Annals of Botany **00**: 1–16, 2026
https://doi.org/10.1093/aob/mcag149, available online at www.academic.oup.com/aob

ANNALS OF BOTANY
Nonprofit since 1887

ORIGINAL ARTICLE

Contrasting responses of pollen and fruit to whole-tree heating in two tropical savannah species

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Received: 27 November 2025 Returned for revision: 13 May 2026 Accepted: 26 May 2026

• **Background and Aims** The Brazilian Cerrado, the most biodiverse savannah in the world, is rapidly warming, potentially threatening thousands of species, in addition to large-scale water supply and carbon storage services. Prediction of possible impacts requires a better understanding of plant physiological responses to increasing temperatures, yet direct investigations of wild and tropical species are lacking. Sexual reproduction is considered particularly sensitive to temperature stress, and high temperature-related reductions in yield are well documented in crop species. Here, we report the first *in situ* experimental heating of entire, mature individuals of tropical woody species aiming to investigate the impacts of warming on reproductive success. We expected elevated temperatures to reduce both pollen viability and fruit set.
• **Methods** Two common and widespread Cerrado species, *Byrsonima pachyphylla* (Malpighiaceae) and *Davilla elliptica* (Dilleniaceae), were heated by 2–3 °C during the daytime throughout reproductive development. The viability of pollen produced (analysed through differential staining) and fruit set (calculated as a proportion of hand-pollinated flowers) were compared between heated and unheated individuals. Pollen viability values were also compared with those of the previous year (prior to heating).
• **Key Results** Unexpectedly, pollen viability increased in both species, indicating a high temperature resilience of pollen development. In contrast, fruit set (in *B. pachyphylla*) declined under heating as anticipated. The results suggest that high temperatures constrain reproduction between pollination and early fruit development, and the divergent responses of pollen and fruit might indicate greater sensitivity of female than male development, unusual in studied species.
• **Conclusions** Given already low natural levels of fruit set, the observed reductions in *B. pachyphylla* under predicted levels of warming, perhaps replicated in other Cerrado species, have serious implications for future recruitment, potential migration to more favourable environments, species persistence, interacting species and community structure. Our results therefore emphasise the urgent need for systematic research into heating impacts on tropical diversity.

Key words: Tropical savannah, Cerrado, *Byrsonima pachyphylla*, *Davilla elliptica*, reproduction, *in situ* heating, whole-tree heating, pollen viability, fruit set.

INTRODUCTION

Anthropogenic climate change, in particular climate warming, is one of the most immediate challenges facing global ecosystems (Bellard *et al.*, 2012; Scheffers *et al.*, 2016). Linked to species distribution changes, range contractions and overall losses in biodiversity (Parmesan, 2006; Pecl *et al.*, 2017; Freeman *et al.*, 2018), it has implications for ecosystem function and service provisioning (Tilman *et al.*, 2014). To help prepare for (and hopefully mitigate) future ecological issues, complex models are often used to try to understand and predict the impacts of climate change (Elith and Leathwick, 2009), although significant gaps remain in our understanding of how individual plants, species or ecosystems will respond to increasing temperatures. Such models are therefore greatly enhanced by the incorporation of

new experimental data (Luo *et al.*, 2011; Feng *et al.*, 2018; Schuwirth *et al.*, 2019). Processes such as photosynthesis and primary production have long been a focus of plant ecophysiological research owing to their direct relationship to the global carbon balance (Lin *et al.*, 2010; Kumarathunge *et al.*, 2019), whereas other processes, such as reproduction and recruitment, have received far less attention (Slot and Winter, 2016). However, sexual reproduction is considered one of the most temperature-sensitive stages of plant development (Hedhly, 2011; Lohani *et al.*, 2020).

Given that they are often grown for their fruits or seeds, the impacts of temperature on reproduction have been studied more extensively in crop species (reviewed by Sage *et al.*, 2015; Lohani *et al.*, 2020; Zhu *et al.*, 2021). High temperatures have been shown to alter the timing and extent of flowering (Albrigo and Galán Saúco, 2004); affect the speed of reproductive development, leading to underdevelopment of anther (male) and pistil (female) tissues and gametophytes (pollen grains and embryo sacs) at anthesis, or an asynchrony between male and female development (Rodrigo and Herrero, 2002; Herrero, 2003; Hedhly *et al.*, 2009; Lora *et al.*, 2011); and cause the deformation, degeneration or lack of function of tissues and gametophytes (Kozai *et al.*, 2004; Djanaguiraman *et al.*, 2018*b*; Bennici *et al.*, 2019; Raja *et al.*, 2019). Overall, this can affect viable pollen release or thermotolerance, impact pollen–pistil interactions during the progamic phase (from pollination to fertilization) and reduce fertilization success (Fang *et al.*, 2010; Song *et al.*, 2015; Wang *et al.*, 2021). High temperatures post-fertilization can also affect embryo development and fruit and seed maturation, further impacting the quantity and quality of seeds produced (Albrigo and Galán Saúco, 2004; Pagamas and Nawata, 2008; Suriyasak *et al.*, 2020). Nevertheless, high temperature-induced reductions in yield are most often attributed to reduced pollen viability causing fertilization failure (Vara Prasad *et al.*, 2001; Slavković *et al.*, 2016; Zhu *et al.*, 2021). Male reproductive development is therefore widely considered to be more sensitive to temperature stress than female (Zinn *et al.*, 2010; Giorno *et al.*, 2013; Pacini and Dolferus, 2016; Santiago and Sharkey, 2019).

If reproduction in wild populations is impacted in a similar negative manner by increasing temperatures, it could have significant implications for species persistence, migration potential (Aitken *et al.*, 2008), species interactions (plant–plant and plant–animal) and, ultimately, community stability (Brooker, 2006; Butt *et al.*, 2015; Vilela *et al.*, 2018; Rabeling *et al.*, 2019). It is therefore increasingly recognized that the regeneration niche (the ecological requirements for successful production, dispersal and germination of seeds and seedling establishment; Grubb, 1977) requires greater consideration if we are to predict the impacts of climate warming more accurately (Bykova *et al.*, 2012; Parmesan and Hanley, 2015; Borghetti *et al.*, 2021; Ferreira *et al.*, 2022). Furthermore, the regeneration niche also encompasses the requirements for successful pollen production and performance (Rosbakh *et al.*, 2018).

Experimental warming can be an effective method for investigating the impacts of increasing temperatures on plant physiology (Frei *et al.*, 2020). Still, existing studies on wild species are predominantly limited to short-stature species (Kudo and Suzuki, 2003; Bokhorst *et al.*, 2011; Elmendorf *et al.*, 2012; Jacques *et al.*, 2015), and reproductive responses to warming are often complex and species specific (Hovenden *et al.*, 2007; Lambrecht *et al.*, 2007; Liu *et al.*, 2012; Tushabe *et al.*, 2023). Tropical species, in particular, might already be growing at temperatures close to their thermal maxima (Sentinella *et al.*, 2020; Araújo *et al.*, 2021; Doughty *et al.*, 2023), and it is unclear to what extent reproductive processes might be able to acclimate or adapt to further warming (Rieu *et al.*, 2017; Flores-Rentería *et al.*, 2018).

Within tropical research, non-forest ecosystems, such as the Brazilian Cerrado biome (a complex mixture of grassland, shrubland and woodland, originally covering $\sim 2 \times 10^6$ km^2; Ratter *et al.*, 1997), have received far less attention, and protection, than forest ecosystems (Overbeck *et al.*, 2015; Bispo *et al.*, 2024). Considered the most biodiverse savannah in the world and a conservation 'hotspot' (Myers *et al.*, 2000; Klink and Machado, 2005; Sano *et al.*, 2019), the Cerrado also provides vital and widespread ecosystem services, including carbon storage, climate regulation and water provisioning (Klink and Machado, 2005; Lima and da Silva, 2007; Sano *et al.*, 2019; Rodrigues *et al.*, 2022). However, heavily threatened by agricultural expansion, less than half of the Cerrado remains as native vegetation (Beuchle *et al.*, 2015; Parente *et al.*, 2021). Furthermore, what remains faces additional climate pressures, because regional models predict temperature increases of 2.8–6.6 °C by 2100 (based on moderate to high emissions scenarios; Ferreira *et al.*, 2024), with significant warming already recorded (Hofmann *et al.*, 2021).

Although the potential impacts of anthropogenic activity and climate change on reproduction in Cerrado species have received some attention, studies to date have focused predominantly on seeds and seedlings (reviewed by Daibes *et al.*, 2022), phenology (Vilela *et al.*, 2018; Martins *et al.*, 2025) and habitat fragmentation (Camargo *et al.*, 2011; Vogado *et al.*, 2016). Indeed, the potentially negative effects of elevated temperatures on floral and fruit development in wild tropical trees have rarely been investigated directly, despite evidence from several tropical woody crop species (Sukhvibul *et al.*, 2000; Lora *et al.*, 2011, 2012; Alves Rodrigues *et al.*, 2018; Distefano *et al.*, 2018; Shafqat *et al.*, 2021; Liu *et al.*, 2023). Recently, however, Slot *et al.* (2023) demonstrated reduced pollen viability in cut branches of the widespread tropical tree *Muntingia calabura* L. exposed to experimental daytime warming, providing one of the first direct indications of these effects in a non-crop species.

More recently, Werkmeister *et al.* (2024) studied common Cerrado tree *Byrsonima pachyphylla*, using small custom-built chambers to heat developing inflorescences individually *in situ*. They found a significant reduction in fruit set (the proportion of flowers that develop into fruits/seeds) under ~3 °C of daytime warming, a result that could have serious implications for future reproductive success. In contrast, pre-anthesis heating had no impact on pollen viability, suggesting an unexpectedly high temperature resilience of pollen production. Alternatively, Werkmeister *et al.* (2024) note that late initiation (after partial inflorescence development) and the targeted nature (excluding vegetative tissues) of their heating treatment might have limited its potential impact. It is therefore plausible that a heating treatment

initiated earlier and including vegetative tissues would elicit a negative response in pollen viability (as in the study by Slot *et al.*, 2023) and in fruit set.

Here, we have expanded on the previous inflorescence heating experiment of Werkmeister *et al.* (2024) by using a novel whole-tree heating methodology (described by Werkmeister *et al.*, 2022) to gain a better understanding of the impacts that increasing temperatures will have on reproduction in *B. pachyphylla*, and an additional woody Cerrado species, *Davilla elliptica*. We exposed entire individuals to elevated daytime temperatures (initiated prior to inflorescence development) to quantify the impact on pollen viability and fruit set, hypothesising that both viable pollen production and fruit set would be reduced in the heated individuals.

MATERIALS AND METHODS

Study site and species

The field site (14°42′30.1″S, 52°21′01.0″W) was located in an area of Cerrado *típico*, or 'typical Cerrado', in the Bacaba Municipal Park reserve in Nova Xavantina (Mato Grosso, Brazil), situated in a region of transition between the Cerrado biome and Amazon forest (Marimon-Junior and Haridasan, 2005; Araújo *et al.*, 2021). Typical Cerrado, which is a sub-classification of Cerrado *sensu stricto* (tree and shrub woodland) exhibiting 20–50 % tree cover with an average height of 3–6 m (Ribeiro and Walter, 2008), is a dominant vegetation type within the reserve (Mews *et al.*, 2011). The climate (classified as Aw by the Köppen system; Peel *et al.*, 2007) exhibits pronounced wet (from mid-October to April) and dry (from May to October) seasons, reaching peak temperatures towards the end of the dry season (from August to October). Average monthly temperatures are 25 °C and annual precipitation 1300–1500 mm (Marimon *et al.*, 2010), although over recent decades the region has experienced rapid warming and more frequent extreme heatwaves (Araújo *et al.*, 2021; Tiwari *et al.*, 2021).

The investigation focused on two native woody species common to the typical Cerrado, both in the study area (Marimon-Junior and Haridasan, 2005; Mews *et al.*, 2011) and across the Cerrado biome (Ratter *et al.*, 2003): *Davilla elliptica* A.St.-Hil. (Dilleniaceae) and *Byrsonima pachyphylla* A.Juss. (Malpighiaceae, synonymous with *Byrsonima crassa* Nied.; Francener, 2023). Both species are ecologically and socioeconomically important, providing resources to insects (particularly bee pollinators; Martins, 2005; Pessoa-Queiroz *et al.*, 2008), animals (Purificação *et al.*, 2014) and humans (Guilhon-Simplicio and Pereira, 2011; Sousa *et al.*, 2020; Passos, 2023).

Both *D. elliptica* and *B. pachyphylla* flower during the dry season, with flowering peaks in May/June and July/August, respectively; fruits mature in September/October and October/November, respectively (Silvério and Lenza, 2010; G. A. Werkmeister, personal observation). Both species have bisexual flowers (for detailed descriptions, see Supplementary Data Appendix S1.1) that open around dawn and are susceptible only on the day of anthesis (Gottsberger, 1977; Boas *et al.*, 2013).

Experimental design

This investigation was conducted in two phases over 2 years. In 2020 (the pre-treatment year), we carried out a preliminary study of pollen viability in local individuals of *D. elliptica* and *B. pachyphylla* under ambient conditions to gain a better understanding of the natural levels of viability and variation within and between individuals and species. In 2021 (the treatment year), we began the *in situ* whole-tree heating experiment, during which a subset of the individuals studied in 2020 ('treatment individuals') were exposed to elevated daytime temperatures using whole-tree heating structures (WTHSs). To assess the effects of long-term warming on reproductive development in 2021, pollen viability and fruit set were compared between treatment and control individuals. Additionally, pollen viability of both treatment and control individuals was compared between 2020 (when no individuals were heated) and 2021 (when treatment individuals were heated).

In 2020 (the pre-treatment year), 16 healthy, reproductively mature individuals of each species were selected, with mean (±s.d.) height and diameter at stump height (or 30 cm) of 2.5 m (±0.5) and 8.1 cm (±1.8) for *D. elliptica*, and 2.9 m (±0.5) and 9.3 cm (±0.1) for *B. pachyphylla*. During flowering, their pollen was collected for the preliminary study of pollen viability, which was analysed through differential staining. Of these 16 individuals (per species), 6 were randomly selected to be treatment (heated) individuals the following year (reflecting the labour-intensive nature of building WTHSs *in situ*), leaving 10 as controls. Mean height and diameter at stump height were equivalent between treatment and control groups.

In 2021 (the treatment year), WTHSs were built around the six treatment individuals of each species, initiating the whole-tree heating experiment in early March for *B. pachyphylla* and in early April for *D. elliptica* (see Supplementary Data Fig. S1). To capture all stages of floral and fruit development, the WTHSs were erected prior to inflorescence development (beginning earlier in *B. pachyphylla*) and maintained until fruits had matured. During flowering, pollen samples were collected and analysed, and selected flowers were hand pollinated. Fruits were later counted to calculate fruit set, both at an early stage (immediately after flowering) and when mature.

Heating methodology

To heat entire individuals of *D. elliptica* and *B. pachyphylla in situ*, we used novel passive WTHSs previously developed and tested by Werkmeister *et al.* (2022). They were designed to raise internal daytime air temperatures by 2–3 °C, in line with mid-range climate predictions for the Cerrado (Ferreira *et al.*, 2024). Similar to a large open-top chamber, each WTHS (Supplementary Data Fig. S2) was 3.5 m tall, with six straight translucent plastic sides ~2 m long, an entirely open 'roof', and a permeable black plastic base that facilitated passive heating (for details, see Supplementary Data Appendix S1.2). In contrast to classic open-top chamber designs (Marion *et al.*, 1997), the large size, straight vertical sides and open roof of the WTHSs maximized light transmission and facilitated air movement. This

prevented overheating and minimized impacts on variables such as internal humidity and gas concentrations.

Climate data collection

During the treatment year (2021), air temperature and relative humidity (RH) were monitored continuously using Maxim temperature sensors (DS18B20+; accuracy ±0.5 °C) and Elitech Data Loggers (RC-51H; accuracy ±3–5 %), respectively, each mounted at 1.5 m. To minimize the effects of solar radiation, temperature sensors were painted white and sheathed in white heat-resistant cable sleeving, and all sensors were contained in custom 3D-printed radiation shields (Supplementary Data Fig. S3).

Measurement of air temperature began in March 2021, although sensor installation continued until late June (Supplementary Data Appendix S1.3). By this point, sensors were installed at all four sides of three control individuals and six treatments, including four *D. elliptica* and five *B. pachyphylla* (Supplementary Data Table S1). RH sensors were installed in July at the north and south sides of two treatment individuals and one control (all *B. pachyphylla*). Hourly, 2 m surface air temperature measurements from 2010 to the end of 2021 were also acquired from the data assimilation based ERA5-land dataset (9 km resolution; Muñoz Sabater, 2019) for the closest grid reference to the Bacaba field site (14°43′12.0″S, 52°21′36.0″W), providing an uninterrupted long-term climate record.

Pollen viability

Pollen sampling. In June and July 2020 (the pre-treatment year; sampling periods shown in Supplementary Data Fig. S1), pollen samples were collected from the 16 selected individuals of *D. elliptica* and 11 of the 16 individuals of *B. pachyphylla* (reflecting time constraints). Six simultaneous samples were collected from each individual (for details, see Supplementary Data Appendix S1.4), with no temporal replicates. Pollen samples were collected early in the morning on the day of anthesis to minimize contamination (before 10:00 h local time; BRT = UTC − 3). For each sample, all anthers of a single flower were removed using tweezers and placed into a 2 mL Eppendorf tube. Samples were then taken directly to the nearby laboratories at the Nova Xavantina campus of the University of Mato Grosso (UNEMAT) for viability analysis.

Between May and July 2021 (the treatment year; sampling periods in Supplementary Data Fig. S1), pollen samples were collected from all *D. elliptica* and *B. pachyphylla* individuals as they began to flower, attempting to collect samples from both treatments and controls each day. To maximize the number of individuals sampled per day, four samples per individual were collected at any one time (for details, see Supplementary Data Appendix S1.4). Each individual was sampled on multiple days, producing an average of three temporal replicates for *D. elliptica* individuals and four for *B. pachyphylla*. At the time of sampling, treatment individuals had been exposed to higher temperatures for 24–71 days in *D. elliptica* and 107–127 days in *B. pachyphylla* (reflecting its longer period of floral development).

Viability analysis. Pollen sample viability was analysed through differential staining of aborted and non-aborted pollen grains (discussed in Supplementary Data Appendix S1.4) using a simplified version of the classic Alexander stain (as in the study by Peterson *et al.*, 2010). Every day after sample collection, each sample was immediately macerated with 400 μL of the staining solution (Supplementary Data Table S2; previously optimized for the study species and local laboratory conditions). Next, 30 μL of each sample mixture was transferred to microscope slides and gently heated (following the protocol of Peterson *et al.*, 2010). Slides were observed at ×100 magnification under an Eclipse E200 microscope (Nikon, Tokyo, Japan) paired with a Nikon DS-Fi2-U3 camera system. At least five images (of unique microscopic fields) were taken per sample to count and classify pollen grains as aborted (cell walls stained blue/purple) or non-aborted (presumed to be viable; cell protoplasm stained orange/red).

Image analysis (pollen grain classification) was carried out manually using ImageJ software (v.1.51; Rasband, 2018). All pollen grains in each image were counted, with *D. elliptica* and *B. pachyphylla* samples averaging 79 and 314 grains per image, respectively. Pollen viability of a sample was estimated as the percentage of all grains per image that stained orange/red (non-aborted), averaged over all images per sample. Samples of poor quality or containing very few pollen grains were excluded from further analysis.

Fruit set

Hand pollination. Prior to flowering in 2021 (the treatment year), three bud-bearing branches (*D. elliptica*) or inflorescences (*B. pachyphylla*) on each treatment and control individual were selected for hand pollination, evenly distributed around the midsection of each crown. These were excluded from pollen viability sampling. Every morning during flowering, two pollination samples (one per species) were collected from individuals outside the experiment. Each sample contained the anthers of two flowers from three individuals (six flowers in total) that remained constant throughout. The freshly collected conspecific pollen was mixed with a paintbrush and carefully applied to the stigmas of any newly opened flowers on the selected branches/inflorescences, avoiding damage while also ensuring rupture of the stigmatic cuticle present in *B. pachyphylla* (Boas *et al.*, 2013; botanical description in Supplementary Data Appendix S1.1). Hand pollinations continued (May–July in *D. elliptica* and June–September in *B. pachyphylla*) until all flowers on each selected branch/inflorescence had been pollinated. Each was then enclosed within an agricultural net bag to prevent falling or herbivory of fruits and seeds.

Fruit production and analysis. Given that *D. elliptica* sepals form capsules that enclose the ovary after flowering (persisting even when empty; botanical description in Supplementary Data Appendix S1.1), the presence or absence of seeds could not be determined at an early stage. Once mature, capsules were to be collected and counted. However, storms prior to collection caused the loss of

many experimental branches of *D. elliptica*, rendering fruit set data for *D. elliptica* unobtainable.

In *B. pachyphylla*, 2 days after the completion of hand pollination, any developing fruits on each inflorescence were counted. Early fruit set per inflorescence was then calculated as the percentage of pollinated flowers developing into fruits at this stage. Once mature, fruits were collected and counted again. However, storms also caused early detachment and decay of *B. pachyphylla* fruits inside the net bags. Final counts therefore included any fruits within the bags that appeared fully developed and of reasonable size, although not necessarily fully mature. Final fruit set per inflorescence was calculated as a percentage of flowers pollinated. Fruit retention was also calculated as the percentage of developing fruits at the early count that remained until the final count.

Data analysis

Climate data. Field sensor temperature and RH measurements were initially averaged across all sensors installed on each individual, then further averaged across all treatment or control individuals. A continuous record of the heating effect produced by the WTHSs was calculated as the difference between the mean temperature records for treatments and controls. Daily mean values of temperature, heating effect and RH were calculated for the daytime (06:30–18:30 h local time), night-time (18:30–06:30 h) and 'peak hours' (09:00–17:00 h) during which the WTHSs were previously found to be most effective (Werkmeister *et al.*, 2022). Mean diurnal patterns of temperature (treatment and control) and heating effect were also calculated. The insertion of black plastic bases into all WTHSs was erroneously delayed until 21 April; therefore, separate diurnal patterns were calculated for the heating effect pre- and post-base insertion (e.g. Supplementary Data Fig. S4).

Although agreement was not exact, the acquired ERA5-land air temperature dataset (a hybrid of observed data and physics-based time-stepped modelling) showed strong correlation with recorded field sensor data (compared using time series and scatter plots). To produce a complete temperature record for 2021 (including periods without field sensor data) and allow for year-to-year comparisons, the ERA5-land data were therefore taken as 'estimated' control temperatures (although not the real temperatures experienced by our individuals). 'Estimated' treatment temperatures (for both *D. elliptica* and *B. pachyphylla*) were then extrapolated from these using the mean diurnal patterns of WTHS heating effect (pre- and post-base insertion).

Pollen viability and fruit set. For each individual sampled in 2020, pollen viability was calculated as an average of all samples (up to six per individual, collected on a single day). In 2021, given that each individual was sampled across multiple days (with up to four samples taken per day), individual-level viability was calculated as an average of daily mean values. Days with only one sample taken or remaining in the analysis were excluded owing to low reliability. By this point, all 2021 samples from three of the ten *D. elliptica* control individuals had been excluded from further analysis (see Supplementary Data Appendix S1.4). For the remaining study individuals, 3–20 samples were retained in the analysis, averaging 11 per *D. elliptica* individual (collected over 3 days) and 16 per *B. pachyphylla* (over 4 days).

Individual-level fruit set (early and final) and fruit retention values were calculated as the mean of the three branches studied per individual. Treatment and control group means of pollen viability and fruit set were calculated from individual-level results. To quantify variability between individuals, coefficients of variation (CVs) for group-level results were calculated as the s.d. divided by the mean (expressed as a percentage).

Owing to the small sample sizes and sometimes skewed distributions of our group-level data, non-parametric Wilcoxon tests were used for data analysis. Wilcoxon unpaired rank-sum tests were used to assess the significance of differences in individual-level pollen viability and fruit set between the treatment and control groups for each species, both in 2020 (pre-treatment; pollen viability only) and in 2021 (post-treatment). Wilcoxon paired signed-rank tests were used to assess the significance of changes in pollen viability for each individual within the treatment and control groups between the two years. All data analyses were performed using R software (R Core Team, 2021).

RESULTS

Preliminary study pollen viability

Under natural climate conditions in 2020 (the pre-treatment year), all *B. pachyphylla* individuals sampled produced a high percentage of viable pollen grains (mean ± s.e. viability of 92 ± 1 %; Supplementary Data Table S3), displaying low variation both within individuals (Fig. 1) and between individuals (4 % CV; Supplementary Data Table S3). Pollen viability in *D. elliptica* was lower (mean ± s.e. of 70 ± 2 %), with greater variation within (Fig. 1) and between individuals (13 % CV; Supplementary Data Table S3). Pollen viability did not differ significantly between treatment and control groups of *B. pachyphylla* ($R = 0.11$, $P = 0.79$) or *D. elliptica* ($R = 0.03$, $P = 0.96$; Supplementary Data Table S4).

Whole-tree heating experiment

Experimental temperatures. From the start of recording in March 2021 (the treatment year), daytime air temperatures remained relatively stable until August (Fig. 2B), then increased steadily, peaking in September with maximum recorded temperatures of ~44 °C for controls and 49 °C for treatments (although no control sensors recorded on the hottest days), before decreasing again in October. The passive WTHSs erected in early 2021 performed as expected, raising internal air temperatures during the daytime and producing a strong and consistent level of heating during the peak hours (09:00–17:00 h; Fig. 2A), with no discernible impact on night-time temperatures or RH. The heating effect produced by the WTHSs (post-base insertion) was consistent throughout the different stages of the experiment (Fig. 2B; Supplementary Data Table S5), and treatment and control temperatures displayed corresponding responses to natural climate variation (day-to-day and seasonal; Fig. 2B).

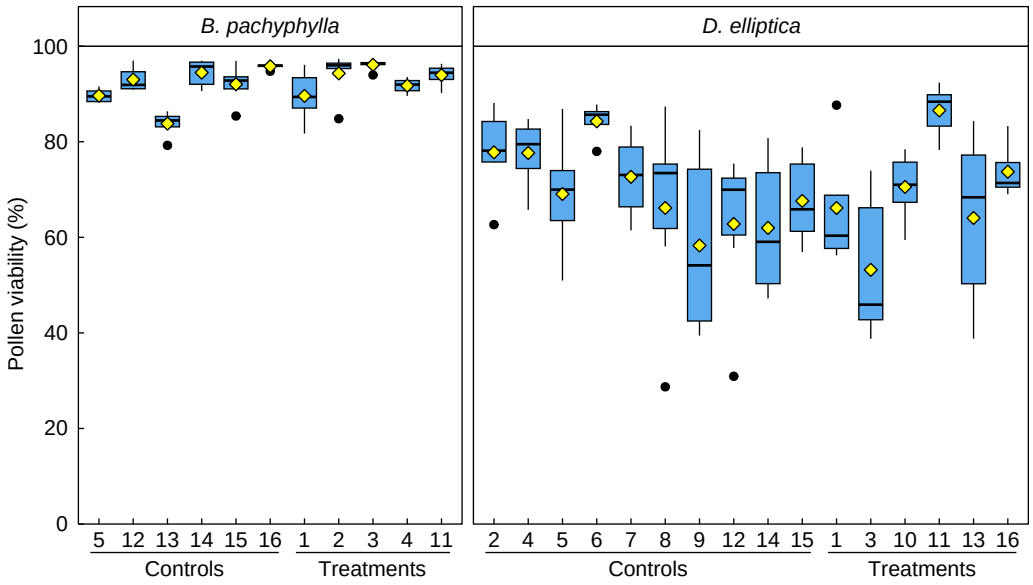

FIG. 1. Pollen viability of samples taken in the pre-treatment year (2020) from tagged individuals (1–16) of each species, showing the division of individuals into control and treatment groups. Yellow diamonds denote mean values.

From the initiation of full-scale heating (black base insertion; 21 April) until the end of flowering (final hand pollinations of *B. pachyphylla*; 26 August; Fig. 2B), the WTHSs produced an average daytime heating effect of 2.2 ± 0.3 °C (s.d.), which rose to 3.0 ± 0.3 °C during the peak hours. Mean daytime temperatures were 29.8 ± 2.3 °C for control individuals and 31.9 ± 2.2 °C for treatments, and peak hour temperatures were 33.4 ± 2.6 and 36.2 ± 2.6 °C, for controls and treatments, respectively. Peak hour treatment temperatures were therefore comparable to daily maximum control temperatures of 36.6 ± 2.6 °C. Treatments experienced mean daily maxima of 39.9 ± 2.4 °C.

Although natural climate variation resulted in partial overlap of temperatures experienced by treatment and control individuals (Fig. 2B), mean and (in particular) maximum temperatures experienced by treatment individuals on pollination days were still distinct from those experienced by the controls (Supplementary Data Fig. S5). Furthermore, comparing the ERA5-land data (estimated ambient/control temperatures) with the complete record of estimated treatment temperatures (Supplementary Data Fig. S1), treatment individuals clearly and consistently experienced daytime temperatures significantly higher than controls (Supplementary Data Fig. S6). Additionally, when comparing the estimated treatment temperatures (2021) with the ERA5-land data from 2010 onwards (e.g. looking specifically at the peak hours; Fig. 2C), treatment individuals were exposed to high temperatures more frequently and to a greater degree in 2021 than in any previous year. Our heating treatment therefore exposed treatment individuals to unprecedented thermal conditions. Ambient temperatures in 2020 and 2021 were not markedly different from one another (Supplementary Data Fig. S1) or from the previous years.

Pollen viability. In 2021 (the treatment year), the heating treatment had a significant positive impact on pollen viability in both species (Fig. 3A; for individual results, see Supplementary Data Fig. S7). Mean ± s.e. viability was 12 ± 3 % higher in the treatment group than in the control group for *B. pachyphylla* ($R = 0.79$, $P = 0.0005$) and 24 ± 9 % higher for *D. elliptica* ($R = 0.67$, $P = 0.014$; Supplementary Data Table S4).

Comparing pollen viability of individuals between 2020 and 2021 also revealed divergent patterns of change between treatments and controls in both species. Of the control individuals sampled in both years, the majority displayed reduced viability in 2021 (five of six *B. pachyphylla* and five of seven *D. elliptica*; Fig. 3B), although not statistically significant at the 95 % confidence level (Fig. 3B; Supplementary Data Table S6). In the treatment individuals (heated in 2021), viability remained similar between years in *B. pachyphylla*, whereas it increased strongly in five of the six *D. elliptica* individuals (Fig. 3B). However, these changes were also not statistically significant (Fig. 3B; Supplementary Data Table S6), potentially owing to the small sample sizes.

Fruit set. In contrast to pollen, there was a significant negative impact of the heating treatment on fruit production in *B. pachyphylla* in 2021 (Fig. 4). Fruit set displayed high variability, both within and between individuals and groups (Fig. 4; Supplementary Data Fig. S8); for example, CVs in early fruit set were 40 and 45 % for the control and treatment groups, respectively (Supplementary Data Table S7). In the control individuals, mean ± s.e. fruit set was 56 ± 7 % at the early count and 48 ± 7 % at the final count (Fig. 4; Supplementary Data Table S7). In the treatment individuals, fruit set was significantly lower at both the early (27 ± 5 %, $R = 0.65$, $P = 0.0075$) and final counts (22 ± 5 %, $R = 0.60$, $P = 0.016$; Fig. 4; Supplementary Data Table S7). Although final fruit set was lower than early fruit set in almost all individuals (Supplementary Data Fig. S8), fruit retention was equivalent between controls and treatments (85 ± 4 and 84 ± 6 %,

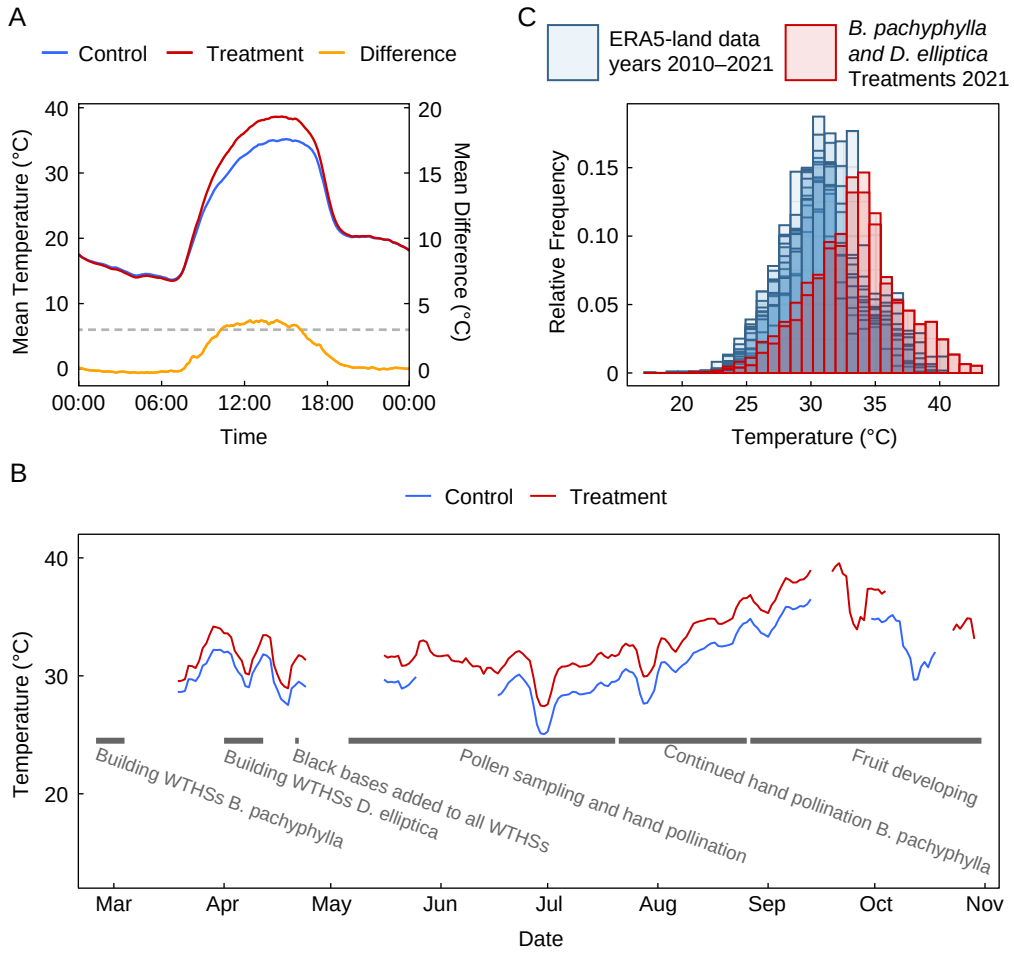

FIG. 2. Temperatures during the whole-tree heating experiment in 2021. (A) Example mean diurnal pattern of 5 min control and treatment temperatures (July 2021), showing the difference between control and treatment (heating effect) on the right-hand axis for clarity. Dashed line indicates target heating of 3 °C. (B) Five-day moving averages of mean daytime (06:30–18:30 h) temperatures in 2021 recorded by field sensors, showing marked periods of the experiment (temperatures summarized in Supplementary Data Table S5). (C) Peak hour (09:00–17:00 h) temperatures between March and November, comparing the ERA5-land data (estimated ambient temperatures) from 2010 to 2021 (inclusive) with the 2021 treatment temperatures for *Davilla elliptica* and *Byrsonima pachyphylla* (estimated using ERA5-land data and diurnal heating patterns).

respectively; Supplementary Data Table S7). Fruiting data for *D. elliptica* were unobtainable owing to storm damage.

DISCUSSION

This experiment, novel in its approach of heating entire, mature individuals of wild tropical tree species *in situ*, is also one of few to assess the impacts of any form of direct heating on their reproductive success (others being: Slot *et al.*, 2023; Werkmeister *et al.*, 2024). Temperatures in the study area have been increasing markedly over recent decades (Marimon *et al.*, 2020; Araújo *et al.*, 2021; Tiwari *et al.*, 2021), implying that local individuals might already be growing at or beyond their thermal optima (Sentinella *et al.*, 2020; Araújo *et al.*, 2021; Tiwari *et al.*, 2021; Doughty *et al.*, 2023). Our experiment added substantial further daytime heating, increasing the potential for temporary exceedance of physiological thresholds, with the expectation that reproduction would be adversely affected.

We examined two processes central to reproduction, namely viable pollen production and fruit set. As expected, fruit set was significantly lower in heated individuals of *B. pachyphylla*, supporting the hypothesis that reproduction at this already very warm site will be negatively impacted by further warming. However, contrary to our hypothesis (and notable given the well-documented thermal sensitivity of pollen development), pollen viability at anthesis was significantly higher under heating in both *B. pachyphylla* and *D. elliptica*. Interestingly, the contrasting responses in pollen and fruit production might suggest a higher sensitivity of female reproductive development in *B. pachyphylla*, challenging the common assumption that male development is the most sensitive to temperature stress.

Pollen viability

Significantly higher pollen viability in treatment individuals (compared with controls) of both study species under heating in 2021 (Fig. 3A) suggests that viable pollen development was not only resilient to, but was positively impacted by, the elevated temperatures to which they were exposed inside the WTHSs. The absence of significant differences in pollen viability between treatment and control groups

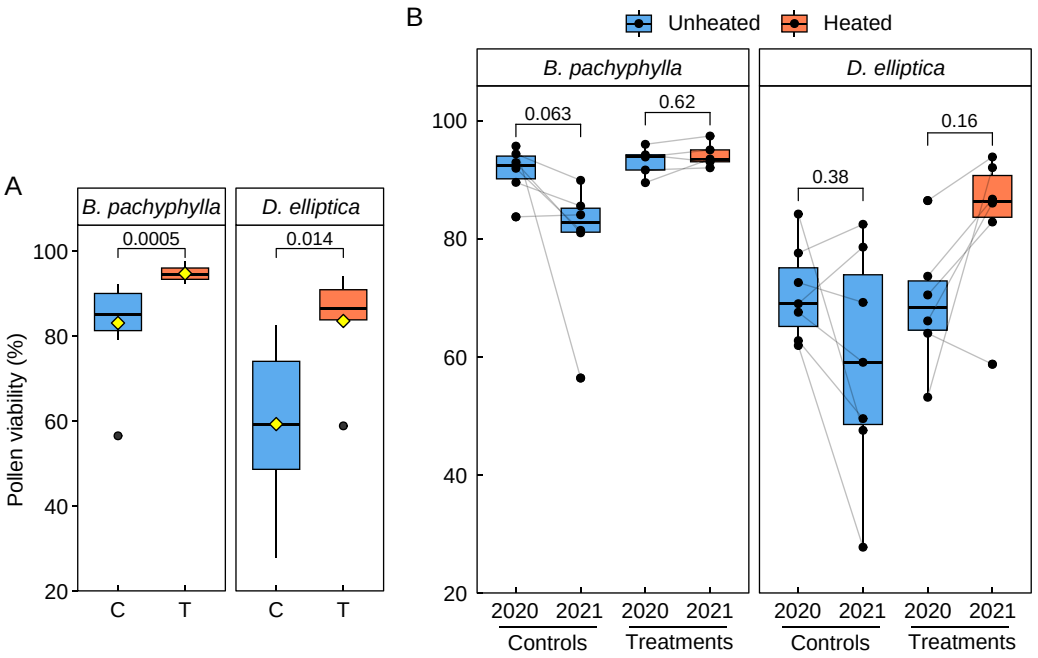

FIG. 3. Pollen viability of: (A) all individuals sampled in 2021 (treatment year), comparing control (C) and treatment (T) groups; and (B) each individual (points connected by grey lines) sampled in both 2020 (pre-treatment year) and 2021, comparing group results between years. Yellow diamonds denote group means. Numbers denote *P*-values of Wilcoxon unpaired rank-sum tests in A and Wilcoxon paired signed-rank tests in B.

under ambient conditions in 2020 (the pre-treatment year; Supplementary Data Table S4), together with the divergent (although not statistically significant) changes in pollen viability of treatment and control individuals from 2020 to 2021 (Fig. 3B), further support the finding that pollen development was enhanced by the elevated temperatures.

In the only previous direct investigation of the effects of temperature on reproduction in Cerrado species, Werkmeister *et al.* (2024) found no significant impact (positive or negative) of daytime heating on pollen viability in *B. pachyphylla*. Although this suggested a strong resilience of pollen development to high temperature, the targeted nature (heating only inflorescences) and delayed initiation of the heating treatment applied by Werkmeister *et al.* (2024) might also have lessened its potential impacts on vegetative tissues, microsporogenesis and pollen development overall. Male reproductive development is energetically demanding, relying heavily on foliar photosynthesis and translocation of carbohydrates to developing anthers and pollen (Ferguson *et al.*, 2021; Liu *et al.*, 2021). The proportion of viable pollen produced at anthesis has also been linked to nutrient provision and competition between developing pollen grains (Carrizo García *et al.*, 2017). By applying whole-tree heating from the earliest possible developmental stages, our experiment addressed the methodological limitations of the study by Werkmeister *et al.* (2024) and, contrary to expectation, resulted in increased pollen viability in both study species. This not only corroborates the previous result of Werkmeister *et al.* (2024) and demonstrates a similar response in *D. elliptica*, but also suggests that the increases in pollen viability under warming might reflect enhanced resource availability owing to the additional heating of vegetative tissues.

This interpretation would suggest that our species are growing below their thermal optima at ambient

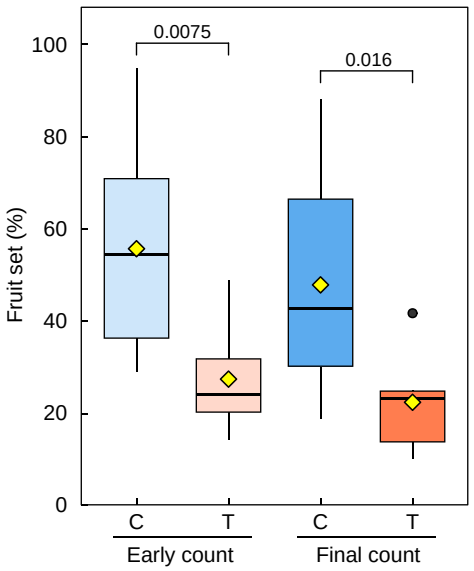

FIG. 4. Early and final fruit set in *Byrsonima pachyphylla* individuals in 2021, comparing control (C) and treatment (T) groups. Yellow diamonds denote group means; numbers denote *P*-values of Wilcoxon rank-sum tests.

temperatures. Optimum temperatures for photosynthesis in tropical forest trees have been suggested to be related closely to their mean maximum daytime temperatures (Slot and Winter, 2017*b*). Given that mean treatment temperatures during peak hours (09:00–17:00 h) were comparable to maximum ambient temperatures (Supplementary Data Table S5), treatment individuals might have experienced optimal temperatures more frequently than controls.

This could have enhanced photosynthetic rates, providing more energy for reproductive development and a greater supply of photosynthates to developing pollen, thereby reducing competition and increasing pollen viability (Carrizo García *et al.*, 2017).

However, this explanation is contradicted by one study of local species that suggests Cerrado trees are growing close to their thermal maxima (rather than optima) for photosynthesis and are already stressed at the onset of the dry season (Araújo *et al.*, 2021), which coincides with floral development in our study species. Nevertheless, Cerrado temperatures peak in August and September (Fig. 2B), exceeding those experienced earlier in the dry season, and local species might be able to acclimate their photosynthetic and respiratory mechanisms to maintain homeostasis during this time (Tiwari *et al.*, 2021; Werkmeister *et al.*, 2022). This includes increasing the thermotolerance of leaf photosystems, raising thermal optima for photosynthesis and downregulating respiration rates (Sastry and Barua, 2017; Slot and Winter, 2017*a*; Cox *et al.*, 2023). It is therefore plausible that long-term warming inside our WTHSs induced physiological acclimation in treatment individuals, positively impacting pollen viability by, for example, altering the balance between photosynthesis and respiration, thus providing more photosynthates to developing pollen (Carrizo García *et al.*, 2017). Given that we did not measure photosynthetic and respiratory activity, both explanations remain speculative. Future investigations would therefore benefit from parallel measurement of such variables.

Although whole-tree physiological responses might partly explain the observed increases in pollen viability, the persistence of viable pollen production under unusually high temperatures also suggests an inherently high thermal tolerance of reproductive development in both study species. Such resilience is particularly surprising given that male reproductive development and viable pollen production are considered highly sensitive to temperature (Sage *et al.*, 2015; Lohani *et al.*, 2020; Goel *et al.*, 2023), especially during the initial stages (microsporogenesis; Pacini and Dolferus, 2016; Raja *et al.*, 2019). Indeed, high growth temperatures (>25–30 °C) have been shown to negatively impact pollen viability in numerous crop species (Luo, 2011; Zhu *et al.*, 2021), including several tropical and sub-tropical tree crops (Higuchi *et al.*, 1998; Kozai *et al.*, 2004; Nava *et al.*, 2009; Lora *et al.*, 2012; Distefano *et al.*, 2018; Bennici *et al.*, 2019). Crop species are, however, bred for high yield in optimal environments, making them more susceptible to stresses (Kapazoglou *et al.*, 2023), and are often studied in controlled environments, which can elicit different responses from field experiments (Mesihovic *et al.*, 2016). This might explain the contrasting results of our *in situ* study on non-crop tropical tree species, which – poorly studied to date – appear to exhibit greater thermal resilience in male reproductive development than inferred from crop-based research.

Nevertheless, our results also contrast with the only other comparable direct warming study of a non-crop tropical tree species, which reported reduced pollen viability in *M. calabura* under passive daytime warming (Slot *et al.*, 2023). However, *M. calabura* is widespread across the tropics, whereas *B. pachyphylla* and *D. elliptica* are prevalent across the Cerrado biome (Ratter *et al.*, 2003; Bridgewater *et al.*, 2004), which is a strongly seasonal environment. The Cerrado dry season is characterized by limited rainfall, low RH, intense irradiance, high temperatures and frequent fires (de Castro *et al.*, 2020), conditions that impose persistent physiological stress. Although both studies focus on tropical trees, the divergent responses observed here and by Slot *et al.* (2023) not only highlight the species-specific nature of reproductive responses to temperature, but are also likely to reflect adaptation of our study species to their more extreme growing conditions (Franco *et al.*, 2008).

Indeed, the study region, throughout which these species are common (Marimon-Junior and Haridasan, 2005; Mews *et al.*, 2011), has been experiencing steady increases in both baseline temperatures and the strength and frequency of heatwaves (Marimon *et al.*, 2020; Araújo *et al.*, 2021; Tiwari *et al.*, 2021). Sustained pollen viability at unusually high temperatures could therefore also reflect local adaptation of reproductive development or, more specifically, viable pollen development to their highly variable high-temperature growth environment (Rieu *et al.*, 2017; Driedonks *et al.*, 2018). Although little evidence of such adaptation has been documented in tree species (Slot *et al.*, 2023), optimum temperatures for pollen germination and tube growth have recently been shown to vary with growth temperature in a limited number of woody species (Hsu and Kim, 2024; Kumarathunge *et al.*, 2024), suggesting that such traits might be more plastic than previously assumed. It is therefore possible that understudied species in extreme environments, such as the Cerrado, might possess adaptive capacities not yet represented in the literature. Expanding our experiment across Cerrado regions with different baseline temperatures could provide valuable insights into the adaptive capacity of reproductive development.

Regardless of the underlying mechanism, initial interpretation of our results would suggest that viable pollen production in both study species is likely to persist and might even increase in the future with the projected rise in Cerrado temperatures. However, this will not necessarily lead to continued or improved reproductive success. Development at high temperatures can also cause less conspicuous variations in pollen grain fitness, which can limit fertilization success, lower the quality of seed produced or even affect seedling growth (Higuchi *et al.*, 1998; Rosbakh *et al.*, 2018). Moreover, the combined stresses of baseline warming, heatwaves and higher night-time temperatures might elicit different responses in pollen viability and vigour (Djanaguiraman *et al.*, 2013; Rosenberger *et al.*, 2024). This study therefore emphasises the need for further investigation and highlights the limitations of studying reproduction in isolation without accounting for the influence of other physiological processes, such as photosynthesis and respiration.

Fruit set

As predicted, higher daytime temperatures significantly reduced fruit set in *B. pachyphylla*. This is consistent with observations in tropical crop species (Higuchi *et al.*, 1998; Chu and Chang, 2020; Matsuda and Higuchi, 2020; Shafqat *et al.*, 2021) and confirms the previous results from targeted heating of independent inflorescences in local

B. pachyphylla individuals (Werkmeister *et al.*, 2024). Average fruit set in the heated individuals was approximately half that of controls (Fig. 4; Supplementary Data Table S7), mirroring the effect observed by Werkmeister *et al.* (2024). Reproductive development and fruit set, like pollen development, are energy-demanding processes that require the production and transport of photosynthates from vegetative tissues, which can be disrupted by heating (Snider *et al.*, 2009; Ruan *et al.*, 2012; Ferguson *et al.*, 2021). However, equivalent reductions in fruit set under both targeted and whole-tree heating, coupled with the positive response in pollen viability under whole-tree heating, suggest that the additional heating of vegetative tissues did not further impair reproductive development. Fruit set was therefore likely affected by high-temperature impacts at the inflorescences specifically.

As outlined in the Introduction, high temperatures can act at any stage (from floral organ initiation to seed maturation) to negatively impact reproductive output (Sage *et al.*, 2015; Wang *et al.*, 2021), although isolated effects post-fertilization (e.g. on embryo development and fruit retention) are much less well studied (Hedhly *et al.*, 2009). In this experiment, fruit set was already significantly lower in treatment individuals than in controls at the early count after pollination (Fig. 4), yet both groups retained ~85 % of their fruits to maturity (Supplementary Data Table S7). The higher treatment temperatures are therefore likely to have acted before the early count (before, during or immediately after fertilization) to reduce fruit set, rather than during fruit development. Additionally, the high fruit retention observed in both groups suggests that fruit development and maturation in *B. pachyphylla* (at least in local individuals) are resilient to the extremely high temperatures experienced during the peak of seasonal heating in September. These findings build on the previous investigation of *B. pachyphylla* by Werkmeister *et al.* (2024), which measured fruit set at maturation alone, by providing further insight into the timing and nature of the impacts of temperature on fruit development.

Owing in part to the greater exposure of the male tissues and gametophytes to the environment, male reproductive development is generally considered more temperature sensitive than female reproductive development (Zinn *et al.*, 2010; Hedhly, 2011; Pacini and Dolferus, 2016). Heat-induced declines in fruit set in many species have consequently been attributed to compromised pollen viability and performance (Sage *et al.*, 2015; Rosbakh *et al.*, 2018; Lohani *et al.*, 2020). In our experiment, however, both treatment and control individuals were subject to the same hand-pollination procedure using a mixture of freshly collected conspecific pollen from additional unheated individuals, which should have provided an excess of viable, compatible pollen to all flowers. Although flowers remained open to insect visitation, and this might have occured more often in controls (regardless of the openness of the WTHSs), available evidence suggests that hand cross-pollination in *B. pachyphylla* is at least as efficient as insect-mediated pollination (Boas *et al.*, 2013; Hughes, 2021). Limited availability of viable pollen was therefore unlikely to be the cause of the observed reduction in fruit set.

High treatment temperatures could still have compromised fruit set by negatively impacting the normal functioning of pollen during the progamic phase (from pollination to fertilization). This includes pollen adhesion, hydration and germination on the stigma; pollen tube growth through the stigma and style to the ovary; and double fertilization of the egg and endosperm mother cells, all of which are vulnerable to temperature stress (Hedhly, 2011; Rosbakh *et al.*, 2018; Raja *et al.*, 2019). Nevertheless, pollen germination and tube growth have been shown to persist (although limited) at temperatures of >40 °C in several tropical species (tested *in vitro*; Kakani *et al.*, 2002, 2005; Hebbar *et al.*, 2018; Mog *et al.*, 2023) and, as previously mentioned, optimum temperatures might be adaptable to growth temperature (Hsu and Kim, 2024; Kumarathunge *et al.*, 2024). Furthermore, pollen is considered to be considerably more sensitive to temperature stress during development than during the progamic phase (Higuchi *et al.*, 1998; Distefano *et al.*, 2018; Raja *et al.*, 2019; Chu and Chang, 2022), and our results indicate that pollen development in *B. pachyphylla* was highly resilient to the treatment temperatures, responding positively to heating. Although untested, this points to an even greater temperature resilience of *B. pachyphylla* pollen during the progamic phase and suggests that reduced fruit set under heating did not result from impaired pollen function.

An alternative explanation might lie in the female tissues. Post-pollination processes also involve complex physical and biochemical pollen–pistil interactions that are highly regulated by the female tissues and gametophytes. Their development and function can be impaired by high temperatures applied pre- or post-anthesis, as reported in a number of tropical and tree crop species (Rodrigo and Herrero, 2002; Hedhly *et al.*, 2003, 2005; Nava *et al.*, 2009; Benlloch-González *et al.*, 2018; Lohani *et al.*, 2020). This can lead, for example, to reduced stigma receptivity; sugar starvation of the pollen tube; reduced levels of attractants (that guide the pollen tube); imbalance of important hormones or reactive oxygen species; fertilization failure; incorrect embryo or endosperm development; or early fruit drop (reviewed by Lohani *et al.*, 2020; Wang *et al.*, 2021). Having not monitored these processes *in vivo*, we cannot pinpoint which were most affected. Nevertheless, the demonstrated resilience of pollen development (and potentially pollen performance) in *B. pachyphylla* implies that temperature-induced limitations on female tissue function might have played a key role in the reduced fruit set observed in heated individuals.

Contrasting responses of pollen and fruit

Taken together, our findings provide important insights into the processes potentially limiting reproduction under warming in our study species, and possibly in other Cerrado taxa. Contrary to common assumptions about the impacts of heat stress on viable pollen production, our results suggest that reproductive success in *B. pachyphylla* might instead be constrained by high-temperature impacts on processes occurring between pollination and early fruit development. Although reduced fruit set could have resulted from impacts on female reproductive function, post-pollination pollen performance, or a combination of the two, the contrasting responses of pollen viability and fruit

set suggest that female reproductive processes might be more temperature sensitive than male reproductive processes. While this has been reported in a very limited number of crop species (e.g. pearl millet and peach; Kozai *et al.*, 2004; Gupta *et al.*, 2015; Djanaguiraman *et al.*, 2018*a*) it is an uncommon observation in species studied to date. Indeed, temperature impacts on female reproductive processes are rarely studied in isolation, and in non-crop species, including tropical trees, even less is known about female development than male development. Our results therefore highlight the importance of considering female function when predicting reproductive outcomes under warming and demonstrate that pollen viability alone is not always a good indicator of reproductive success.

Ecological implications

Although the precise mechanisms remain undetermined, the concurrent findings of this experiment and that of Werkmeister *et al.* (2024) suggest that rising Cerrado temperatures might impose significant limitations on fruit (and therefore seed) production in *B. pachyphylla*, despite potential increases in pollen viability. Fruit set in control individuals was already <50 % given hand pollination and might be even lower under natural pollination (Boas *et al.*, 2013). The decline in fruit set observed in both studies (~50 % reduction under 2–3 °C of heating) could therefore have serious consequences for species recruitment and persistence locally, and potentially across the Cerrado, under projected warming scenarios. Declines in fruiting could also reduce the dispersal capacity of *B. pachyphylla* and limit migration to areas with more favourable environmental conditions (Daibes *et al.*, 2022; McNichol and Russo, 2023), potentially affecting long-term resilience to climate change.

Interestingly, sustained (or enhanced) pollen viability under warming might prove nutritionally advantageous for associated bee pollinators of both study species (Yeamans *et al.*, 2014). Nevertheless, rising temperatures are also likely to affect pollinator phenology, physiology, behaviour and habitat suitability, potentially limiting the likelihood or success of pollination events (Giannini *et al.*, 2012; Lima and Marchioro, 2021; Walters *et al.*, 2022). In addition, changes in flowering phenology (caused by altered environmental cues) and continued fragmentation of the Cerrado biome might cause further reductions in fecundity owing to pollinator limitation, genetic drift, and altered relationships with pollinators and pests (Athayde and Morellato, 2014; Melo *et al.*, 2014; Vilela *et al.*, 2018; Gérard *et al.*, 2020). These combined effects could have further repercussions for pollinators and other fauna (Butt *et al.*, 2015; Rabeling *et al.*, 2019) and for people, given the socioeconomic and ethnopharmacological uses of *B. pachyphylla* (Bonacorsi *et al.*, 2011; Guilhon-Simplicio and Pereira, 2011; Passos, 2023).

Although the high temperature resilience of pollen development in both study species might point to a trend among Cerrado species, the absence of fruit set data for *D. elliptica* means that we cannot say whether it would demonstrate the same, ultimately negative response to heating as *B. pachyphylla*. The species-specific nature of reproductive responses to temperature (Hovenden *et al.*, 2007; Gray and Brady, 2016) also means that it remains uncertain whether our results would be replicated in other unstudied Cerrado species. Nevertheless, possibly owing to a combination of water, nutrient and pollen limitation, many Cerrado plants already exhibit low fruit set in natural conditions (Montesinos and Oliveira, 2015). Many woody species also flower during the dry season, often during the peak of seasonal heating (Batalha and Martins, 2004; Rabeling *et al.*, 2019) when potentially already experiencing significant heat and water stress. Reproduction might therefore be particularly vulnerable to additional warming. It is thus highly plausible that additional species, both here and in other comparably extreme ecosystems, will exhibit similar declines in reproductive success under climate warming, with interspecific variation eventually leading to possible changes in species composition and community structure (Grubb, 1977; Vilela *et al.*, 2018; Borghetti *et al.*, 2021; Daibes *et al.*, 2022; Hofmann *et al.*, 2025). Further investigation into reproductive thermal thresholds is therefore warranted, potentially through the expansion of our methodology to other Cerrado species and physiognomies, and even other tropical savannah ecosystems.

CONCLUSION

This investigation of reproduction under *in situ* whole-tree heating provides novel evidence for how common woody Cerrado species might respond to increasing temperatures. Although pollen viability in both *B. pachyphylla* and *D. elliptica* was significantly higher under warming, demonstrating an unexpected resilience to elevated daytime temperatures, fruit set in *B. pachyphylla* declined significantly. This suggests that reproductive success might instead be constrained by post-pollination processes, potentially associated with temperature impacts on female tissue development or function, which remain comparatively understudied. Our findings emphasise the importance of considering whole-tree physiological responses to warming and evaluating both female and male components of reproduction when assessing reproductive resilience to climate change.

The overall negative effects of warming on reproductive success could have important implications for species persistence and, ultimately, community structure and function. Although further investigation is required to determine whether these responses might be widespread across Cerrado species, this study represents an important initial step towards understanding how reproduction in the Cerrado, and perhaps other tropical savannah ecosystems, will respond to a changing climate. More broadly, it highlights the need for expanding the literature on the impacts of increasing temperatures on tropical species reproduction and demonstrates the potential for direct environmental manipulation experiments in understudied ecosystems.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following. Appendix S1: supplementary methodological information. Figure S1: mean daytime and

night-time temperatures for the years in which pollen samples were collected (based on the ERA5-land data and estimated treatment temperatures), indicating the sampling periods. Figure S2: image of the first whole-tree heating structure erected in the Cerrado field site. Figure S3: images of the 3D printed radiation shield. Figure S4: mean diurnal pattern of heating effect produced by whole-tree heating structures post-base insertion, based on recorded temperatures. Figure S5: mean and maximum recorded daytime air temperatures experienced by *Byrsonima pachyphylla* individuals on pollination days. Figure S6: estimated hourly daytime temperatures experienced by control and treatment individuals of both study species between March and November 2021. Figure S7: individual-level pollen viability 2021. Figure S8: individual-level early and final fruit set for *Byrsonima pachyphylla* in 2021. Table S1: summary of temperature sensors being deployed in the field. Table S2: staining solution. Table S3: mean pollen viability of each group and species in each year. Table S4: comparisons of pollen viability between control and treatment groups of each species in each year, including results of Wilcoxon unpaired rank-sum tests. Table S5: summary of recorded control and treatment temperatures and heating effect throughout different periods of the whole-tree heating experiment. Table S6: Wilcoxon paired signed-rank test results comparing pollen viability values between 2020 and 2021 for individuals sampled in both years. Table S7: fruit set and fruit retention of control and treatment individuals of *Byrsonima pachyphylla* in 2021, showing the differences between groups and results of Wilcoxon unpaired rank-sum tests.

FUNDING

This work was supported primarily by the Natural Environment Research Council (NERC) SPHERES Doctoral Training Partnership under grant NE/L002574/1, the NERC grant ARBOLES (NE/S011811/1), the Royal Society grant FORAMA (ICA\R1\180100), and the Climate Research Bursary Fund awarded by the Priestley Centre for Climate Futures (University of Leeds, UK). Additionally, we thank the National Council for Scientific and Technological Development (CNPq) for financial support of the projects PELD (441572/2020-0) and FAPEMAT (0346321/2021).

ACKNOWLEDGEMENTS

We thank David Ashley and Santiago Clerici (University of Leeds, UK) for their technical support throughout, and all members of the Laboratório de Ecologia Vegetal at the Nova Xavantina campus of UNEMAT (Universidade do Estado de Mato Grosso, Brazil) who supported the investigation teams. Further thanks to Professor Rodrigo Reis and Professora Karina de Cassia Faria for the use of space and equipment in the Laboratórios de Sementes e Genética (UNEMAT), respectively.

AUTHOR CONTRIBUTIONS

Georgina A. Werkmeister: Conceptualization, Methodology, Funding acquisition, Resources, Project administration (lead), Investigation, Formal analysis, Data curation, Visualization, Writing—original draft, Writing—review and editing. David R. Galbraith & Emanuel Gloor: Conceptualization, Methodology, Funding acquisition, Supervision (lead), Writing—review and editing. Márcia Cardoso Silva: Project administration, Investigation. Jairo Matos Rocha: Methodology, Project administration, Investigation. Paulo Alves Silva: Project administration, Investigation. Bruno Gonçalves Lopes: Investigation. Daniel Ferreira Oliveira: Project administration, Investigation. Regiane Batista Santos: Investigation. Denilson Mendes Santos: Investigation. Beatriz Schwantes Marimon & Ben Hur Marimon-Junior: Conceptualization, Funding acquisition, Resources, Supervision, Writing—review and editing. Oliver L. Phillips: Funding acquisition, Writing—review and editing.

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