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RESEARCH ARTICLE

The temperature optima for pollen germination and pollen tube growth of coconut (*Cocos nucifera* L.) strongly depend on the growth temperature

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Abstract

Understanding trait variation in response to temperature is important to predict how crops respond to rising temperature. Although we have a sound understanding of the effects of increasing temperature on growth and development of crops, a robust assessment of how crop reproductive processes are affected by climate warming is still lacking. In this study, we experimentally investigate how the growth temperature affects the cardinal temperatures of in vitro pollen germination of widely distributed tree crop species *Cocos nucifera* L. (cultivar Sri Lankan Tall). We hypothesize that temperature optima for pollen germination and pollen tube growth would be determined by the growth temperature. Our results showed that the temperature optima of pollen germination and pollen tube growth were higher at relatively warmer sites (sites where the mean annual temperature $\sim 28^{\circ}\text{C}$) compared to the cooler sites (sites where the mean annual temperature $\sim 22^{\circ}\text{C}$). The two processes were better coordinated at warmer sites. We speculate that tropical tree species that are currently growing in relatively cooler environments may have the capacity to perform their reproductive physiological functions in future warmer climates without any substantial negative impacts. Findings of this study should prove useful in quantifying the potential impacts of climate warming on tropical agroecosystems, improving the representation of plant reproduction in crop models.

Keywords: Global warming; tree crops; thermal niche; coconut; crop models

Introduction

Global warming has been causing significant adverse impacts on natural environmental systems. It is expected that the global average temperature will increase by 0.3 to 0.7°C during the period 2016–2030 (IPCC, 2014). Additionally, a 2–4°C increase is predicted with frequent extreme temperature events such as heat waves in the latter part of the 21st century (Huntingford *et al.*, 2012; Wang *et al.*, 2023). With the increasing concern over the effects of climate change on plants, understanding the responses of crops to increasing atmospheric temperature has become of paramount importance (Battisti and Naylor, 2009). Temperature is one of the principal factors affecting growth and development of crops; therefore, understanding how these processes respond to temperature is important to make predictions on how crops will respond to warming in future

climates. Although we have a sound understanding of the impact of rising temperature on growth and development of crops including trees (Choury *et al.*, 2022; Drake *et al.*, 2017; Kumarathunge *et al.*, 2020; Lizumi *et al.*, 2017), we lack a robust quantitative assessment of how crop reproductive processes are affected by global warming. The reproductive phase of plants is considered one of the most sensitive and vulnerable stages to increasing temperature (Hedhly *et al.*, 2005). Even though past studies provide evidence for the negative impacts of rising temperatures on the reproductive physiology of crops, including tree crops (Abhayapala *et al.*, 2018; Battisti and Naylor, 2009; Firon *et al.*, 2006; Rodriguez-Garay and Barrow, 1988), empirical information on how crop reproduction processes are affected by the climate of their growing environment is still not available in past literature, limiting accurate representation of the crop reproduction process in crop models.

The impacts of increasing temperature on crop reproductive performances mainly depend on whether the given reproductive process is operated at temperatures above or below the thermal optimum of that process. Many authors have attempted to describe reproductive heat tolerance of crops by investigating the cardinal temperatures (i.e. the minimum, optimum, and maximum temperature) for *in vitro* pollen germination. For example, Kakani *et al.* (2002) reported that pollen viability and germination in groundnut reduce at temperatures above 33°C. Similarly, reduced boll retention and yield have been reported for cotton at temperatures above 30°C during flowering (Kakani *et al.*, 2005). Several authors provide evidence for reduced pollen germination, pollen tube growth, and fruit set due to high temperature in tree crops such as coconut (Amarasinghe *et al.*, 2014; Ranasinghe *et al.*, 2010; Ranasinghe *et al.*, 2018; Hebbar *et al.*, 2020), almond (Sorkheh *et al.*, 2011, 2018), mango (Sukhvibul *et al.*, 2000), and peach (Hedhly *et al.*, 2005). These cardinal temperatures have been widely used for selecting crop varieties for high-temperature tolerance.

Empirical studies have shown that the optimum temperature for plant physiological processes such as photosynthesis varies geographically due to the long-term adaptation of species to the thermal environment of the location of origin (see Kumarathunge *et al.*, 2019). Additionally, plants have the capacity to temporarily adjust these optimum temperatures in response to the seasonal changes in the temperature of the plants' growing environment, a response known as temperature acclimation (Way and Sage, 2008; Yamaguchi *et al.*, 2016). Much of our current understanding of temperature adaptation and acclimation of plant physiological processes has been principally limited to physiological processes such as photosynthesis, respiration, and plant water relations (Kumarathunge *et al.*, 2019; Atkin *et al.*, 2015; Blackman *et al.*, 2019; Blackman *et al.*, 2017). Studies on temperature adaptation or acclimation of plants' reproductive physiological processes are extremely rare in past literature, making it difficult to accurately predict the impact of global warming on plants in general, and crops in particular in future climates using crop models.

In this study, we attempted to resolve how the air temperature of plants' growing environment affects the reproductive physiology of tree crops by investigating the cardinal temperatures of *in vitro* pollen germination. We utilized *Cocos nucifera* L. (cultivar Sri Lankan Tall), a tropical tree crop species, as a test crop, which grows across a wide temperature range from 22 to 35°C in Sri Lanka and countries in humid and sub-humid tropics. We hypothesize that temperature optima for pollen germination and pollen tube growth would be determined by the growth temperature; therefore, temperature-response curves with different optimum temperatures may be observed for trees growing in cooler and warmer environments, respectively. We tested this hypothesis against the alternative hypothesis of similar temperature-response curves of pollen germination and pollen tube growth for trees growing in contrasting thermal environments: relatively warmer sites (where the mean annual air temperature \sim 28°C) and cooler sites (where the mean annual air temperature \sim 22°C). We collected pollen from coconut palms growing across a temperature gradient of 7°C and characterized the temperature response of *in vitro* pollen germination and pollen tube growth. Our primary objective was to describe the effect of different growth thermal environments on the temperature response of pollen germination and pollen tube growth of tree crops using coconut as a test crop.

Materials and Methods

Experimental sites, growth conditions, and planting material

Six mature coconut plantations distributed across an elevation gradient from 2 to 838 m were selected to determine the effect of growth temperature on the temperature-response functions of pollen germination and pollen tube growth. The mean annual temperature of different sites ranged from 22 to 28°C (Table 1). The locations were Lunuwila, Puttalm, Maduruoya, Doluwa, Bowala, and Pussellawa. These six sites can be broadly categorized into two contrasting growth temperature groups: sites with low growth temperatures (where the mean annual air temperature ~ 22°C, 3 locations) and sites with relatively high growth temperatures (where the mean annual air temperature ~ 28°C, 3 locations, Table 1). To avoid potential confounding effects of other environmental and soil variables on the measured temperature responses other than the sites' mean growth temperature, the following factors were considered when selecting plantations and individual palms within the selected plantations for sample collection. All the six plantations were 25–30 years old and belonged to the land suitability classes S3 or S4 (Somasiri *et al.*, 1994) as classified by the Coconut Research Institute of Sri Lanka (CRISL) and were managed according to the recommended management practices by the CRISL. Inflorescence sampling was performed during the latter part of the rainy season to make sure that the individual palms were not affected by soil moisture stress during the sampling period.

Inflorescence sampling and in vitro pollen germination

From each plantation, six representative coconut palms were used for pollen sample collection. A recently opened inflorescence (2–6 days after spathe opening) was selected from each tree to harvest the male flowers. Mature, unopened male flowers were harvested from the middle part of the inflorescence between 8.00 and 10.00 am (Ranasinghe *et al.*, 2018) in June–July 2019. To avoid pollen desiccation, soon after sampling, the collected male flowers were kept in an insulated box half filled with ice and transported to the laboratory on the same day and stored at 7°C before processing and further analysis (Kakani *et al.*, 2002, Ranasinghe *et al.*, 2010, Ranasinghe *et al.*, 2018).

Pollen individual male flowers were extracted by slicing anthers using a needle. The male flowers of two palms (out of six) were randomly pooled and three sub-samples were generated before using them for the pollen germination test to minimize any confounding effects due to inherent variation between individual palms on the temperature responses (Ranasinghe *et al.*, 2010). Hence, the analysis contained three biological replicates. A growing media was prepared for in vitro pollen germination following Ranasinghe *et al.* (2010) as described below. In total, 100 g of sucrose, 0.125 g of boric acid, 0.54 g of calcium nitrate, 0.1 g of magnesium sulfate, and 0.1 g of potassium nitrate were added to a 1-liter flask and filled up using distilled water up to 1 liter. Two sets of pollen were prepared to determine pollen germination and pollen tube growth, respectively. Pollen was dusted into sample tubes (i.e., 1.5 ml microcentrifuge tubes with safety lid) containing 0.5 ml of growth medium. For each biological replicate, three microcentrifuge tubes per incubation temperature treatment were used for the germination test and pollen tube growth measurements. The tubes were then incubated at temperatures ranging from 22 to 40°C at 2°C intervals (MIR-254-PE Cooled Incubator, PHC, Europe). Relative humidity of the incubator was maintained at 75–80% at each temperature.

Ranasinghe *et al.* (2010) suggested that pollen germination of coconut under room temperature starts within the first 30 min after incubation and stops after 16 h. Therefore, after 24 h of incubation, the number of germinated and non-germinated pollen at each incubation temperature was counted under the light microscope (magnification $\times 10$). A pollen grain was considered germinated if it had produced a pollen tube that was longer than the diameter of the pollen grain (Kakani *et al.*, 2002; Ranasinghe *et al.*, 2018). Three microscopic slides were prepared from one

Table 1. Parameters of the temperature response of pollen germination and pollen tube growth (Equation (1))

Site	Latitude	Longitude	Mean annual temperature (°C)	T_{opt} (Pollen germination; °C)	T_{opt} (Pollen tube growth; °C)	P_{max} (pollen germination; %)	P_{max} (pollen tube growth; μm)	Ω (pollen germination; °C)	Ω (pollen tube growth; °C)
Site with low growth temperature									
Paradeka	7.107	80.605	22.6	25.6 (0.3)	15.7 (7.8)	69.7 (1.4)	37.9 (7.6)	9.6 (0.4)	21.6 (6.3)
Bowala	7.164	80.643	22.9	24.6 (0.5)	17.1 (5.1)	71.7 (1.1)	35.9 (4.4)	13.0 (0.6)	20.9 (4.3)
Doluwa	7.177	80.556	23.8	25.8 (0.3)	14.5 (8.1)	68.0 (1.2)	37.3 (7.5)	9.4 (0.4)	23.3 (6.5)
Site with high growth temperature									
Maduruoya	7.829	81.138	27.2	26.8 (0.2)	25.8 (0.6)	58.7 (0.9)	31.0 (0.8)	10.1 (0.3)	12.1 (0.8)
Bandirippuwa	7.337	79.877	27.4	30.3 (0.2)	29.7 (0.2)	65.5 (1.8)	34.7 (1.2)	7.0 (0.2)	7.7 (0.4)
Puttalam	8.035	79.896	27.7	28.6 (0.2)	27.6 (0.2)	60.3 (1.4)	40.5 (1.0)	7.4 (0.2)	8.2 (0.3)
P -value of ANOVA for the comparison between cool vs warm sites	-	-	-	0.039	0.001	0.023	0.590	0.178	0.001

T_{opt} (Pollen germination) – temperature optimum for pollen germination, T_{opt} (Pollen tube growth) – temperature optimum for pollen tube growth, P_{max} (pollen germination) – pollen germination percentage at the optimum temperature, P_{max} (pollen tube growth) – pollen tube length at the optimum temperature, Ω (pollen germination; °C) – the temperature difference from T_{opt} where the pollen germination rate falls to 37% of its pollen germination rate at T_{opt} , Ω (pollen tube growth; °C) – the temperature difference from T_{opt} where the pollen tube length falls to 37% of its pollen tube length at T_{opt} . Values within the parentheses are standard errors of estimates.

microcentrifuge tube of pollen and were used to count pollen germination at each incubation temperature treatment. The pollen germination percentage was determined by dividing the number of germinated pollen grains by the total number of pollen grains per field of view and expressed as a percentage (Ranasinghe *et al.*, 2010; Ranasinghe *et al.*, 2018). The average germination percentage of three slides was recorded as the germination percentage value for a given biological replicate.

Similar to the pollen germination test, a separate set of microcentrifuge tubes of pollen with growth medium was prepared to measure the pollen tube length at different incubation temperatures. However, to avoid measurement errors due to lengthy pollen tubes after 24 h of incubation, pollen tube length was measured after three hours of incubation time. The pollen tube lengths were measured using an ocular micrometer fitted to the eyepiece of the microscope (magnification $\times 40$). Similar to pollen germination measurements, three microscopic slides were prepared from one microfuge tube (i.e. one replicate) of pollen and were used to measure pollen tube length at each incubation temperature treatment. Three microscopic fields per slide were observed, and the mean of three random pollen tube lengths was taken. The average pollen tube length of three slides was recorded as the pollen tube length value for each biological replicate.

Estimation of temperature-response parameters of pollen germination and pollen tube growth

A mathematical model was fitted to describe the temperature-response curves of pollen germination and pollen tube growth. The model was of the form (Equation (1))

$$P(T_i) = P(T_0) e^{-\left(\frac{T_i - T_0}{\Omega}\right)^2} \quad (1)$$

Where $P(T_i)$ is the rate of the pollen germination at the in situ temperature T_i and $P(T_0)$ is the rate of the pollen germination at the optimum temperature T_0 . Ω is the difference in temperature from T_0 , where the pollen germination falls to e^{-1} of its value at T_0 (the temperature difference from T_0 where the pollen germination rate falls to 37% of its pollen germination rate at T_0). Large values of Ω reflect wider temperature-response curves, while small values of Ω reflect narrow curves. The model, which was originally derived by June *et al.* (2004) to describe the temperature response of photosynthetic electron transport rate, has been widely used in past literature to describe the rate temperature response of biological processes, including net photosynthetic rate (Drake *et al.*, 2017; Kumarathunge *et al.*, 2020) data sets. The equation assumes the process rate is symmetric around the optimum temperature, and it appeared to be appropriate for the data presented in this study.

Statistical analysis

The parameters of equation 1 were estimated in a non-linear regression framework using the *nls* function within the *nlme* package in R version 3.5.1 (R Development Core Team, 2012). The 95% confidence intervals of the temperature-response curve and its parameters were estimated using the *confint2* function within the *nlstools* R package. The least squares linear regression (*lm* function within *Car* R package) was used to test the relationship between the temperature-response parameters and growth temperature. Analysis of variance was used to detect significant differences in parameters between warmer and cooler growing environments. The dataset used for this study and the analysis code to reproduce all the results, including the figures and tables, are available at (<https://bitbucket.org/Kumarathunge/pollenger>).

Results

Temperature response of pollen germination

The temperature response of pollen germination showed a peaked response to temperature at sites with different growth temperatures (Figure 1). At relatively warmer sites, the response displayed a 'full' curve within the bounds of measurement temperature range, 22–40°C (Figure 1a, b, and c).

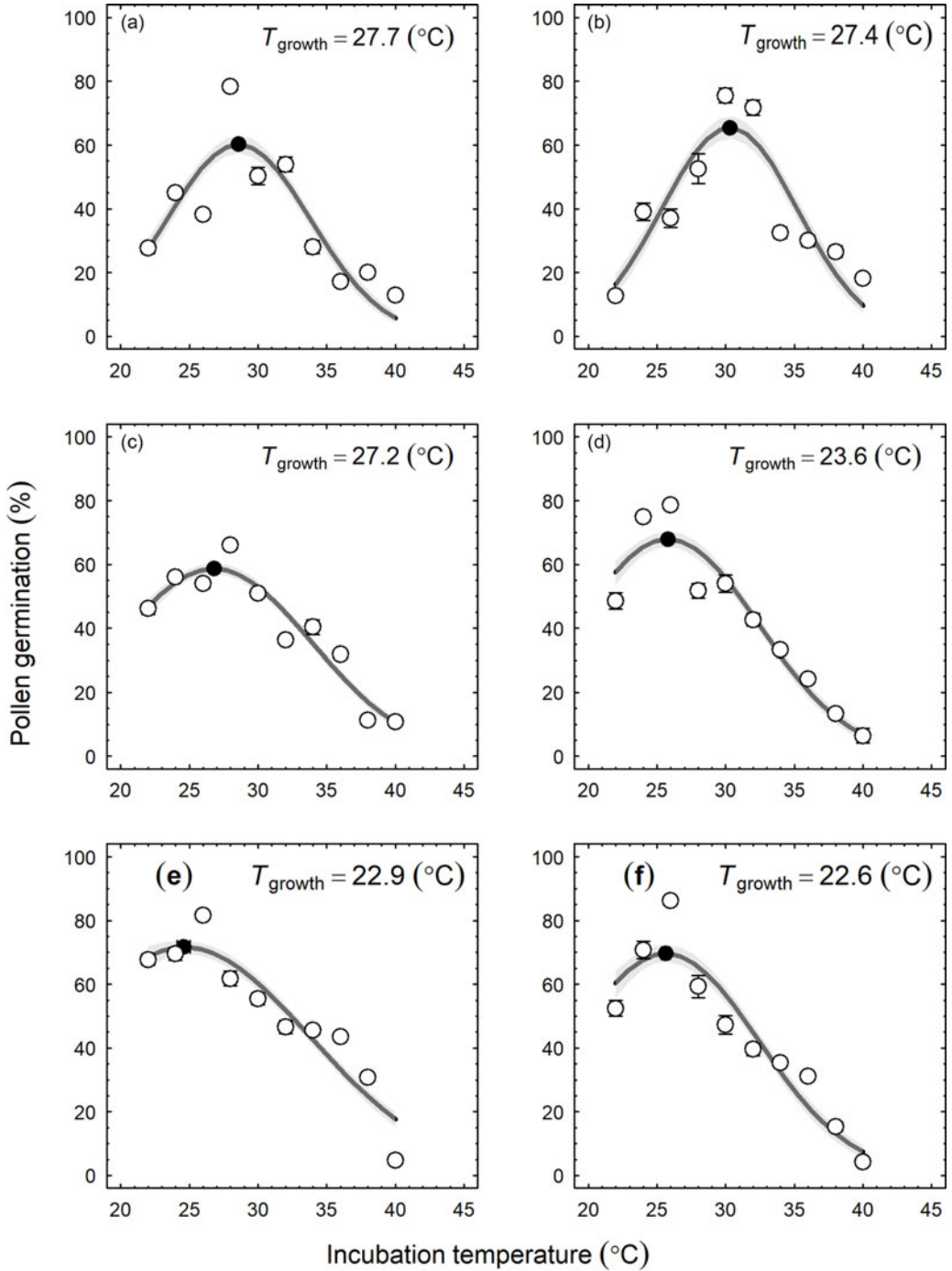


Figure 1. Temperature response of in vitro pollen germination of coconut (cultivar Sri Lankan Tall) growing at different thermal environments. Points reflect the mean ($\pm 1\text{SE}$, $n = 8$), lines reflect functions fit to the data, and the shaded areas reflect 95% CI for the model predictions.

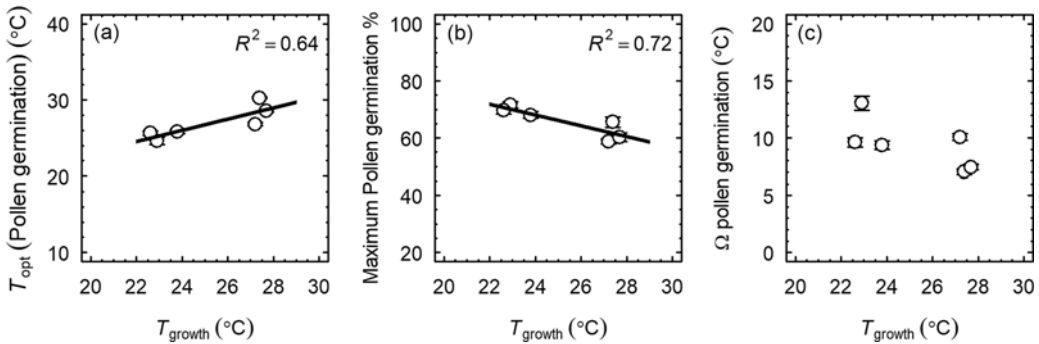


Figure 2. Temperature response parameters of pollen germination: (a) optimum temperature for in vitro pollen germination, (b) maximum pollen germination percentage, and (c) breadth of the temperature-response curve of coconut (cultivar Sri Lankan Tall) growing at different thermal environments. Points reflect the mean ($\pm 1SE$, $n = 8$), and lines reflect the least square regression fit to the data.

However, at relatively cooler sites, the temperature-response curve showed a peak followed by a declining trend with increasing measurement temperature, which contrasts with the clear peaked relationship observed at the warmer sites (Figure 1d, e, and f).

The optimum temperature for pollen germination showed an increasing trend with the growth temperature. The optimum temperature was significantly higher ($p < 0.05$) at the sites where the growth temperature was high compared to the sites with low growth temperatures (Figure 2a, Table 1). However, when considering warmer and cooler sites separately, within-site variability of the temperature optimum for pollen germination was not significantly different. The pollen germination percentage at the optimum temperature also showed a decreasing trend with the growth temperature, where the pollen germination percentage was significantly higher at the cooler sites compared to the warmer sites (Figure 2b, Table 1).

The breadth of the temperature-response curves (Ω) of pollen germination percentage of coconut growing at different thermal environments did not show a significantly different trend ($p > 0.05$) with growth temperature (Figure 2c, Table 1). Hence, the breadth of the temperature-response curve was similar across the growth temperature range.

Temperature response of pollen tube growth

Similar to pollen germination, temperature response of pollen tube growth showed a peaked distribution with temperature. At relatively warmer sites, the response showed a clear peaked pattern (Figures 3a, b, and c), but at relatively cooler sites, the response showed a declining trend without a clear peak with increasing temperature (Figures 3e, f, and g). The optimum temperature for pollen tube growth was significantly higher ($p < 0.05$) at warmer sites compared to the cooler sites (Figure 4a, Table 1). However, when considering warmer and cooler sites separately, within-site variability of the temperature optimum for pollen growth was not significantly different.

In contrast to the pollen germination percentage at the optimum temperature, pollen tube length at the optimum temperature was not significantly different ($p > 0.05$) between warmer and cooler sites (Figure 4b, Table 1). However, the breadth of the temperature-response curves of pollen tube growth (Ω pollen tube growth) showed a negative relationship with increasing temperature (Figure 4c, Table 1) where at cooler growth temperatures, the temperature-response curve becomes narrower (smaller Ω) compared to the broader temperature-response curves observed at higher growth temperature (larger Ω).

Figure 5 shows the relationship between the optimum temperature for pollen germination and the optimum temperature for pollen tube growth. In relatively warmer sites, the optimum

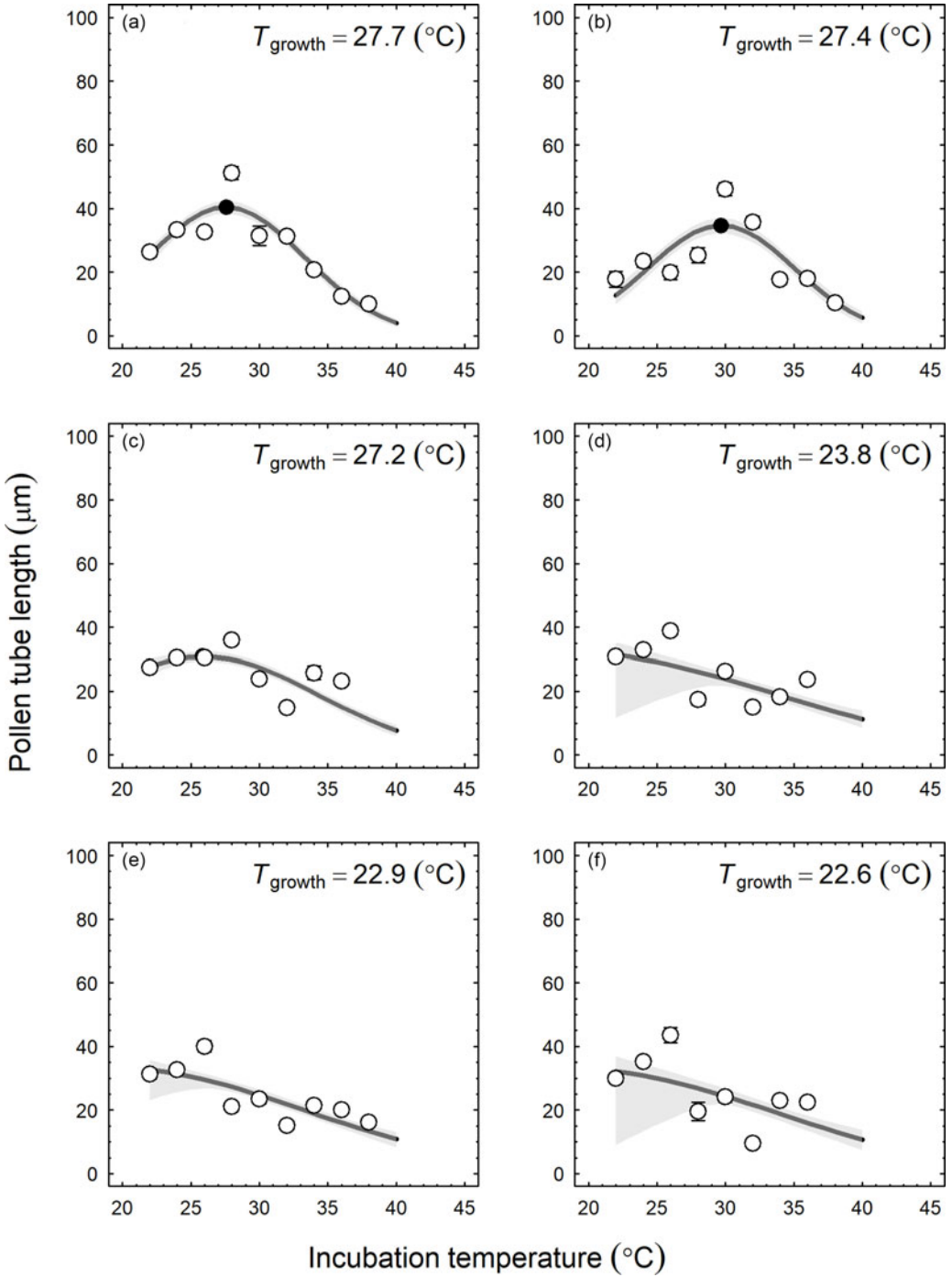


Figure 3. Temperature response of in vitro pollen tube growth of coconut (cultivar Sri Lankan Tall) growing at different thermal environments. Points reflect the mean ($\pm 1\text{SE}$, $n = 8$), lines reflect functions fit to the data, and the shaded areas reflect 95% CI for the model predictions.

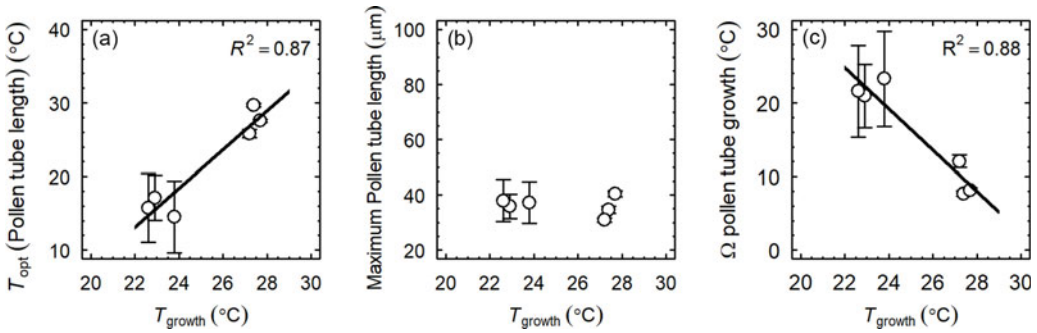


Figure 4. Temperature response parameters of pollen tube growth (a) optimum temperature for in vitro pollen tube growth, (b) maximum pollen tube length, and (c) breadth of the temperature-response curve pollen tube growth of coconut (cultivar Sri Lankan Tall) growing at different thermal environments. Points reflect the mean ($\pm 1SE$, $n = 8$), and lines reflect least square regression fit to the data.

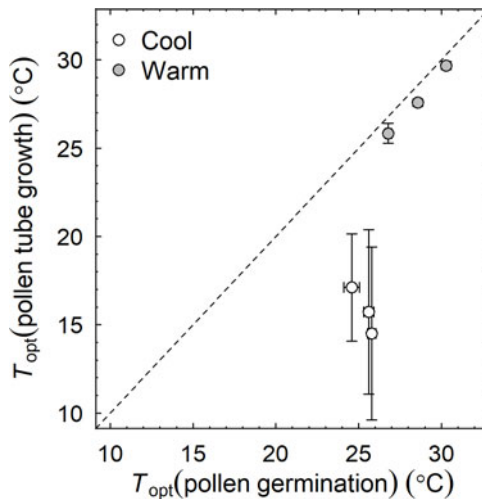


Figure 5. Relationship between the optimum temperature for pollen tube growth and the optimum temperature for pollen germination of coconut (cultivar Sri Lankan Tall) growing at different thermal environments. Points depict the temperature optimum values ($\pm 1SE$) and the dashed line depicts the 1:1 relationship.

temperature for pollen germination was similar to the optimum temperature for pollen tube growth. However, at cooler sites, the optimum temperature for pollen tube growth was 8–10°C lower than the optimum temperature for pollen germination. Taken together, these results suggest that in relatively warmer sites, both processes, pollen germination and pollen tube growth, are strongly coordinated compared to the cooler sites.

Discussion

This study provides clear evidence that the temperature response of coconut pollen germination and pollen tube growth is strongly determined by the growth temperature. At relatively warmer sites, the temperature optima for pollen germination and pollen tube growth were higher compared to the cooler sites. Further, at warmer sites, the temperature-response curves were broader compared to the narrow response curves observed at sites with low growth temperatures.

Hence, the results of this study support our hypothesis that pollen germination and pollen tube growth of coconut responded to increasing temperature in a manner that reflect differentiated temperature-response curves relative to the temperature of the species' growing environment.

Results of this study further suggest that pollen germination and pollen tube growth of a widely distributed coconut species (*viz.* Sri Lankan Tall) responded to warming in a manner that reflected differentiated temperature-response curves despite the broader climate distribution of the species. Hence, it would reflect the potential of species' ability to adjust its pollen germination and pollen tube growth responses across wide-ranging thermal environments. Many empirical studies show that temperature responses of plant physiological processes vary geographically, suggesting adaptation of species to their thermal environment of origin (Blackman *et al.*, 2017; Gunderson *et al.*, 2009; Kumarathunge *et al.*, 2019). Additionally, plants have the capacity to change their temperature responses following seasonal changes in ambient temperature (Atkin and Tjoelker 2003; Crous *et al.*, 2013; Hall *et al.*, 2013; Way *et al.*, 2017; Yamaguchi *et al.*, 2016). Our results on increasing temperature optima of pollen germination and pollen tube growth with increasing growth temperature are consistent with the observations reported for other physiological processes such as photosynthesis (Hikosaka *et al.*, 2006; Kattge and Knorr, 2007). For example, Kumarathunge *et al.* (2019) showed that the temperature optimum for plant photosynthesis linearly increases with increasing growth temperature. Even though there are several studies that investigated temperature response of pollen germination process (Hedhly *et al.*, 2005; Kakani *et al.*, 2002; Kakani *et al.*, 2005), past studies on the temperature adaptation or acclimation of plant reproductive physiological processes are extremely rare. To our knowledge, our study would be the first to investigate the temperature response of the pollen germination process of tree crops in relation to the growth temperature. However, our study inherently assumed that the observed responses are totally due to differences in growth temperature, as our experimental design does not allow us to infer the effect of the temperature at the climate of origin of the species. We suggest that further studies are necessary to quantify the relative contribution of the two processes: adaptation and acclimation to the observed temperature responses for the pollen germination process.

Our data provide strong evidence that, in relatively warm climates, both pollen germination and pollen tube growth processes are coordinated, therefore, both processes have similar thermal optimum. For successful fertilization of the egg cell, both pollen germination and pollen tube growth are important, therefore at relatively warm sites, this coordination between the two processes ensures a successful fertilization. However, at cooler sites, the two processes are less coordinated (*i.e.* divergent temperature optima between the two processes), therefore, at growth temperatures, where the pollen germination is maximized, pollen tube growth would be negatively affected due to its low temperature optimum compared to the pollen germination. Hence we speculate that, with climate warming, pollination and fertilization processes of tree crops growing in cooler climates may be negatively affected due to poor pollen tube growth even though there would be a successful pollen germination even at high temperatures due to its higher thermal optima.

Results of this study have several implications in predicting the fate of tropical perennial cropping systems under climate warming. Our data suggested that pollen germination in tree crops has the capacity to regulate its temperature-response curves depending on the changes in the temperature of the growing environment. Therefore, it is likely that tree species currently growing in environments with relatively low growth temperatures may be able to perform in a similar manner in future warm environments as they can adjust their thermal response of pollen germination to fit the new climate. As tree crops like coconut have long economic lifespan of 65–70 years (Ranasinghe *et al.*, 2015) the capacity to adjust the thermal response of pollen germination would be very important to continue the reproductive process without any adverse impact of rising temperatures. However, our data do not provide information to determine how the pollen germination process of plants that are currently growing in warmer environments will

change under climate warming. Several authors have reported that tropical tree species are operating at their upper thermal limits; therefore, further warming would cause a negative impact on plant physiological processes (Mercado *et al.*, 2018; Slot and Winter, 2018; Scafaro *et al.*, 2017). However, such information is not available for the reproductive physiology of tropical tree species, therefore, accurate predicting of how the pollen germination process of plants growing in warmer environments will be affected by climate warming becomes challenging. Carefully designed experiments with controlled environmental facilities to simulate future climate scenarios are necessary for generating such information. The findings of this study demonstrate that the resilience of tropical perennial cropping systems to climate warming can be increased by introducing tree crops such as coconut to environments with moderate to relatively cooler, so the trees may be able to adjust their thermal responses to warming.

Conclusions

This study demonstrates that pollen germination and pollen tube growth of coconut responded to warming in a manner that reflects differentiated temperature optima depending on the species' growth temperature. The work highlights that tropical tree species that are currently growing in relatively cooler environments may have the capacity to perform their reproductive physiological functions in future warmer climates without any substantial negative impacts. Collectively, our findings of the temperature dependency of tree crop pollen germination should prove useful in quantifying the potential impacts of climate warming on tropical agro-ecosystems, improving the representation of plant reproduction in crop models.

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Author contribution statement. DPK conceived the project, and led the data collection, analysis, and manuscript writing. LKW, RKS, and NG made substantial contributions to the data interpretation and writing.

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