Physical Constraints on Temperature Difference in Some Thermogenic Aroid Inflorescences

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INTRODUCTION

Thermogenesis in reproductive organs is known from several plant families: Araceae, Annonaceae, Arecaceae, Cycadaceae, Cyclanthaceae, Magnoliaceae, Nymphaeaceae and Zamiaceae (Prance and Arias, 1975; Tang, 1987, Cucurbitaceae, Scrophulariaceae, and Zamiaceae (Prance and Arias, 1975; Tang, 1987, or a specialized appendix (Meeuse, 1987, 1993; Gottsberger, 1990; Uemura et al., 1993; Seymour and Schultz-Motel, 1998; Azuma et al., 1999; Dieringer et al., 1999; Bernhardt, 2000; Thien et al., 2000; Lamprecht et al., 2002a, b). A few taxa are even able to control their inflorescence temperature (i.e. thermoregulate) at a given value regardless of the ambient temperature (Seymour et al., 1983; Seymour and Schultz-Motel, 1996; Seymour, 1999, 2004; Ito et al., 2003). Heat production is generally associated with the emission of fragrance and the arrival of pollinators, and it has been particularly well documented in the family Araceae (Knutson, 1974; Moodie, 1976; Seymour et al., 1983; Meuse and Raskin, 1988; Yafuso, 1993; Seymour and Schultz-Motel, 1997, 1998, 1999; Seymour, 1999; Barabé and Gibernau, 2000; Barabé et al., 2002; Angiò et al., 2004). Although the most obvious role of the thermogenic process appears to be the dispersion into the air of scented compounds, thermogenic activities play other roles not linked with pollinator attraction, and may also be related to the unfolding of the spathe, and physiological processes such as flower development, pollen maturation, insect warming or pollen release (Seymour, 1999; Seymour and Schultz-Motel, 1999; Wada and Uemura, 2000; Barabé et al., 2002; Albre et al., 2003). Recently, it has been shown that heat may represent an energetic reward for some types of pollinators (e.g. beetles), but not for others (e.g. flies) (Seymour et al., 2003a, b).

The inflorescences of Araceae are typically composed of a spadix into which are inserted minute flowers surrounded by a modified bract, the spathe. In the subfamily Aroideae (sensu Mayo et al., 1997), the spadix bears unisexual flowers and heat is generally produced by the male flowers (fertile and sterile) or a specialized appendix (Meuse, 1975, 1978; Skubatz et al., 1990, 1991; Bermadinger-Stabentheiner and Stabentheiner, 1995; Seymour, 1999). This increase in temperature is produced by a particular biosynthetic pathway, the cyanide-insensitive respiration that uses starch or lipids as a source of energy and results in the production of heat instead of ATP, and which is triggered by salicylic acid (James and Beevers, 1950; Lance, 1972; Nagy et al., 1972; Wedding et al., 1973; ap Rees et al., 1976, 1977; Chauveau and Lance, 1982; Dieringer et al., 1993; Seymour et al., 1999, 2002; Albre et al., 2003). Recently, it has been shown that heat may represent an energetic reward for some types of pollinators (e.g. beetles), but not for others (e.g. flies) (Seymour et al., 2003a, b).

Methods

Spadix temperature was measured in 18 species from eight genera of tropical Araceae from the basal clade of Aroideae, both in French Guiana and in the glasshouses of the Montreal Botanical Garden.

Key Results

A significant logarithmic relationship was found between the volume of the thermogenic spadix zone and the maximum temperature difference between the spadix and ambient air. Four heat transfer models were applied to the data (conductive heat transfer alone, convective heat transfer alone, radiative heat transfer alone, and convective and radiative heat transfers) to test if physical (geometric and thermic) constraints apply. Which heat transfer model was the most probable was determined by using the criterion of a classical minimization process represented by the least-squares method. Two heat transfer models appeared to fit the data well and were equivalent: conductive heat transfer alone, and convective plus radiative heat transfers.

Conclusions

The increase in the temperature difference between the spadix and ambient air appears to be physically constrained and corresponds to the value of a thermal model of heat conduction in an insulated cylinder with an internal heat source. In the models, a heat metabolic rate of 29.5 mW g⁻¹ was used, which was an acceptable value for an overall metabolic heat rate in aroid inflorescences.

Key words: Aglaonema, Anubias, Araceae, Cercestis, Cucurbita, heat transfer model, Montrichardia, Philodendron, thermogenesis.
The regulation of this biosynthetic pathway at the mitochondrial level depends on the ubiquinone, the alternative oxidase (e.g. a membrane protein) and a species-specific uncoupling protein (Wagner and Krab, 1995; Leach et al., 1996; Laloi et al., 1997; Wagner et al., 1998; Ito, 1999; Ito et al., 2003).

Numerous observations have been made on the production of heat by inflorescences of Araceae, mostly in relation to physiological processes, respiration rates and heat production involved in temperature increases, or the characterization of thermogenic patterns (Knutson, 1972, 1974; Nagy et al., 1972; Chen and Meuse, 1975; Seymour et al., 1983; Young, 1986; Raskin et al., 1987; Skubatz et al., 1990, 1991; Bermadinger-Stabentheiner and Stabentheiner, 1995; Seymour, 1999; Gibernau and Barabé, 2000; Barabé et al., 2002). Although many analyses of thermogenesis in the Araceae have been conducted, only one study has discussed the relationship between the physical dimensions of the spadix (e.g. the mass) and the amplitude of heat production across two aroid species (Seymour et al., 1983). In fact, this aspect brings to the fore the question of the relationships between biological constraints and physical constraints during the evolution of organisms.

It has been shown that during their development and evolution organisms suffer different types of constraints. In evolutionary biology, ‘constraints represents a bias or imposition of a restriction on the range of possible responses of an organism to selection’ (Hall, 1992, p.75). Maynard Smith et al. (1985) recognize two general categories of developmental constraints in evolution: universal constraints and local constraints. Universal constraints are the direct consequences of the laws of physics or mathematics and apply to all physical systems and organisms. Local constraints result from the biological properties of organisms (e.g. physiology, genetics, mode of development), and can be limited to a particular taxon. In this paper, we use the terms ‘physical’ (including mathematical laws) and ‘biological’, respectively, to designate these two types of constraints.

It has been shown that there is a possible link between the amplitude of the thermogenic peak and the size or the mass of the spadix in some non-thermoregulating Aroids (Gibernau and Barabé, 2000; Wada and Uemura, 2000), while no such relationship has been found in thermoregulating species (Seymour and Blaylock, 1999; Seymour, 2004). It is obvious that all characteristics (e.g. size, colour, form, physiological properties) of the inflorescences of a given species are derived from its genetic background. However, in this case, we can hypothesize that the size of the inflorescence would constitute a physical constraint, and the morphological and physiological properties involved in the thermogenesis represent a biological constraint.

Very few studies have dealt with the relationship of the increase of temperature according to the size of the spadix (Seymour et al., 1983; Breidenbach et al., 1997; see Tang, 1987 for cycads). By using simple thermal models it may be possible to quantify the relationship between size of the inflorescence and the maximum temperature difference with the ambient air. Four models of heat transfer (conduction, convection, radiation, and conduction plus radiation), which assumed that the inflorescence is a cylinder, were developed.

The general goals of this study were: (1) to compare the maximum temperature increase in relation to spadix size (i.e. the volume of the male zone) among 18 tropical species of Araceae with unisexual flowers belonging to the subfamily Aroideae (or the tribes Philodendraceae, Homalomenaceae, Anubiaceae, Culcasiaceae, Montrichardiaceae, Dieffenbachiacae sense Mayo et al., 1997); (2) to determine if the quantitative variation of heat production among species and inflorescences of different sizes follow a physical law of heat transfer; and (3) can this physical law simply represent a cylinder surface temperature caused by an internal heat source?

MATERIAL AND METHODS

All the genera studied, which belong to the subfamily Aroideae, sense Mayo et al. (1997), are characterized by inflorescences having a male zone in the upper part and a female zone in the lower part. In the genus Philodendron there is also a sterile male zone in the middle of the inflorescence, varying in length depending on the species. For example, in Philodendron solimoense the intermediate zone occupies 35–52 % of the total length of the inflorescence while in P. melinonii this area occupies no more than 22 %. The male zone and sterile zone are composed of morphologically similar organs, and both zones follow the same qualitative thermogenic pattern (Barabé et al., 2002). Considering that all inflorescences belong to the same morphological type, it may therefore be possible to establish a quantitative relationship between the volume of the inflorescence’s male (or sterile) zone and temperature differences between the surface of the inflorescence and the ambient air in different species.

Inflorescence temperature was measured on 28 inflorescences from 18 species belonging to eight genera. Specimens were studied in French Guiana and at the Montreal Botanical Garden (MBG) in 1998 and 1999 (Gibernau et al., 1999; Barabé and Gibernau, 2000; Gibernau and Barabé, 2000, 2002; Gibernau et al., 2000, 2003).

The nine original temperature measures presented in this study were taken in 1999 between 9 August and 15 September at the MBG on the following species (the number in brackets represents the registration number at the MBG): Aglaonema crispum (24–76) (voucher at MT: Barabé & Archambault 198), Anubias barteri (3548–85) (voucher at MT: Barabé and Lavoie 138), Anubias barteri var. caladiifolia (1649–86) (voucher at Marie-Victorin Herbarium Montreal (MT): Barabé 268), Cercestis stigmaticus (4088–84) (voucher at MT: Barabé and Lavoie 139), Culcasi saxatilis (4094–840 (voucher at MT: Barabé & Chanta 91), Culcasi sp. (1072–86) (no voucher available), Culcasi sp. (1073–86) (no voucher available), Philodendron distantiolobum (2601–59) (voucher at MT: Barabé 267), Philodendron cannifolium (2424–46) (voucher at MT: Barabé 266). The other data come from previously published studies of thermogenic patterns present in different...
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The boundary layer can occur only through conduction. To produce heat at a constant rate, and the heat loss across a uniform temperature. We also assumed that the stem tissue boundary layer, the air is assumed to be well mixed and at a uniform temperature. This estimation is a simplification of the process, as in fact the axis of the spadix does not produce much heat, but only male flowers are responsible (Nagy et al., 1972; Seymour, 2001).

Previous studies have shown that the floral cycle is comparable between specimens at the Montreal Botanical Garden and in the wild (Gibernau and Barabé, 2000; Gibernau et al., 2000; M. Gibernau and D. Barabé, unpubl. res.). The environmental conditions (e.g. the ambient temperature) in the tropical greenhouses of MBG (mean ± s.d. = 22.9 ± 2.4 °C) and in the field (mean ± s.d. = 24.1 ± 0.9 °C) being comparable (t-test: $t_{26} = 1.43, P = 0.16$), increases in spadix temperature can thus be integrated into a comparative analysis (Appendix 1).

\[ V = \pi D^2 L/4 \]

\[ D \] is the diameter and \[ L \] the length of the male zone (see Appendix 2 for full list of abbreviations). This case of conductive heat transfer alone. We first consider a layer of stagnant air at a thickness of \( \delta \). Outside this boundary layer, the air is assumed to be well mixed and at a uniform temperature. We also assumed that the stem tissue produces heat at a constant rate, and the heat loss across the boundary layer can occur only through conduction. To calculate the temperature of the tissue, we employed the same equation used to measure the heating of an insulated wire by an internal heat source (Carslaw and Jaeger, 1959; Breidenbach et al., 1997; Fig. 1). Based on the results obtained from the heat conduction equation, the increase above ambient temperature is given by:

\[ \Phi_V = -\pi r^2 L \rho_\phi \]

\[ \Phi = -\lambda \text{grad}T \]

we can calculate eqn (3), which represents the flux dissipated on the lateral surface of the inflorescence. Note that we have neglected the heat transfer occurring at the top and bottom surfaces of the cylinder representing the inflorescence:

\[ \Phi_{(r)} = -\lambda 2\pi r L \frac{dT}{dr} \]

where \( T \) is the surface temperature of the inflorescence. If we assume that these two equations are equal, we can easily obtain the value of the surface temperature of the inflorescence:

\[ T_{(r)} = \frac{r^2 \rho_\phi}{4\lambda} + T_C \]

where \( T_C \) is a constant to be determined. We can obtain the flux liberated by the inflorescence over the entire volume of the cylinder by calculating the mean logarithmic difference:

\[ \Phi_{(r=R_s)} = \frac{T_{(R_s)} - T_{\infty}}{\ln(R_s + \delta)/8} \]

\[ \lambda_s \] conductivity coefficient of stagnant air (W m$^{-1}$ K$^{-1}$).
By again applying Fourier’s law to the radius of the cylinder, we obtain:

$$\Phi_{(r=R_s)} = -\lambda 2\pi R_s L \left( \frac{dT}{dr} \right)_{(r=R_s)}$$ (6)

The equality of eqns (5) and (6) leads finally to the value of \( T_C \), thus:

$$T_C = \frac{R_s^2 p_v}{r \lambda_s} \ln \left( 1 + \frac{\delta}{R_s} \right) + \frac{R_s^2 p_v}{4 \lambda_s} + T_\infty$$ (7)

Substituting the value for \( T_C \) in eqn (4) allows us to obtain the temperature distribution inside the inflorescence:

$$T_{(r)} = \frac{r^2 p_v}{4 \lambda_s} + \frac{R_s^2 p_v}{r \lambda_s} \ln \left( 1 + \frac{\delta}{R_s} \right) + \frac{R_s^2 p_v}{4 \lambda_s} + T_\infty$$ (8)

By using the temperature difference \( \Delta T_V = T_{(r)} - T_\infty \) and \( r = R_s \) we obtain a simplified expression:

$$\Delta T_V = \frac{R_s^2 p_v}{\lambda_s} \ln \left( 1 + \frac{\delta}{R_s} \right)$$ (9)

This expression is analogous to the heating of an insulated wire by an internal heat source (Carslaw and Jaeger, 1959), which has also been reported in Breidenbach et al. (1997).

The case of convective heat transfer alone. In eqn (6) it was assumed that the internal energy dissipated on the lateral surface of the flower by conduction only obeys Fourier’s law, but in reality this lateral heat transfer is certainly also subject to convective phenomena:

$$\Phi_V = h_{CV} S \left( T_{(r=R_s)} - T_\infty \right)$$ (10)

where \( h_{CV} \) is the convective heat exchange coefficient determined by Bejan (1993) and calculated as follows:

$$h_{CV} = \frac{N_{th} \lambda_s}{L}$$ (11)

With:

$$N_{th} = 4 \left[ \frac{7 R_{th} \rho \tau}{5 (20 + 21 \Pr)} \right]^{1/4} + 4 \frac{(272 + 315 \Pr)}{35 (64 + 63 \Pr)} \times \frac{L}{D}$$ (11a)

and

$$R_{th} = \frac{g \Delta T L^3}{\nu^2 \Pr}$$ (11b)

By again using eqn (2) = eqn (9) we obtain a new value for \( \Delta T_V \):

$$\Delta T_V = \frac{p_v R_s}{2 h_{CV}}$$ (12)

The case of radiative heat transfer alone. Temperature differences in terms of radiative exchange are shown in eqn (13):

$$\Delta T_V = \frac{p_v R_s}{2 h_t}$$ (13)

To estimate the level of radiative heat exchange, we evaluated a linearized radiative heat exchange coefficient (Sacadura, 1993):

$$h_t = \frac{e \sigma (T_{(r=R_s)} - T_\infty)^4}{T_{(r=R_s)} - T_\infty} \approx 4 \sigma e T_m^3$$ (14)

Taking into account the constant values for a grey and diffusing surface (see below), for \( h_t \) we obtained an estimation of 5.1 Wm\(^{-2}\) K\(^{-1}\) for the inflorescence.

$$e = 0.9$$

$$\sigma = 5.67 \times 10^{-8} \text{ Wm}^{-2} \text{ K}^{-4}$$

$$T_m = \frac{T_{(r=R_s)} + T_\infty}{2} = 293 \text{ (K)}$$ (14a)

The case of convective plus radiative heat transfers. Finally, eqn (15) shows temperature differences in terms of the two types of simultaneous heat transfers:

$$\Delta T_V = \frac{p_v R_s}{2 (h_{CV} + h_t)}$$ (15)

Applications

Two data sets were considered: first temperature measures related only to Philodendron (eight species, 13 measurements); second, all the data (eight genera, 18 species, 28 measurements). The four thermal models were applied to the two data sets assuming that:

1. The volume-specific heat production rate of the flower is equal to 29,500 Wm\(^{-3}\). This value minimizes the different least-square sums of all the models. A value 29.8 mW g\(^{-1}\) is mentioned for the spadix Philodendron selloum (Lamprecht et al., 2002b).
2. The thickness of the subviscous layer is equal to 0.003 m (Cuniasse-Languans, 1998).

Relationship between male zone size and temperature excess. A strong logarithmic correlation exists between the volume of the male zone and the temperature difference between the inflorescence and the ambient air (Fig. 2; \( y = 3.1845 \ln(x) + 1.4505, R^2 = 0.89 \); see data presented in Appendix 1). Hence the increase in temperature difference is steeper for small volumes (up to 10 cm\(^3\)) and then

Figure 2. Relationship between the volume of the thermogenic zone (male or male-sterile according to the aroid species) and the maximum of the temperature difference between the inflorescence and the ambient air.
flatter for larger inflorescence volumes. The maximum temperature difference between the air and the spadix increases and seems to reach a maximum around 15 K for a spadix with a male zone volume of 50–60 cm³.

**Table 1.** Results ($K^2$) of the minimization process (method of the least sum of squared differences) between the calculated temperature according to four heat transfer models and the measured temperatures for the eight *Philodendron* species and for all the species

<table>
<thead>
<tr>
<th></th>
<th>Conductive heat transfer alone</th>
<th>Convective heat transfer alone</th>
<th>Radiative heat transfer alone</th>
<th>Convective and radiative heat transfers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eight <em>Philodendron</em> species</td>
<td>38.9</td>
<td>729.6</td>
<td>1494.0</td>
<td>42.2</td>
</tr>
<tr>
<td>All species</td>
<td>81.9</td>
<td>1148.9</td>
<td>2630.6</td>
<td>84.7</td>
</tr>
</tbody>
</table>

**Fig. 3.** Relationships between the volume of the thermogenic zone and the maximum temperature difference between the inflorescence and the ambient air for the eight *Philodendron* species studied. Measured temperatures (dashed line) are shown together with calculated temperatures (solid lines) according to the four different heat transfer models (see text for full explanation).

**Fig. 4.** Relationships between the volume of the thermogenic zone and the maximum temperature difference between the inflorescence and the ambient air for all the species studied. Measured temperatures (dashed line) are shown together with calculated temperatures (solid lines) according to the four different heat transfer models (see text for full explanation).

**DISCUSSION**

Our results show that the conductive heat transfer model and the convective plus radiative heat transfer model best represent the data measured. This can be explained if we consider two facts. First, there is no reason that the different kinds of heat transfer occur separately. In reality, when a temperature difference is observed at a solid–air interface...
(e.g. the wall of a dwelling) two types of heat transfer (convective and radiative) happen simultaneously (Trombe et al., 2004). Second, we chose for the calculations of the conductive heat transfer alone an air thickness giving an equivalent resistance to convective and radiative phenomena (Cuniasse-Languans, 1998). It should be noted that our results are in accordance with those obtained by Breidenbach et al. (1997) who also used a model of conductive heat transfer (eqn 9) to calculate temperature increases in the inflorescence of Philodendron selloum with respect to volume.

The point distribution along the curve does not follow a phylogenetic pattern. Although the point in the asymptotic part of the curve corresponds mainly to the genera Philodendron, Homalomena and Montrichardia, there is no concordance between the grouping of taxa and the empirical values in the other part of the curve. For example, if there was a correlation between phylogeny and the empirical values in the other part of the curve. For example, is no concordance between the grouping of taxa and the Philodendron part of the curve corresponds mainly to the genera phylogenetic pattern. Although the point in the asymptotic

Philodendron selloum increases in the inflorescence of

conductive heat transfer (eqn 9) to calculate temperature

by Breidenbach that our results are in accordance with those obtained

an equivalent resistance to convective and radiative phe-

the conductive heat transfer alone an air thickness giving

et al. (1997). For example, in our

analysis, there are no members of the tribes Areae and Peltandreae. All members of the selected genera have a common ‘bauplan’ organization of the inflorescence. This would explain why the correlation between the size of the inflorescence and the maximum amount of heat produced corresponds to a particular theoretical curve. The heat is produced by the male and/or the sterile male zones of the inflorescence. The thermogenic process appears to be linked to the metabolic power and structure of the inflorescence (Lamprecht et al., 2002b). It may be supposed that the heat metabolic rate represents the biological constraint and the structure of the inflorescence the physical one. In our models a volume heat metabolic rate of 29 500 Wm$^{-3}$ was used, which corresponds to the value that minimizes the different sums of squares. If we consider that the inflorescence, as a plant tissue, has a density close to 1 g cm$^{-3}$, (1·07 in Seymour, 2001) then we can estimate a corresponding mass heat metabolic rate of 29·5 mW g$^{-1}$, which can be compared with mass metabolic heat rates documented for other species. Focusing on Aroids, individuals florets may have very high heat rates: 170 mW g$^{-1}$ in Symplocarpus foetidus (Knutson, 1974; Seymour and Blaylock, 1999), 175 mW g$^{-1}$ in Philodendron selloum (Seymour et al., 1983; Seymour, 1999) or 400 mW g$^{-1}$ in Arum maculatum (Lance, 1974). These values are much higher than overall inflorescence metabolic heat rates: 25 mW g$^{-1}$ in Amorphophallus paeonifolius (Lamprecht et al., 2002a), 34·1 mW g$^{-1}$ in Dracunculus vulgaris (Seymour and Schulz-About, 1999), 40–70 mW g$^{-1}$ in Philodendron selloum (Seymour et al., 1983), 68–130 mW g$^{-1}$ in Symplocarpus foetidus (Seymour and Blaylock, 1999). Except Symplocarpus foetidus, which is a species with bisexual flowers, our estimated metabolic heat rate is a little lower than those measured, but this value is not an aberrant overall mean heat rate. The difference can be explained by the fact that temperature measurements do not take into account evaporation, which is a powerful mechanism of heat dissipation (Seymour, 2001). In fact, in Philodendron, the evaporative heat loss increased with spadix temperature in an exponential fashion such that it is multiplied by a factor of 4·3 between 30 and 45 °C (Seymour et al., 1983).
If in *Pholidendron selloum* less than 8% of the metabolic heat production is lost by evaporative heat loss, in *Dracunculus vulgaris* the appendix can evaporate more heat than it generates (Seymour et al., 1983; Seymour and Schultz-Motel, 1999; Seymour, 2001).

In order to know if the obtained empirical curve is valuable for the entire family, one may test if the same relationship exists in clades with a different types of inflorescence and thermogenic patterns. For example, is this relationship also true in the tribe Araceae where the spadix has a specialized appendix to produce heat that can be empty inside, or in the subfamily Pothoiideae where the flowers are bisexual and the thermogenic pattern is about three weeks long?

In conclusion, the maximum temperature difference produced by an aroid inflorescence (from the basal clades of the subfamily Aroideae) corresponds to the value of a thermal model of heat conduction in a cylinder with an internal heat source, suggesting that strong physical constraints apply on this character. However, biological constraints cannot be ruled out as they are of great importance in the thermoregulated phase of *Symplocarpus* (Seymour, 2004), particularly variations in metabolic heat rates among species or over time. To date, all the available models and simulations are based on fixed parameters and/or a reduced part of the thermogenic process, and do not take into account evaporative heat loss. Further studies are thus necessary in order to understand and simulate the dynamics of the thermogenic process and its evolution.

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LITERATURE CITED


tissue of the voodoo lily (Sauromatum guttatum Schott).  

Thermochimica Acta 349: 135–140.


### APPENDIX 1

List of aroid specimens and measured data used in this study.

<table>
<thead>
<tr>
<th>Species</th>
<th>Spadix temperature (°C)</th>
<th>Air temperature (°C)</th>
<th>Male zone length (cm)</th>
<th>Diameter (cm)</th>
<th>Volume (cm³)</th>
<th>Site*</th>
<th>Source†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Philodendron solimoesense</td>
<td>39.7</td>
<td>24.6</td>
<td>17</td>
<td>2</td>
<td>53.38</td>
<td>FG 2</td>
<td></td>
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<tr>
<td>P. solimoesense</td>
<td>37.7</td>
<td>23.6</td>
<td>15.5</td>
<td>1.9</td>
<td>43.92</td>
<td>FG 1</td>
<td></td>
</tr>
<tr>
<td>P. acutatum</td>
<td>39.0</td>
<td>25.0</td>
<td>13.8</td>
<td>1.7</td>
<td>31.31</td>
<td>FG 2</td>
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<tr>
<td>P. acutatum</td>
<td>36.9</td>
<td>23.5</td>
<td>13</td>
<td>1.7</td>
<td>29.49</td>
<td>FG 2</td>
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<tr>
<td>P. melinonii</td>
<td>36.9</td>
<td>23.4</td>
<td>11</td>
<td>1.6</td>
<td>22.11</td>
<td>FG 3</td>
<td></td>
</tr>
<tr>
<td>P. pedatum</td>
<td>34.6</td>
<td>22.8</td>
<td>9.2</td>
<td>1.4</td>
<td>14.16</td>
<td>FG 2</td>
<td></td>
</tr>
<tr>
<td>Montrichardia aborescens</td>
<td>35.5</td>
<td>24.2</td>
<td>8</td>
<td>1.7</td>
<td>18.15</td>
<td>FG 5</td>
<td></td>
</tr>
<tr>
<td>Homanolema rubescens</td>
<td>31.8</td>
<td>21.3</td>
<td>6.1</td>
<td>1.3</td>
<td>8.09</td>
<td>MBG 6</td>
<td></td>
</tr>
<tr>
<td>P. melinonii</td>
<td>34.7</td>
<td>24.6</td>
<td>11.4</td>
<td>1.6</td>
<td>22.91</td>
<td>MBG 3</td>
<td></td>
</tr>
<tr>
<td>M. aborescens</td>
<td>35.4</td>
<td>25.8</td>
<td>9</td>
<td>1.5</td>
<td>15.90</td>
<td>FG 5</td>
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<tr>
<td>P. pterotum</td>
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<td>22.4</td>
<td>13</td>
<td>1.2</td>
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* Site: FG, French Guiana; MBG, Montreal Botanical Garden.
† Sources: 1, Gibernau et al. (1999); 2, Gibernau and Barabé (2000); 3, Gibernau et al. (2000); 4, Gibernau and Barabé (2002); 5, Gibernau et al. (2003); 6, Barabé and Gibernau (2000).

### APPENDIX 2

Abbreviations used in the text.

- **ATP**: Adenosine tri-phosphate
- **D**: Inflorescence diameter (m)
- **g**: Acceleration due to gravity (m s⁻²)
- **L**: Length of male zone inflorescence (m)
- **h_cv**: Convective heat exchange coefficient (W m⁻² K⁻¹)
- **h_r**: Linearized heat exchange coefficient (W m⁻² K⁻¹)
- **Nu_h**: Mean Nusselt’s number
- **Pr**: Prandtl’s number
- **v**: Volume-specific heat production rate of the flower (W m⁻³)
- **Rao** or **r**: Rayleigh’s number
- **S**: Inflorescence radius (m)
- **S**: Lateral surface of the inflorescence (m²)
- **T_s**: Surface temperature of the inflorescence (°C)
- **T_i**: ith numerically calculated temperature (°C)
- **T_m**: Mean temperature (°C)
- **T_C**: Constant value at the centre of the flower (°C)
- **T_w**: Ambient air temperature (°C)
- **V**: Male zone volume (m³)
- **Y_i**: ith experimentally measured temperature (°C)
- **ΔT_F**: Temperature difference, ΔT_F = T_i – T_w (K)
- **β**: Volumetric expansion coefficient of air (K⁻¹)
- **ε**: Emissivity coefficient
- **σ**: Boltzmann’s constant (W m⁻² K⁻⁴)
- **λ**: Conductivity coefficient of the inflorescence (W m⁻¹ K⁻¹)
- **λ_v**: Conductivity coefficient of stagnant air (W m⁻¹ K⁻¹)
- **δ**: Thickness of the conductive boundary layer (m)
- **Φ_F**: Dry heat flux leaving the male zone inflorescence (W)
- **ν**: Kinematics viscosity of air (m² s⁻¹)