amazonia across much of Brazil, making it vital for maintaining large South American watersheds (Lima & da Silva, 2007). Although considered a tropical savannah, it comprises a range of vegetation types, from dense grassland to shrubland and woodland (Ratter et al., 1997), containing such high levels of species richness and endemism—while facing significant anthropogenic pressure—that it is categorized as a "hotspot" for biodiversity conservation (Klink & Machado, 2005; Myers et al., 2000). Nevertheless, historically undervalued, the Cerrado remains understudied, and less protected than the Amazon region (Murphy et al., 2016; Overbeck et al., 2015). Remaining intact vegetation is under immediate threat from agriculture-driven deforestation (Garcia & Ballester, 2016; Strassburg et al., 2017) and potentially climate change (Silva et al., 2019; Velazco et al., 2019). Regional climate models predict temperature increases of 1–5°C across the Cerrado biome by 2100 (IPCC, 2013), and significant temperature increases have already been detected (Hofmann et al., 2021).

High temperatures can impact many aspects of plant growth and function (Hasanuzzaman et al., 2013); one of the most temperature-sensitive developmental stages being sexual reproduction (Hedhly, 2011). As a species' ability to persist depends largely on continued reproduction and recruitment (i.e., producing, dispersing, and germinating seeds, and establishing seedlings), habitat suitability is partly determined by the environmental conditions required for these processes (the regeneration niche; Grubb, 1977). Changes in temperature can alter the timing and extent of flowering and fruiting events (reproductive phenology; Butt et al., 2015; Mendoza et al., 2017) and potentially take species outside of their regeneration niche, limiting reproductive success (Rosbakh et al., 2018; Sage et al., 2015). Such changes can have further consequences for species interactions (e.g., with other plants, pollinators, herbivores, or seed dispersers; Butt et al., 2015; Rabeling et al., 2019; Vilela et al., 2018), species persistence, community structure, and ecosystem functioning (Brooker, 2006; Vilela et al., 2018). Investigating the potential impacts of increasing temperatures on Cerrado species reproduction is therefore necessary to better predict the future composition and function of native plant communities, and perhaps strengthen the evidence base for minimizing climate warming.

How temperature affects reproduction has been extensively studied in crop species (often cultivated for their fruits and seeds). Elevated temperatures can inhibit floral bud initiation (Albrigo & Galán Saúco, 2004) or alter or accelerate floral tissue development (Distefano et al., 2018; Prasad & Djanaguiraman, 2014; Rodrigo & Herrero, 2002), adversely affecting pollination or ovule fertilization and frequently leading to reduced crop quality or yield (Jagadish, 2020; Shafqat et al., 2021). While the heat-sensitivity of many stages of both male and female reproductive development—from pre- to post-anthesis (flower opening)—has been demonstrated across a variety of species (reviewed in Lohani et al., 2020; Sage et al., 2015), male development has often been identified as the most vulnerable (Lohani et al., 2020; Pacini & Dolferus, 2016; Santiago & Sharkey, 2019). High temperatures can, for example, induce irregular development or degradation of male reproductive tissues or pollen grains (Bennici et al., 2019; Raja et al., 2019), particularly affecting microsporogenesis (early pollen development; Iovane & Aronne, 2022; Liu, Zhou, et al., 2023); disrupt the supply of water, nutrients, or metabolites to tissues and developing pollen (Pacini & Dolferus, 2016; Paupière et al., 2014); or disturb reactive oxygen species homeostasis, leading to oxidative damage (Djanaguiraman, Perumal, Jagadish, et al., 2018). Such effects can lead to lower quantities or viability of pollen grains released at anthesis or thermotolerance post-anthesis (Lohani et al., 2020; Paupière et al., 2014). Reductions in reproductive success—often measured as fruit set (the proportion of flowers that develop into fruit)—at high temperatures have therefore been largely attributed to losses in pollen viability leading to fertilization failure (Rosbakh et al., 2018; Sage et al., 2015).

In non-crop species, and particularly tropical species, the effects of temperature on reproduction are far less well studied. In situ warming experiments can provide valuable insights into the temperature responses of established plant communities (Ettinger et al., 2019), and several studies have documented warming-induced changes in the reproductive phenology or output of wild temperate species (although complex and species-specific; De Frenne et al., 2011; del Cacho et al., 2013; Hovenden et al., 2007; Jacques et al., 2015; Kudo & Suzuki, 2003; Lambrecht et al., 2007; Liu et al., 2012; Marchin et al., 2015). However, such experiments focus predominantly on short-stature species (herbs and shrubs) as environmental manipulation is more challenging for larger woody species (trees; Chung et al., 2013). These are often studied instead as juveniles in controlled environments (Drake et al., 2019; Johnsen et al., 1995; Webber et al., 2005). Nonetheless, a recent global meta-analysis of simulated warming experiments found evidence of an overall decline in fruit production under warming (Zi et al., 2023), although no tropical studies were included.

Research on the reproductive responses of wild tropical species to temperature has focused mainly on phenological changes (e.g., Numata et al., 2022; Vilela et al., 2018), and studies on Cerrado species are largely limited to seed experiments (reviewed in Daibes et al., 2022) or those utilizing ecological gradients (such as between the edge and center of vegetation fragments; Athayde & Morellato, 2014; Camargo et al., 2011; Melo et al., 2014; Vogado et al., 2016). Nevertheless, since high temperatures have been shown to negatively impact reproduction in a number of tropical tree crops (including peach, mango, date palm, *Annona*, and *Citrus* species; Alves Rodrigues et al., 2018; Distefano et al., 2018; Hedhly et al., 2005; Liu, Xiao, et al., 2023; Lora et al., 2011, 2012; Nava et al., 2009; Shafqat et al., 2021; Slavković et al., 2016; Sukhvibul et al., 2000), it is plausible that wild tropical woody species, including those native to the Cerrado, would also be negatively affected.

To investigate how increasing temperatures might affect the reproduction of woody Cerrado species, we carried out a direct heating experiment in situ on inflorescences of native tree species *Byrsonima pachyphylla* A.Juss. (Malpighiaceae) using novel passive heating chambers. To the best of our knowledge, this was the first direct heating experiment attempted in situ on any native Cerrado vegetation. We hypothesized that inflorescences that developed at higher temperatures would: (a) produce pollen of lower viability than those at ambient temperatures (analyzed through two complementary techniques of in vitro pollen germination and staining); and (b) have lower percentages of fruit set (given manual pollination).

2 | METHODS

2.1 | Study site and species

This study was conducted between June and November 2019 in an area of Cerrado típico or "typical Cerrado" (a subcategory of Cerrado sensu stricto; Ribeiro & Walter, 2008) in the Bacaba Municipal Park reserve (14°42′28.8″ S, 52°21′03.9″ W) in Nova Xavantina, Mato Grosso, Brazil. Typical Cerrado is a dominant vegetation type of the reserve (Mews et al., 2011), comprised of tree and shrub woodland with 20%–50% tree cover of average height 3–6 m (Ribeiro & Walter, 2008). The climate is classified as Aw (Köppen system; Peel et al., 2007), with a pronounced wet (mid-October–April) and dry season, with peak temperatures coinciding with the end of the dry season (August–October; Figure S5). The region is characterized by 1300–1500 mm annual precipitation and average monthly temperatures of 25°C (Brazilian Meteorological Service; Marimon et al., 2010), although it has experienced recent and rapid warming (Marimon et al., 2020; Tiwari et al., 2021). According to the long-term ERA5-Land dataset (Muñoz Sabater, 2019; data assimilation based dataset with 9 km resolution, see Supporting Information Appendix S1 for details), 2010–2020 mean annual daytime and night-time temperatures locally were 28.6 ± 0.2°C (SD) and 24.6 ± 0.2°C respectively.

Byrsonima pachyphylla (also known by synonym *Byrsonima crassa*; Francener, 2023) is a widespread tree of the Cerrado biome (Bridgewater et al., 2004) and among the 10 most common species of the typical Cerrado vegetation in Bacaba Park (Mews et al., 2011). Its pollen and floral oils are collected by specialist pollinators (predominantly bees of the genera *Centris* and *Epicharis*; Boas et al., 2013); its fruits are consumed by animals, for example, birds (Purificação et al., 2014) and to some extent humans (Passos, 2023); and its leaves and bark have medicinal properties (Guilhon-Simplicio & Pereira, 2011; Sannomiya et al., 2005), making it both socially and ecologically important. Flowering can occur throughout the dry season, but peaks in July and August (Silvério & Lenza, 2010). The fruits begin to develop soon after flowering, maturing in November. Flowers are zygomorphic with five yellow petals, oil glands at the base of the calyx, and a diameter of ~13 mm (Figure 1a); bisexual with ten stamens and three carpels; and borne on terminal, racemose inflorescences ~8 cm long (Figure 1c). Most flowers open in the morning around 06:00 h and are receptive for 1 day (Boas et al., 2013), changing color to orange and red on the days after anthesis. *Byrsonima pachyphylla* is self-incompatible (Boas et al., 2013), with stigmas covered by a thin cuticle that prevents pollen from adhering and germinating unless broken by pollinators.

FIGURE 1 *Byrsonima pachyphylla*, showing (a) individual flower; (b) developing inflorescence at the stage at which the heating chambers were set up; and (c) inflorescence during flowering with yellow buds nearing anthesis, yellow flowers open on the day of anthesis, and orange and red flowers that have opened on previous days.

2.2 | Heating experiment

To heat inflorescences in situ, we developed an elevated open-topped chamber (25 × 25 cm) with a telescopic support structure (Figure S1b), designed to passively heat the air surrounding the inflorescences (and developing flower buds) during sunny periods. Each chamber was comprised of two parts, a square base 75% covered with black polythene (part A; Figure S1a), and a transparent acetate upper section (part B; Figure S1a), with the top left completely uncovered. See Supporting Information (Appendix S1) for a more detailed description and discussion of this heating methodology.

Five healthy, mature *B. pachyphylla* individuals were selected (>20 m apart; dimensions in Table S4), each displaying at least six inflorescences at the same, early developmental stage (Figure 1b; the earliest stage possible given delays initiating the experiment). Between June 12th and 18th, heating chambers were installed around three developing inflorescences per individual (treatment inflorescences; T1–T3). Three further inflorescences per individual were chosen as unheated controls (C1–C3), each physically close to a treatment (heated) inflorescence (although not on the same branch) to reduce variation in microclimatic variables (other than temperature) between corresponding treatment and control inflorescences.

2.3 | Measurement of climatic variables

On each *B. pachyphylla* individual, temperature sensors (Maxim DS18B20+; accurate to ± 0.5°C) were placed at two treatment (heated) inflorescences and at their two corresponding control inflorescences, while temperature and relative humidity (RH) were measured together (using Adafruit DHT22 sensors; accurate to ± 0.5°C and ± 2%–5% RH) at the third treatment inflorescence and its corresponding control. All sensors were housed in custom radiation shields (see Figure S1b). Data were recorded every minute.

2.4 | Experimental temperatures

Between the initiation of heating and the end of flowering (approximately 8 weeks), control inflorescences experienced average daytime (6:30–18:30 h local time; BRT = UTC-3) and night-time (18:30–6:30 h) air temperatures of 29.4 ± 1.5°C (SD) and 18.7 ± 2.1°C respectively, reaching mean maximum (daytime) temperatures of 36.7 ± 2.1°C (Table S1). Treatment (heating chamber) air temperatures correlated closely with controls (Figure 2a) but rose on average 2.7 ± 1.0°C higher in the daytime (Table S1). The strongest and most consistent period of heating (peak heating) occurred between 9:00 and 17:00 h each day, when treatment temperatures rose to 4.0 ± 1.4°C above controls (Table S1). Mean treatment temperatures were 32.1 ± 2.0°C in the daytime and 36.8 ± 2.5°C during peak heating, reaching mean maximum temperatures of 42.3 ± 2.9°C (Table S1).

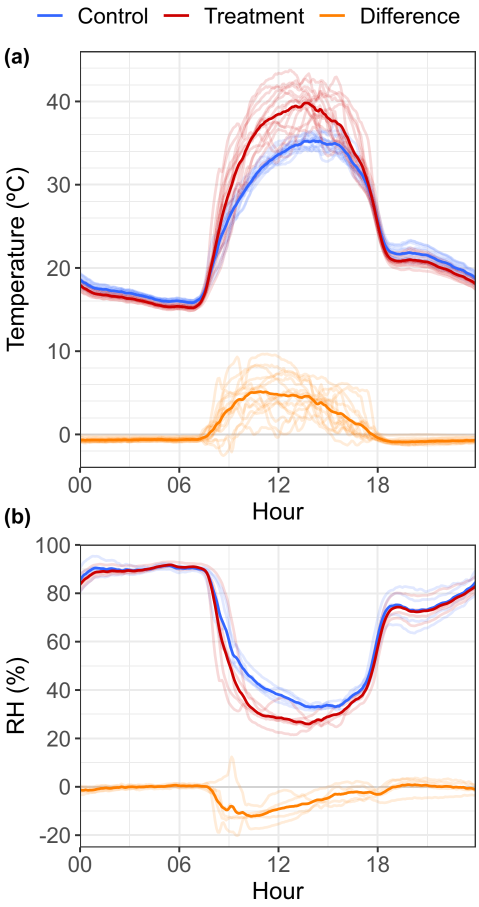

FIGURE 2 Mean diurnal patterns of (a) temperature and (b) relative humidity (RH) for control and treatment inflorescences, with differences in temperature and RH calculated between the treatment inflorescences and their corresponding controls. Values averaged across every 5 min interval of each day of recorded data, between the initiation of heating and the end of flowering. Faded lines show mean diurnal patterns for each inflorescence.

Following flowering, temperatures rose seasonally throughout August towards the wet season (Figure S4a; Table S3), reaching mean daily maxima of 42.0 ± 2.4°C in September (controls). Despite increasing cloud cover, the chambers continued to produce a strong heating effect (Table S3), exposing treatment inflorescences to even higher maximum temperatures of 47.4 ± 2.5°C on average in September (during fruit development).

According to the ERA5-Land dataset since 2010 (see Supporting Information Appendix S1 for details), 2019 was a warmer than average year (Figure S5). Furthermore, the standard deviation around monthly mean daytime temperatures (interannual variation) over the last 10 years was on average ± 0.9°C (and lower for the study period, June–September; Figure S5). Therefore, the treatment chambers produced temperatures above those frequently experienced locally during the same period of previous years.

2.5 | Pollen sampling and analysis

To investigate the effect that heating during floral development had on *B. pachyphylla* pollen viability, pollen samples from treatment (heated) and control flowers were analyzed using two complementary techniques (detailed below): in vitro pollen germination (successfully germinated pollen grains presumed viable) and differential staining of aborted and non-aborted pollen grains (non-aborted pollen grains presumed viable; Dafni & Firmage, 2000). Flowering began on June 24. On each day from July 3 to 19, pollen samples (anthers) were collected (before 10:00 h and preceding hand-pollinations) from any experimental inflorescences displaying flowers at anthesis. From each of up to three newly opened flowers per inflorescence, two anthers were collected for analysis by pollen staining, and two for analysis by pollen germination. Although aiming to collect at least five repeat samples (on different days) from each inflorescence, variations in flowering resulted in 2–10 repeats per inflorescence (6 on average). Treatment flowers had undergone heating for 14–35 days (25 on average) prior to sampling.

2.5.1 | In vitro pollen germination

Prior to experiment initiation, a protocol for in vitro pollen germination was developed based on the hanging-drop method (Shivanna & Rangaswamy, 1992) and variations of the classic Brewbaker and Kwack (1963) pollen germination medium and germination conditions were tested and optimized for *B. pachyphylla* (Table S5). Pollen germinated well at 30°C (as in some other tropical species; Hebbar et al., 2018; Reddy & Kakani, 2007; Youmbi et al., 2011). Prehydration of pollen was not required.

During the experiment, each sample (anthers) taken for analysis by germination was macerated with the germination medium (Table S5) and 40 μL drops of each solution were transferred to petri dishes and inverted over moistened filter paper. By 12:00 h the same day, dishes were sealed with petroleum jelly and incubated at 30°C in the dark for 24 h. Drops were then transferred to microscope slides and observed under an Eclipse E200 microscope (Nikon, Tokyo, Japan) paired with a Nikon DS-Fi2-U3 camera system at 100× magnification. At least four images (unique microscopic fields) were taken per sample (Figure S6a) and all grains were counted per image (mean of 51). Pollen grains were classified as germinated if possessing a pollen tube of length at least equal to the grain diameter (Dafni & Firmage, 2000). Sample viability was estimated as the percentage of germinated grains in each image, averaged over all images per sample.

2.5.2 | Differential pollen staining

Prior to experiment initiation, a modified version of Alexander's staining solution (Peterson et al., 2010) was optimized for *B. pachyphylla* pollen and local lab conditions (Table S6). During the experiment, each sample taken for analysis by staining was macerated with the staining solution and 30 μL of this mixture was transferred to a microscope slide, heated gently (protocol as in Peterson et al., 2010), and observed using the same microscope and camera system as above to differentiate between aborted (cell walls stained blue/purple) and non-aborted (presumed viable; cell protoplasm stained orange/red) pollen grains (Figure S6b). At least four images were taken per sample, and all grains counted per image (mean of 134). Sample viability was estimated as the percentage of all grains per image that stained orange/red (non-aborted), averaged over all images per sample. Image analysis (pollen grain classification and counting) was carried out manually using ImageJ software (Version 1.51; Rasband, 2018).

2.6 | Hand-pollination and fruit set analysis

Every day during the flowering period (June 24–August 9) any flowers at anthesis on each of the experimental inflorescences were counted and hand-pollinated to provide them with an equal chance of receiving compatible pollen. The pollen for this was collected fresh each day from two newly-opened flowers on each of three non-experimental individuals of *B. pachyphylla* (six flowers in total), using the same three individuals throughout (located >80 m from the experimental individuals). The pollen was mixed together using a thin paintbrush (mixture on the first day showing 78% viability analyzed by staining) and applied vigorously to break the stigmatic cuticle (necessary for fertilization). Care was taken not to damage the flowers.

Following flowering, experimental inflorescences were contained within net bags (sold for agricultural fruit protection) to prevent fruit loss through falling or herbivory. Heating chambers remained in place. Mature fruits were collected and counted in November. Fruit set for each inflorescence was calculated as the percentage of pollinated flowers that developed into mature fruits.

2.7 | Data analysis

Samples containing less than 200 pollen grains were excluded from further analysis due to low reliability. Reliability of the pollen analysis methods was evaluated by comparing viability results for each sample, estimated through germination and staining, using linear regression. For both the pollen germination and staining results, mean pollen viability for each inflorescence (15 control and 15 heated treatment inflorescences) was calculated from repeat sample results, and averaged to estimate treatment-level results. Tree-level ($n = 5$) means were calculated from the inflorescence results, weighted by the number of samples taken per inflorescence. Fruit set results were calculated at the inflorescence level and simply averaged to estimate tree- and treatment-level results. Coefficients of variation (CV) were calculated for tree-level control results to quantify spread in pollen viability and fruit set values relative to their means.

Due to the small sample sizes and highly variable tree-level results, paired Wilcoxon signed-rank tests were used to evaluate the differences between treatment and control results. As our hypotheses were directional—that the heating treatment would induce losses in pollen viability and fruit set—we used one-tailed tests. Tests were repeated considering both inflorescences ($n=15$) and trees ($n=5$) as independent units, as although separate inflorescences on one tree are physically connected, uncertainty exists about the extent of autonomy of tree branches (Auzmendi & Hana, 2020). Additionally, Slavković et al. (2016) demonstrated that separate inflorescences on one tree can respond independently to different temperature treatments, supporting the idea that they can be considered as independent reproductive units. To evaluate whether length of heating influenced treatment sample pollen viability, we examined the slope of regression between the two variables for each tree. All data analyses were carried out in R version 4.1.1 (R Core Team, 2021).

3 | RESULTS

3.1 | Pollen viability

Pollen viability was variable and clearly influenced by the individual tree (Figure 3), with high *CV* in tree-level control results, whether estimated by pollen germination or staining analysis (39% and 38%, respectively). Pollen viability was generally lower when estimated through germination than through staining (Figure 3). Nevertheless, the viability estimates for each sample analyzed by both methods showed a strong linear relationship ($R=0.89$, $p<2.2\text{e}^{-16}$; Figure S7), demonstrating their complementarity and providing confidence in the results when taken together.

Mean pollen viability for the control and treatment (heated) inflorescences was 53.4% ± 4.8% (SE) and 53.9% ± 5.8%, respectively, when estimated by germination, and 72.8% ± 6.5% and 72.5% ± 6.6% when estimated by staining (Table 1). The heating treatment had no significant impact on pollen viability, whether estimated by germination or staining, and whether considering inflorescences ($n=15$) or individual trees ($n=5$) as independent units (all p-values >.5; Table 1).

One of the five trees studied showed a significant negative correlation between heating length and treatment flower pollen viability ($p<.01$; Figure S8). However, the tree displaying a significant correlation differed depending on the pollen analysis method (tree B for germination, E for staining; Figure S8) and all other relationships varied in strength and direction (Figure S8), suggesting no overall impact.

3.2 | Fruit set

Fruit set was low in all inflorescences (maximum 52%) and influenced by tree (*CV* of 90% in tree-level control results; Figure 4). Mean fruit set was 16.6% ± 4.1% (SE) in the control inflorescences and 8.0% ± 3.3% (more than halved) in the treatment (heated)

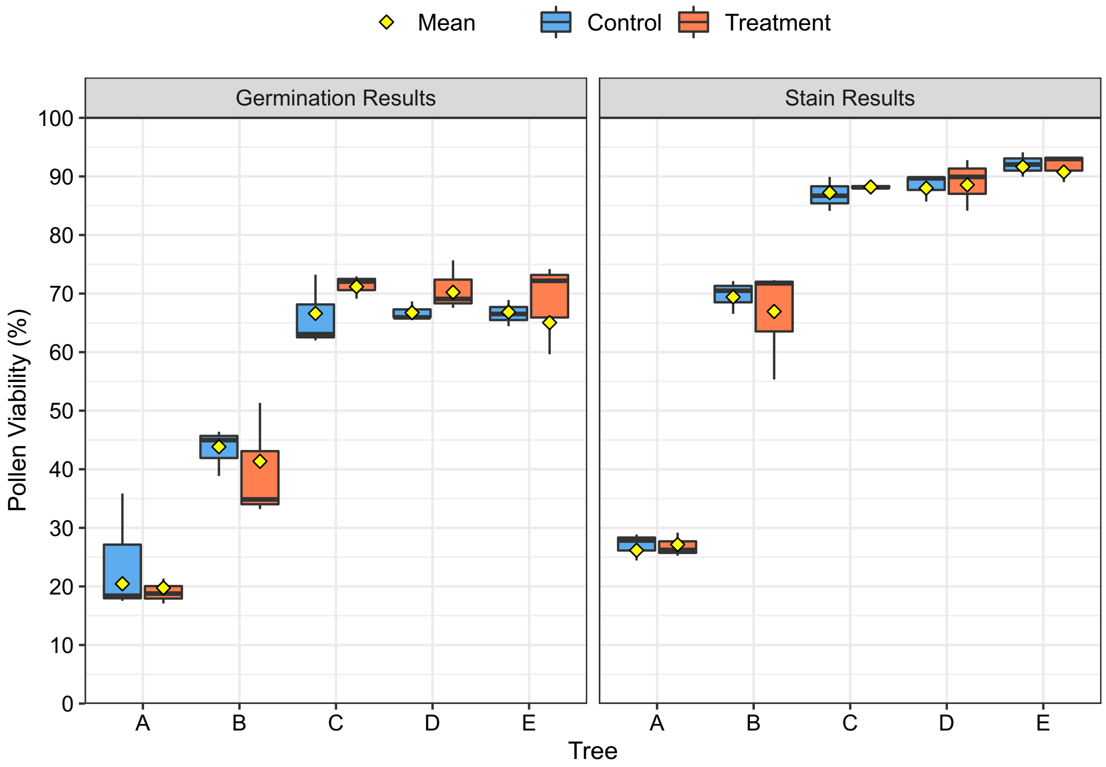

FIGURE 3 Pollen viability for the three control and three treatment inflorescences on each tree (A–E) based on in vitro pollen germination (left) and pollen staining (right) analyses. Tree-level control and treatment means (yellow diamonds) were calculated from the inflorescence values, weighted by the number of repeat samples taken per inflorescence.

TABLE 1 Mean values of pollen viability and fruit set (%±SE) for the control and treatment (heated) inflorescences, including the mean differences between the treatment inflorescences and their corresponding controls; showing the results of paired Wilcoxon signed-rank tests (p, V, R; one-tailed) used to evaluate the significance of these differences, considering either trees ($n=5$) or inflorescences ($n=15$) to be independent units.

	Pollen viability analyzed by		
	Germination	Staining	Fruit set
Controls	53.4±4.8	72.8±6.5	16.6±4.1
Treatments	53.9±5.8	72.5±6.6	08.0±3.3
Differences	00.6±2.1	−0.4±1.4	−8.5±3.6
$n=5$	$p=.69$ $V=6$ $R=.18$	$p=.59$ $V=7$ $R=.06$	$p=.03$** $V=15$ $R=.91$
$n=15$	$p=.70$ $V=51$ $R=.13$	$p=.72$ $V=50$ $R=.15$	$p=.01$** $V=89$ $R=.59$

**Strongly significant result ($p<.05$).

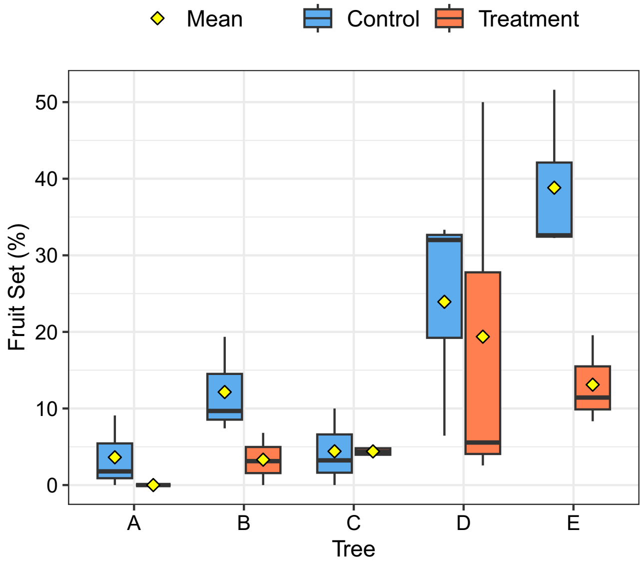

FIGURE 4 Fruit set for the three control and three treatment inflorescences on each tree (A–E).

inflorescences (Table 1). This difference was significant whether considering inflorescences ($p=.01$, $n=15$) or trees ($p=.03$; $n=5$; Table 1) as independent units.

4 | DISCUSSION

This study was the first direct investigation of the impacts of higher temperatures on the reproductive success of any Cerrado species. In line with mid-range predictions of future warming across the Cerrado (IPCC, 2013), our novel passive heating chambers effectively heated developing *B. pachyphylla* inflorescences and fruits by 3–4°C during the day, exposing them to daytime temperatures above those often experienced during the same period of previous years. Contrary to our first hypothesis, viable pollen production was unaffected by higher daytime temperatures during floral development. In contrast, fruit production was negatively affected by warming, which could have a significant impact on the success of *B. pachyphylla* reproduction and recruitment in a future, hotter Cerrado.

4.1 | Pollen viability

Pre-anthesis temperatures above 25°C have been shown to disrupt viable pollen development in many species, including several tropical tree crops (Bennici et al., 2019; Distefano et al., 2018; Higuchi et al., 1998; Kozai et al., 2004; Lora et al., 2012; Nava et al., 2009). Although control temperatures during bud development in our study frequently rose above this threshold, all control inflorescences produced viable pollen (Figure 3). Furthermore, our elevated treatment temperatures unexpectedly had no impact on pollen viability. This suggests that, in local individuals of *B. pachyphylla*, male reproductive tissue and pollen grain development can be maintained at unusually high temperatures (compared to previously studied species) and up to a very high threshold (>40°C).

The Cerrado experiences strong seasonal warming towards the wet season (Figure S5)—daily maxima in September 2019 reached ~42°C—and fires are also common (Miranda et al., 2009). Many native species are therefore physically and physiologically adapted to withstand extreme temperatures (Araújo et al., 2021; Simon & Pennington, 2012), which could explain why heating of 3–4°C did not impact pollen development. It is also possible that *B. pachyphylla* individuals have developed an effective heat stress response and acquired thermotolerance following previous exposure to extreme temperatures (Giorno et al., 2013; Qu et al., 2013). Our heating treatment may have activated elements of this response in the treatment inflorescences during floral development, preventing damage, and maintaining physiological homeostasis (and viable pollen production; Raja et al., 2019; Rieu et al., 2017).

Alternatively, aspects of our heating methodology may have mitigated its impact on pollen viability. Reproductive development is energy-demanding, relying on foliar photosynthesis and metabolite transport (Liu et al., 2021), processes which can be disrupted by high-temperature impacts on vegetative or reproductive tissues (Ferguson et al., 2021). While we chose to heat only inflorescences to allow pairwise comparisons between treatment and control inflorescences on the same tree (having anticipated high variability in pollen viability and fruit set values at the tree level; Augspurger, 1983; Melo et al., 2014), this also excluded any potential effects of heating vegetative tissues from the experiment. Furthermore, elevated night-time temperatures (alone) can impact pollen viability (Djanaguiraman et al., 2013) but were unattainable through passive heating. Continuous heating of entire trees might therefore have elicited a different response in pollen viability. Nevertheless, we can still infer that daily exposure of *B. pachyphylla* inflorescences to very high maximum temperatures did not disturb reproductive tissue development enough to disrupt pollen development, or indeed metabolite transport from vegetative tissues.

It is also possible, however, that the initial and most temperature-sensitive stages of pollen development (namely microsporogenesis; Hedhly, 2011; Sage et al., 2015) were unaffected by our heating treatment. While treatment inflorescences were heated from an early stage, we could not commence heating entirely prior to bud development and the timing of microsporogenesis in *B. pachyphylla* is unknown. However, as racemose inflorescences develop successionally, buds that opened later in the experiment were heated from an earlier developmental stage. Nevertheless, length of heating had no clear impact on treatment sample viability (Figure S8), indicating that the timing of heating initiation did not reduce its impact on pollen development. We can therefore surmise that viable pollen development in *B. pachyphylla* is indeed resistant to very high temperatures.

As Nova Xavantina is at the higher end of temperatures experienced within the Cerrado (Araújo et al., 2021), our results suggest that pollen viability of *B. pachyphylla* in other areas will not be affected by increasing daytime temperatures for some time. Sustained pollen viability could be advantageous for the continued reproductive success of *B. pachyphylla*—and nutrition of its associated pollinators (Boas et al., 2013; Yeamans et al., 2014)—into the future as temperatures increase. This is especially true considering the possibility of plant-pollinator mismatches or potential reductions in pollen availability due to phenological changes and the impacts of further habitat fragmentation and climate warming on pollinators themselves (Melo et al., 2014; Gérard et al., 2020; Giannini et al., 2012; Rabeling et al., 2019).

4.2 | Fruit set

Agreeing with our second hypothesis, higher daytime temperatures negatively impacted fruit set in *B. pachyphylla*, as reported in a range of crop species (Lohani et al., 2020; Sage et al., 2015; Shafqat et al., 2021) and in keeping with the trend found in previous non-crop temperature manipulation studies (Zi et al., 2023). A lack of viable pollen can lead to low fruit set (Knight et al., 2005); however, hand-pollination of all experimental flowers using a mixture of fresh conspecific pollen (collected daily from multiple non-experimental individuals) should have provided surplus viable, compatible pollen to each.

Nevertheless, high temperatures during pollination can limit germination of viable pollen on the stigma or growth of the pollen tube, preventing fertilization and fruit set (Distefano et al., 2018; Liu, Xiao, et al.,2023; Sukhvibul et al., 2000). Although *B. pachyphylla* pollen germinated readily in vitro at 30°C (high for many studied species; Beltrán et al., 2019; Sage et al., 2015), experimental inflorescences regularly experienced temperatures above 30°C during flowering, potentially limiting pollen germination (or tube growth) in vivo. Treatment inflorescences—which experienced high temperatures more often and to a greater degree than controls (Figure S3)—could have been impacted more strongly, leading to their lower fruit set. However, pollen germination and tube growth in several tropical species can persist (although limited) at temperatures above 40°C (Hebbar et al., 2018; Kakani et al., 2002, 2005; Mog et al., 2023). Furthermore, pollen germination is thought to be less sensitive to temperature stress than pollen development (Chu & Chang, 2022; Distefano et al., 2018; Higuchi et al., 1998), which we have shown was resistant to the treatment temperatures. This might suggest that reduced fruit set under heating resulted from impacts on female development rather than reduced pollen germination.

Male reproductive development is generally considered more sensitive to high temperatures than female (Hedhly, 2011; Rosbakh et al., 2018); nevertheless, female tissues have been found to be more sensitive than pollen in some species (e.g., pearl millet and peach; Djanaguiraman, Perumal, Ciampitti, et al., 2018; Gupta et al., 2015; Hedhly et al., 2005; Kozai et al., 2004). High temperatures can potentially disrupt the timing of anthesis or the development of female tissues, resulting in poorly developed structures; reduced stigma receptivity, ovule longevity, or pollen tube attractants; imbalances in reactive oxygen species and important hormones; impaired metabolite provisioning; or disruption of complex male/female interactions (Hedhly, 2011; Wang et al., 2021). Individually or collectively such impacts can cause reductions in fruit and seed development, as observed in several woody tropical and sub-tropical crops (Benlloch-González et al., 2018; Hedhly et al., 2003, 2005; Nava et al., 2009; Rodrigo & Herrero, 2002). A lack of evidence of metabolite limitation during pollen development (discussed earlier) suggests that reproductive tissues were not damaged to an extent that impaired metabolite transport. However, being unable to test the thermal thresholds for *B. pachyphylla* pollen germination, and having not performed microscopic investigation of experimental flowers (e.g., examining ovule viability or pollen tube growth in vivo), we cannot identify definitively which tissues or development stages were most affected to cause the observed reduction in fruit set.

While the mechanism remains undetermined—and although we observed no impact on viable pollen production—our results suggest that *B. pachyphylla* will experience a decrease in fruit production under increasing daytime temperatures. Furthermore, although unachievable given our methodology, we anticipate that elevated night-time temperatures will intensify these negative impacts of warming (Echer et al., 2014; McAusland et al., 2023). This could have serious repercussions for reproductive success and recruitment into the future as the climate of the Cerrado becomes hotter and drier (Hofmann et al., 2021), especially considering fruit set in our hand-pollinated control inflorescences was already low. Declines in fruit and seed production could also limit *B. pachyphylla*'s ability to disperse and migrate in the face of changing environmental conditions (McNichol & Russo, 2023), with potential consequences for species persistence, and knock-on effects for associated animal and insect species (Butt et al., 2015; Purificação et al., 2014; Rabeling et al., 2019), which includes humans (Guilhon-Simplicio & Pereira, 2011; Passos, 2023). Such impacts may be compounded by increased fragmentation of suitable habitat (further limiting reproductive success; Melo et al., 2014), localized heating due to land use change (Rodrigues et al., 2022), and additional effects of warming and fragmentation, for example, on reproductive phenology or pollinator species (Gérard et al., 2020; Giannini et al., 2012; Rabeling et al., 2019; Vilela et al., 2018). Furthermore, higher temperatures are likely to act both during and after fruit and seed production and dispersal, potentially affecting not only the quantity and quality of seed produced, but the longevity and germinability of seeds in the seed bank (well-studied in comparison; Daibes et al., 2022), and seedling establishment (Marimon et al., 2020; Nottingham et al., 2023), further exacerbating their effects on successful reproduction and recruitment.

As limited to one species, this study provides only an initial insight into the potential impacts of higher temperatures on Cerrado species reproduction. However, *B. pachyphylla* (and *Byrsonima* as a genus) is common and widely distributed throughout the Cerrado (Bridgewater et al., 2004; Ratter et al., 2003) giving our findings widespread importance. Cerrado species already show low levels of fertility and fruit set (Athayde & Morellato, 2014; Melo et al., 2014; Montesinos & Oliveira, 2015), and if reduced fruit set under warming is replicated in—even some—other Cerrado species, it could have significant implications for species persistence and richness, community assemblage, and ecosystem function in a future, hotter climate. It is therefore crucial to better understand and integrate the effects of temperature at all stages of growth and development—including reproduction—into ecological models to help predict the possible consequences of increasing temperatures on Cerrado ecosystem structure and function (Borghetti et al., 2021; Correa et al., 2021; Ferreira et al., 2022; Simon et al., 2013; Velazco et al., 2019). Thus, much could be gained by expanding upon this study and employing our methodology to investigate threshold temperatures for reproduction in other Cerrado species and areas, and indeed other tropical ecosystems.

AUTHOR CONTRIBUTIONS

Conceptualization: GAW with DRG, EG, BSM and BHMJr; Support and supervision: EG and DRG (UK) and BSM and BHMJr (Brazil); Heating structure design: GAW with DA; testing, installation and data collection: GAW with MCS, PGT, JMR and MAOL; Sensor systems: SC; Collection and analysis of pollen: GAW with MCS; fruit: MAOL; Data analysis and manuscript: GAW with contributions from all authors, primarily EG, DRG, OLP, and BSM.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: 10.5061/dryad.63xsj3v9k.

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