J Plant Res (2008) 121:73–82
DOI 10.1007/s10265-007-0129-5

REGULAR PAPER

Thermogenesis and flowering biology of *Colocasia gigantea*, Araceae

Anton Ivancic · Olivier Roupsard · José Quero Garcia · Marie Melteras · Tari Molisale · Serge Tara · Vincent Lebot

Received: 10 September 2007 / Accepted: 17 October 2007 / Published online: 6 December 2007

Abstract The thermogenesis and flowering biology of *Colocasia gigantea* (Blume) Hook. f. were studied from December 2005 to February 2006 on Espiritu Santo, Vanuatu (South Pacific). Endogenous thermogenesis was measured in two ways: (1) continuously over 5-day periods, and (2) over 3 h during maximum heating. The study showed that heat was generated by the male part of the spadix and probably the lower zone of the sterile region. The temperatures of the male part peaked twice: (1) between 0625 and 0640 (during the female phase) and (2) 24 h later (during the male phase). The average maximum temperature was 42.25 ± 0.14°C during the female phase (16.63°C above the ambient temperature) and 35.14 ± 0.22°C during the male phase (10.61°C above the ambient temperature). In the lower zone of the sterile region, thermogenesis was documented only during the female phase. The average maximum temperature was 35.44 ± 0.41°C (9.82°C above the ambient temperature). Thermogenic heating appeared to be closely associated with the activities of pollinating insects.

Keywords *Colocasia gigantea* · Flowering biology · Inflorescence morphology · Pollination biology · Thermogenesis

A. Ivancic (✉)
Faculty of Agriculture, University of Maribor,
Vrbanska 30, 2000 Maribor, Slovenia
e-mail: anton.ivancic@uni-mb.si

O. Roupsard · M. Melteras · T. Molisale · S. Tara
Vanuatu Agricultural Research and Training
Center (VARTC), Espiritu Santo, Vanuatu

J. Q. Garcia
INRA, Unité de Recherche sure les Espèces Fruitières,
Domaine de la Grande Ferrade, BP 81,
33883 Villenave D'Ornon, France

V. Lebot
Centre de Coopération Internationale en Recherche
Agronomique pour le Développement (CIRAD),
Port Vila, Vanuatu

Introduction

Thermogenic flowering in aroids was first described by Lamarck (1778) in *Arum italicum* L. Modern investigations were initiated by Leick (1915) and Schmucker (1925). Leick (1915) described thermogenesis in plants belonging to several genera, such as *Arum* L., *Alocasia* (Schott) G. Don, *Monstera* Adans. and *Philodendron* Schott. Schmucker (1925) concentrated on *Arum maculatum* L. To date, thermogenesis has been documented in many aroid genera, such as *Alocasia* (Yafuso 1993; Miyake and Yafuso 2003; Ivancic et al. 2005), *Amorphophallus* Blume ex Decne. (Lamprecht et al. 2002), *Anubias* Schott (Barabé and Gibernau 2000), *Arum* L. (Skubatz et al. 1990; Albre et al. 2003; Barabé et al. 2003), *Cercestis* Schott (Barabé and Gibernau 2000), *Caladium* Vent. (Maia and Schlindwein 2006), *Colocasia* Schott (Ivancic et al. 2004), *Culcasia* P. Beauv. (Gibernau et al. 2005), *Dieffenbachia* Schott (Barabé and Gibernau 2000; Gibernau et al. 2005), *Dracunculus* Mill. (Seymour and Schultze-Motel 1999), *Helicodiceros* Schott ex K. Koch (Seymour et al. 2003), *Homalomena* Schott (Barabé and Gibernau 2000; Gibernau and Barabé 2002), *Montrichardia* Crueg. (Gibernau et al. 2003), *Philodendron* (Nagy et al. 1972; Seymour 1999; Gibernau and Barabé 2000), *Sauromatum* Schott (Raskin

et al. 1989; Skubatz et al. 1991), *Symplocarpus* Salisb. ex Nutt. (Seymour and Blaylock 1999), *Syngonium* Schott (Chouteau et al. 2007) and *Xanthosoma* Schott (Meeuse and Raskin 1988).

Colocasia is a tropical Asian genus which includes about 12 species (Cai et al. 2006). The most important are *C. esculenta* (L.) Schott (taro, "true" taro) and *C. gigantea* (Blume) Hook. f. (giant elephant ear). *C. esculenta* is grown as a root crop in all tropical regions with sufficient rainfall. In some places, its leaves and/or inflorescences are used as a vegetable (Matthews 2004). *C. gigantea* is grown in some parts of South-East Asia as a minor food crop. The leaf stalk is used as a vegetable.

Colocasia gigantea is a herb 1.5–3 m tall, with a large, fibrous, inedible corm, producing at its apex a whorl of large leaves. Inflorescences appear in groups or clusters, usually from three to five. Each inflorescence consists of a spadix covered by a spathe. The spadix is divided into a female part (lower part), a sterile region, a male part and a sterile tip (sterile appendix) (Figs. 1, 2). In the tropical Pacific, *C. gigantea* blooms throughout the year. The best season for flowering, according to our observations, is from the beginning of December to the end of January, during the hottest and the most humid part of the year. The main pollinators are insects. Some of the pollinators of *C. gigantea* and *C. esculenta* belong to the genus *Colocasiomyia* (Diptera, Drosophilidae) (Kramadibrata and Hambali 1983; Takenaka et al. 2006).

This study focused on the dynamics of thermogenic activity, the role of the sterile region between the female and male parts in heating the floral chamber during the female phase, and the relationships between thermogenic activity and pollination.

Materials and methods

Plant material

The investigation took place between 7 December 2005 and 5 February 2006, at the Vanuatu Agricultural Research and Training Centre (VARTC) near Luganville, on the Island of Espiritu Santo, Vanuatu (15°26.7' S: 167°11.5' E). The main reason for selecting the warm and humid environment was the tropical origin of *C. gigantea*. The plant material belonged to a large open pollinated population grown on a medium fertile, unfertilised soil, partly shaded by gliricidia (*Gliricidia sepium* (Jacq.) Kunth ex Walp.) trees.

Inflorescence measurements

To obtain basic data on inflorescence morphology, we measured the dimensions of the peduncles and the main parts of the spadix on a sample of 41 inflorescences in the male phase.

We used another sample of 22 inflorescences for studying changes in the spathe during anthesis. The data were collected during three successive mornings, between 0700 and 0800: 2 days before the release of pollen (day 1), a day later, when the temperature peak was reached (day 2), and on the day when pollen was released (day 3).

Temperature measurements

Based on the results of preliminary experiments that took place at the end of 2002 and the beginning of 2003, the

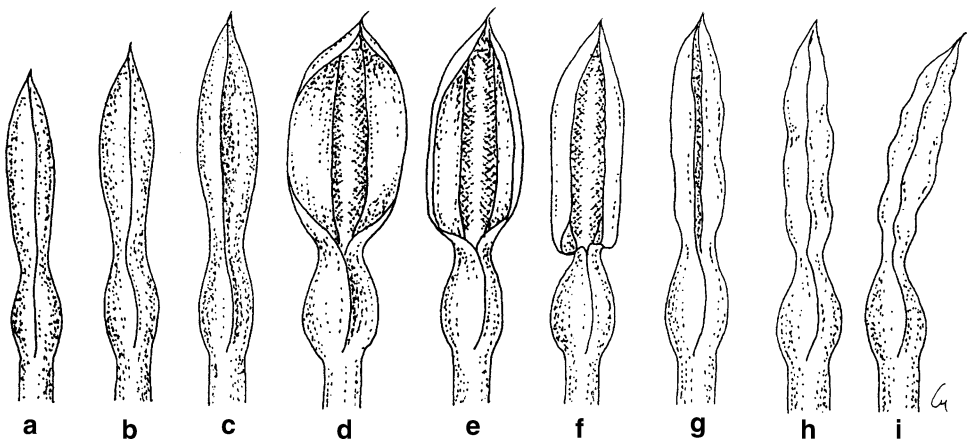

Fig. 1 Development of a *Colocasia gigantea* inflorescence over 8 days. **a** At 0630 (4 days before pollen was released), **b** at 0715 (3 days before pollen was released), **c** at 0730 (2 days before pollen was released, when the spathe was relaxed and its upper part started to change its colour from silvery green to white), **d** at 0630 (1 day before pollen was released, when the temperature in the middle of the male part was 41.3°C), **e** at 0245 (on the day when pollen was released), **f** at 0630, on the same day (the first pollen appeared at 0425), **g** at 0800 (a day later), **h** at 0730 (2 days after pollen was released), **i** 4 days after pollen was released

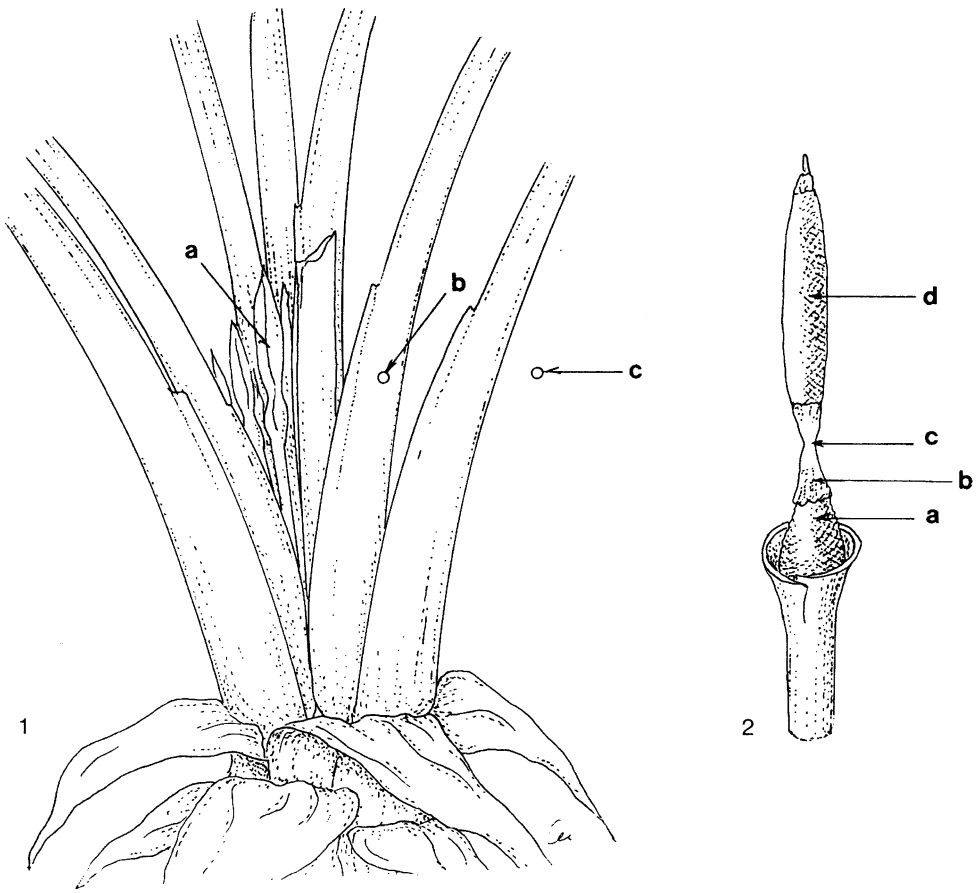

Fig. 2 Main positions of thermocouples. **1** Detail of a *C. gigantea* plant at the beginning of flowering. *a* Sample inflorescence, *b* position of thermocouples for measuring petiole temperature, *c* position of thermocouples for measuring ambient temperature. **2** Positions of thermocouples on the inflorescence. *a* At 0.6 cm below the top of the female part, *b* in the sterile region (0.6 cm above the female part), *c* in the middle of the constricted area, *d* in the middle of the male part

temperatures were measured in the female and male parts of the spadix and in the sterile region. The study involved two approaches: (1) continuous monitoring of three inflorescences over 5 days and (2) monitoring over the 3 h of maximum heating in 48 inflorescences in the female, and 41 inflorescences in the male, phase.

The aim of the first approach was to determine the temperature of various profiles of the spadix, the petiole tissue and the ambient air. The recordings began approximately 41 h before the highest temperatures in the male part (Fig. 1, stage between b and c) and ended approximately 52 h after the release of pollen (Fig. 1, stage between h and i). These 5 days of temperature recordings were obtained by 11 copper-constantan (type T) infra-millimetric thermocouples, which were connected with a Campbell Scientific 10X data logger, located fewer than 2 m from them and sheltered against direct radiation. Voltages (in millivolts) were compared with the internal thermistor reference of the data logger, in differential mode. Temperatures were measured every 10 s and averaged every 15 min. The ambient temperature was recorded at the base of the male part, which was protected from direct solar radiation by a small funnel-shaped shelter of aluminium foil. The leaf temperature was measured in the middle part of the leaf petiole of the largest leaf (Fig. 2–1). The temperatures were recorded in the four crucial positions (Fig. 2–2): 0.6 cm below the top of the female part; in the sterile region (0.6 cm above the top of the female part); in the middle of the constricted area of the sterile region; in the middle of the male part. In the female and male parts of a spadix, thermocouples were inserted into the spongy tissue, whereas in the sterile region they were inserted 2.5 mm deep inside the tissue. The sterile appendix was excluded from the measurements, because this part was too small to allow insertion of the thermocouples without damage (Fig. 2–2).

The aim of the second approach was to determine the number and positions of heating points in the inflorescence. The 3 h-long temperature monitoring during maximum heating was carried out in 13 different tissues. It was assumed that heating of some tissues might have been less expressed and therefore masked by those producing higher temperatures. Temperatures were recorded in the following tissues: the peduncle (5 cm below the base of the spadix), the female part of the spadix (0.6 cm above its base, in the middle, 0.6 cm below its top), the sterile region (0.6 and 1.5 cm above the female part, in the middle of the constricted area, 0.6 cm below the base of the male part), the male part (1.0 cm above its base, at one-third of its length,

in the middle and 1.0 cm below its top), the sterile appendix (0.3 cm above its base) and the ambient air. Temperatures were measured with the electronic handheld thermometer Ebro TFN 1093 SK (sensor NiCr–Ni (thermocouple K), 175 mm × 1.00 mm, having a resolution of 0.1°C and an accuracy ±0.4°C ± 1 digit (−10 … +80°C). The inflorescences used in the female and male phases were not the same, because preliminary experiments had suggested that numerous measurements with the Ebro TFN 1093 SK thermometer during the female phase could have a negative impact on heating during the male phase.

Statistical analyses

Basic statistical parameters and correlation coefficients were calculated with Excel software. Two additional analyses were conducted with Xlsat software: (1) principal component analysis (PCA) was used to analyse which traits contributed most to the size of inflorescence during the male phase; (2) for comparing spathe dimensions measured on 22 inflorescences during three successive days of anthesis, the Levene test for homogeneity of variance was performed, followed by the appropriate *t*-tests for the comparison of means. Principal component analysis belongs to multidimensional descriptive methods. By working with a rectangular matrix of *p* quantitative variables measured on *n* individuals, geometric representations are produced for both individuals and variables. Concerning individuals, the aim is to check for the existence of an a priori unknown structure, within this group of individuals. As for the variables, PCA allows one to study the structure of linear relationships within the subset of chosen variables. We conducted PCA analysis by using all 14 morphological traits measured on 41 inflorescences during the male phase.

Results

Inflorescence morphology

The parameters of the inflorescence morphology are given in Table 1. The spadix was characterised by a thick and short female part, a relatively short, constricted, sterile, region, a long and thick male part, and a remarkably small sterile appendix. The length of the male part was, on average, 3.39-times longer than the female part, and was highly variable. A high variation was also established for the sterile appendix length. As in Table 2, high correlations were observed between the length and width of the spadix, the male and the female part. This means that those parts grow longitudinally with a remarkable horizontal growth.

Table 1 Dimensions of peduncle and various parameters of *Colocasia gigantea* inflorescences measured during male phase ($N = 41$)

Traits (cm)	Minimum	Maximum	Mean	SEM[a]	CV (%)
Peduncle length	24.5	65.4	43.33	1.03	17.84
Peduncle width (long axis[b])	1.2	2.4	1.83	0.03	14.51
Peduncle width (short axis[c])	0.8	2.1	1.49	0.04	19.77
Length of the upper part of spathe	11.5	25.0	18.18	0.36	14.43
Width of the upper part of spathe	5.2	13.8	9.89	0.20	14.93
Length of female part	2.0	4.0	2.82	0.06	15.49
Diameter of female part (long axis[b])	1.4	2.8	2.08	0.03	10.91
Diameter of female part (short axis[c])	1.1	2.5	1.76	0.36	15.50
Diameter of the constriction	0.55	1.20	0.80	0.02	16.51
Length of male part	4.1	13.0	9.56	0.28	21.97
Diameter of male part (long axis[b])	1.3	2.5	1.79	0.04	15.94
Diameter of male part (short axis[c])	1.1	1.8	1.51	0.02	9.76
Appendix length	0.6	1.5	0.98	0.03	20.54
Total length of spadix	9.6	22.3	17.47	0.36	15.63

[a] Standard error of mean

[b, c] Cross-section was, in most cases, elliptical

The length of the male part was highly correlated with the total length of the spadix. This indicates that the large inflorescence of *C. gigantea* has a large male part. In contrast, the sterile appendix had no correlation with any other parts of the inflorescence.

In Table 3, eigenvalues and percentages of variance explained by the first eight principal factors from the PCA analysis are indicated. The first principal factor explained most of the variance (62.13%), and only the projections of observations for axes 1–2 are presented (Fig. 3), since results were not significantly different for projections on axes 1–3 or 2–3 (results not shown). The use of these variables did not result in a clear structure, and individuals formed a spherical cloud, with some isolated points characterised by either a very small (e.g. no. 7) or a very large (e.g. no. 38) inflorescence. The contribution of variables to the axis inertia was concordant with correlation coefficients. Traits that showed the highest correlation coefficients had homogeneous contributions to axis 1 (contributions varying from 5.84% to 9.99%). On the other hand, diameter of the male part on the short axis, and appendix length, which were the least correlated traits, contributed to most of the

Table 2 Correlation coefficients among the most important parameters of *Colocasia gigantea* inflorescences measured during male phase ($N = 41$). *Ap. l.* appendix length, *Con. d.* diameter of the constricted part of the spadix, *Fem. d*. diameter of the female part (at 1/3 of its height), *Fem. l.* length of the female part, *Mal. d.* diameter of the male part (at 1/2 of its height), *Mal. l.* length of the male part, *Ped. d.* peduncle diameter, *Ped. l.* peduncle length, *Spd. l.* spadix length, *Spth. l.* length of the upper part of the spathe, *Spth. w.* width of the upper part of the spathe; diameters of peduncle, female and male parts represent average values (because of the elliptical shape)

Parameter	Ped. l.	Ped. d.	Spth. l.	Spth. w.	Fem. l.	Fem. d.	Con. d.	Mal. l.	Mal. d.	Ap. l.
Ped. d.	0.581**									
Spth. l.	0.718**	0.801**								
Spth. w.	0.642**	0.622**	0.809**							
Fem. l	0.530**	0.503**	0.758**	0.662**						
Fem. d.	0.535**	0.716**	0.769**	0.651**	0.687**					
Con. d.	0.183	0.065	0.108	−0.033	−0.023	0.103				
Mal. l.	0.512**	0.796**	0.822**	0.532**	0.577**	0.699**	0.328*			
Mal. d.	0.557**	0.768**	0.860**	0.686**	0.695**	0.742**	0.245	0.804**		
Ap. l.	0.212	0.217	0.041	0.027	0.037	0.026	−0.168	−0.047	0.084	
Spd. l.	0.569**	0.778**	0.868**	0.591**	0.640**	0.700**	0.234	0.933**	0.847**	0.069

$^{*}P < 0.05$, $^{**}P < 0.01$

Table 3 Eigenvalues, variability and cumulative variability for the first eight principal factors

Principal factor	F1	F2	F3	F4	F5	F6	F7	F8
Eigenvalue	8.69	1.22	1.03	0.91	0.56	0.37	0.32	0.26
Variability (%)	62.13	8.75	7.33	6.49	4.03	2.62	2.27	1.85
Cumulative variability (%)	62.13	70.88	78.21	84.71	88.74	91.36	93.63	95.48

variation explained by axis 2 (40.53% and 28.23%, respectively).

The average number of female flowers per spadix was 573.3 ± 16.47, whereas the average number of synandria was 1,300.4 ± 92.65 ($n = 20$). Sterile and/or deformed female flowers were rare. During anthesis, female flowers on most inflorescences were light green, with well-developed stigmas. Deformed flowers were more frequent on the male part, occurring, in most cases, at the base and on the top of the male part.

Flowering

The blooming sequence from emergence of the upper part of the inflorescence from the membranous flag leaf to pollen release was recorded. It was 8–14 days, which is shorter than the sequence observed in *C. esculenta* (Ivancic and Lebot 1999, 2000). In a few cases, the development of inflorescences stopped for 2–3 days and then they began to grow again and flowered normally.

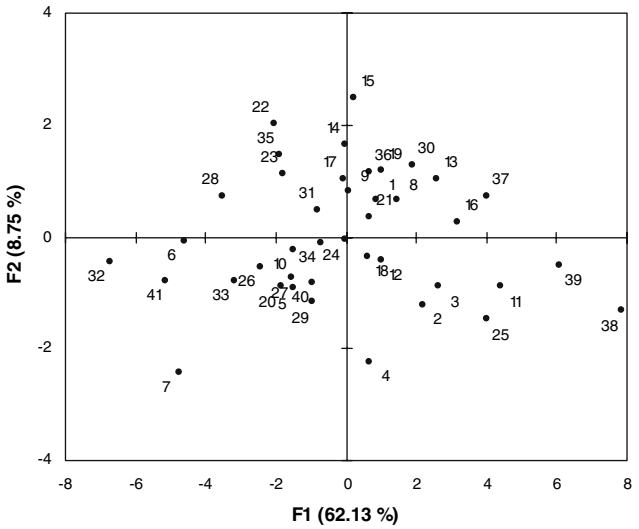

Fig. 3 Projection plots of observations on axes 1 and 2 (corresponding to the principal factors F1 and F2) of a PCA analysis conducted with inflorescence data collected during the male phase. Percentage of variance explained is indicated in *parentheses*

Female phase

The blooming sequence (Fig. 1d–f) lasted 46–50 h. In the morning, 2 days before pollen release, the spathe opened slightly. The colour of the upper part changed from silvery-green to whitish-green. The circumferences of the middle of the lower part of the spathe and the constricted area gradually increased from day 1 to day 2 (Table 4). The floral chamber expanded. On the following morning, when the temperature of the male part of the spadix reached its peak, the upper part of the spathe was already fully open, and its colour was whitish. Its tip was fixed (hooked) by the apex of the sterile appendix. On day 2, the circumferences

Table 4 Changes of various parameters of inflorescences of *Colocasia gigantea* measured during three successive mornings, between 0700 and 0800: 2 days before the release of pollen (day 1), a day later, when the temperature peak was reached (day 2), and on the day when pollen was released (day 3)

Trait (cm)	*N*	Mean values		
		Day 1[a]	Day 2[b]	Day 3[c]
Length of lower part of spathe	22	5.96	6.17	6.53*
Length of upper part of spathe	22	12.26	13.27	13.72*
Spathe circumference—middle of lower part	22	9.19**	11.10	10.51**
Spathe circumference—middle of constriction	22	4.92**	6.65**	5.57**
Length between constriction and appendix base	15	11.40	11.51	11.49
Total length of spadix	22	18.10	18.37	18.59

[a] Test for means measured on days 1 and 2

[b] Test for means measured on days 2 and 3

[c] Test for means measured on days 1 and 3

Significance of *t*-tests for the comparison of means is indicated: $*P < 0.05$; $**P < 0.01$

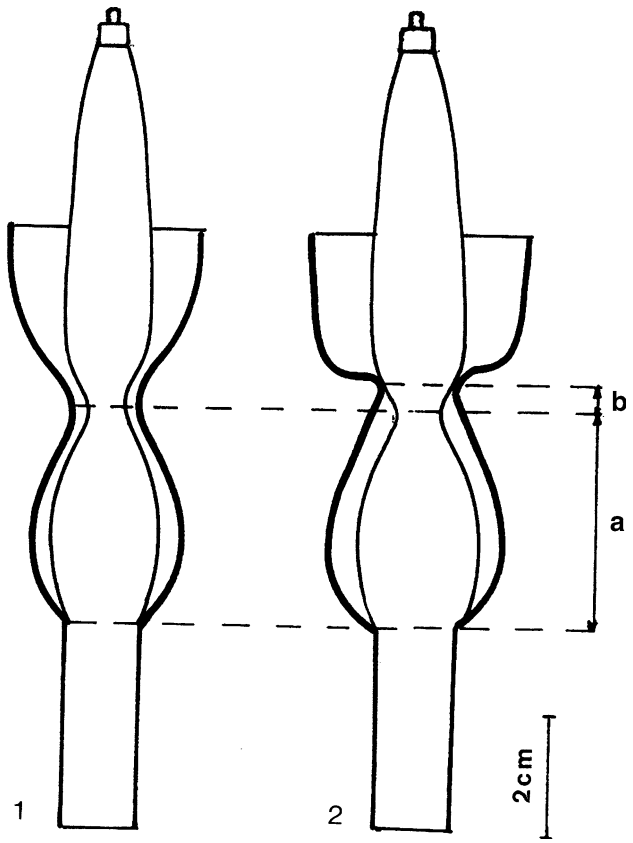

Fig. 4 Floral chamber of a *C. gigantea* inflorescence in the morning hours 1 day before reaching the main temperature peak (**1**) and 2 days later when the first pollen was shed (**2**); *a* height of the lower part of the spathe, *b* change in position of the constricted part of the spathe over 48 h

of the middle of the lower part of the spathe and of the constricted area (consequently the volume of the floral chamber) reached their maximum values. The upper part of the spathe, in most cases, very efficiently protected the spadix from rain drops as well as from cooling (Fig. 1d). However, there were also some inflorescences whose spathe was shorter than the spadix.

On day 2, the stigmas of the female flowers were already fully receptive and looked fresh and wet. At this stage, drosophilid flies were attracted to the inflorescences. The individual number per inflorescence was fewer than 5. Small beetles also visited the inflorescences, although their numbers were low.

In the late morning 1 day before pollen release, the circumferences of the middle of the lower part of the spathe and of the constricted area decreased (Table 4, from day 2 to day 3). Consequently, the volume of the floral chamber decreased, and the opening between overlapping edges of the lower part of the spathe began to close. By mid-afternoon, it was completely closed.

The lower part of the spathe showed the maximum value of average elongation on day 3 (Fig. 4; Table 4). One to two hours before pollen release, it stopped elongating. During the same period, the spadix elongated very little, so that the constricted part of the spathe "moved" upwards towards the thick upper zone of the sterile region and closed tightly around the spadix between the male and the female parts (Figs. 1f, 4–2).

Male phase

The upper part of the spathe remained wide open until late evening. At 2200, it was still wide open. After that, it started to close (Fig. 1, stages e and f), and it became almost white. The floral chamber almost closed after midnight. The first pollen release was observed at 0425, on 29 January 2006. At 0510, pollen was extruded from all inflorescences in the male phase. Pollen in some inflorescences was extruded for 2 days or more. In such cases, a smaller quantity of pollen was released on the first morning, and the rest on the second. After pollen release, the upper part of the spathe enclosed the male part and wilted (Fig. 1g–i).

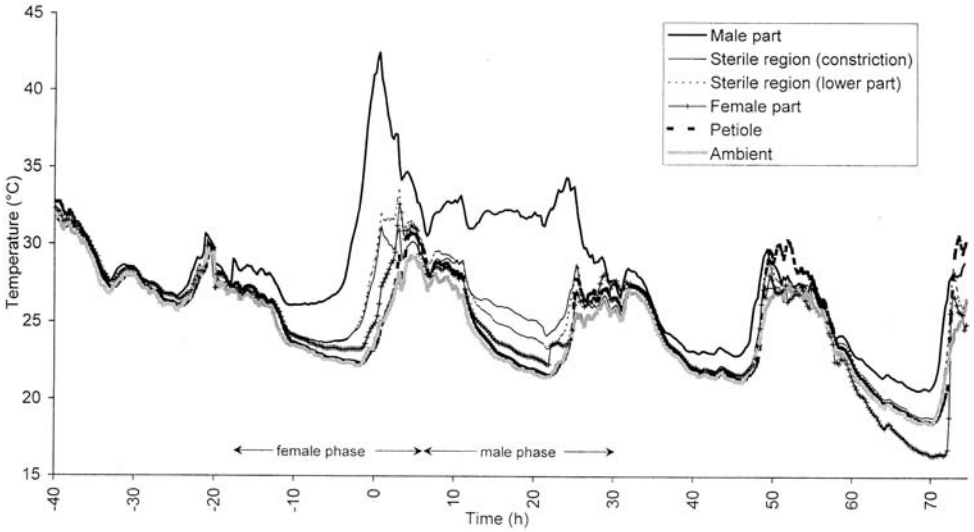

Fig. 5 Temperature course of ambient air, leaf petiole and four main parts of *C. gigantea* spadix over a period of 5 days. Data represent averages obtained from three plants. The first temperature peak of the male part is considered as "time 0"

Thermogenesis

Female phase

The first thermogenic activity was recorded between 1530 and 1730, 36–38 h before pollen release, in the male part. At the beginning, the temperature deviation of the male part from the ambient air was small. It increased after midnight (Fig. 5). The maximum deviation was recorded between 0625 and 0640. Then, the temperature decreased sharply until 1030–1130. The average maximum temperature of 48 inflorescences was recorded at the mid-point of the male part. It was 42.25 ± 0.14°C, and this was 16.63°C above the ambient temperature (Table 5). After reaching the peak, temperatures of the lower part of the male part decreased faster than those of the upper part. At 0815, the maximum temperature was recorded at a point 1.0 cm below the top).

A small increase in temperature, although not statistically significant, was also recorded in the lower zone of the sterile region, above the female part (Fig. 2–2b; Table 5). When thermogenic activity ended, the colour of the lower sterile zone changed from whitish or creamy to light brown or yellow-brown. The average length of this heated sterile zone was 2.015 ± 0.11 cm, and the average diameter was 1.12 ± 0.04 cm. The average maximum temperature in the sterile region was documented 0.6 cm above the top of the female part. It was 35.44 ± 0.41°C (9.82°C above the ambient temperature).

The temperature of the lower zone of the sterile region was higher than temperatures in both the female part and the upper zone of the sterile region (Table 5). The sterile, constricted area of the sterile part above the heating zone was cool, whereas the sterile area above was again warmer than the constricted area. The thermogenic activity in the sterile appendix was not measured, because the part is too small to accommodate the thermocouples.

Male phase

The male phase started approximately 6–7 h after the temperature peak of the female phase (between 1330 and 1430). The temperature increased until 0600–0630 and then decreased sharply until 1100–1130. During this phase, thermogenesis took place only within the male part (Fig. 5). The average maximum temperature of 41 inflorescences was recorded at the midpoint of the male part (Fig. 2–1a). It was 35.14 ± 0.22°C (10.61°C above the ambient temperature) (Table 5).

Discussion

Inflorescence morphology

Principal component analyses showed that the *C. gigantea* inflorescences studied in Vanuatu did not belong to different morphological types, since a continuum of variation was observed. Morphological variations were due mainly to differences in size rather than to differences in the ratios between size parameters. This result would support the hypothesis of the introduction of a relatively small number of *C. gigantea* genotypes in Vanuatu. For better understanding of morphological variation, the same type of analysis should be conducted on inflorescences from the area of origin of *C. gigantea*.

Flowering

Colocasia gigantea is obviously adapted to the humid tropical climate. The structure of the inflorescence, its odour and its thermogenic activity suggest that it is probably a cross-fertilising species, whose main pollinators are

Table 5 Temperatures (in degrees Celsius) of ambient air, peduncle and various parts of the spadix of *C. gigantea* at the temperature peaks during the female phase (measured by handheld thermometer Ebro TFN 1093 SK)

Location of measurement	Minimum	Maximum	Mean	SEM[a]	CV (%)
Female phase ($N = 48$)					
Ambient air	22.3	27.4	25.62	0.16	4.24
Peduncle	23.1	27.9	26.15	0.16	4.13
Female part (0.6 cm above the base)	23.7	31.3	28.19	0.22	5.50
Female part (in the middle of its height)	25.3	32.4	29.33	0.20	4.66
Female part (0.6 cm below its top)	27.6	34.7	31.42	0.24	5.37
Sterile region (0.6 cm above top of female part)	29.4	39.9	35.44	0.41	7.97
Sterile region (1.5 cm above top of female part)	29.4	39.1	35.04	0.36	7.21
Sterile region (constricted part)	29.6	38.9	34.82	0.35	6.94
Sterile region (0.6 cm below base of male part)	31.8	40.6	37.99	0.32	5.86
Male part (1.0 cm above the base)	35.1	43.0	41.66	0.17	2.86
Male part (at 1/3 of its height)	36.0	43.4	42.14	0.16	2.61
Male part (at 1/2 of its height)	37.5	43.7	42.25	0.14	2.30
Male part (1.0 cm below its top)	38.0	43.7	41.74	0.18	2.97
Sterile appendix (0.3 cm above its base)	32.5	39.7	37.44	0.26	4.87
Male phase ($N = 41$)					
Ambient air	22.8	26.9	24.53	0.15	4.57
Peduncle (5 cm below base of female part)	23.1	26.9	24.89	0.13	3.89
Female part (0.6 cm above the base)	23.0	29.0	25.56	0.16	4.71
Female part (in the middle of its height)	23.8	28.6	25.84	0.16	4.72
Female part (0.6 cm below its top)	24.1	29.7	26.21	0.17	4.74
Sterile region (0.6 cm above top of female part)	25.0	29.2	26.74	0.15	4.16
Sterile region (1.5 cm above top of female part)	25.5	29.7	27.13	0.14	3.95
Sterile region (constricted part)	25.5	29.8	27.45	0.14	3.58
Sterile region (0.6 cm below base of male part)	26.6	32.4	28.88	0.18	4.79
Male part (1.0 cm above the base)	29.5	36.7	33.49	0.23	5.25
Male part (at 1/3 of its height)	30.3	37.6	34.69	0.24	5.10
Male part (at 1/2 of its height)	31.3	37.6	35.14	0.22	4.60
Male part (1.0 cm below its top)	30.8	37.7	34.40	0.23	5.09
Sterile appendix (0.3 cm above its base)	27.7	37.5	30.72	0.23	5.68

[a] Standard error of mean

insects. Its entomophylous nature is similar to those observed in *C. esculenta* (Ivancic et al. 2004) and *Alocasia odora* (Miyake and Yafuso (2003). Odour was emitted most strongly after midnight and early in the morning (during the female phase) before the male part reached the maximum temperatures. The protogynous flowering sequence and the physical isolation of female flowers from male flowers in the tightly constricted area of the spathe may be the mechanisms that reduce or prevent self-fertilisation.

Protogyny (the maturation of the female reproductive organs before those of the male), however, cannot completely prevent self-fertilisation, because the period of stigma receptivity and the time of pollen release overlap (Naiola et al. 1984). Our experimentation in different developmental stages showed that the stigmas of female flowers became receptive at least 48 h before the release of pollen, and the receptivity persisted for at least 72 h (unpublished data).

The circumference of the space between female and male parts in the constricted region was rarely tight enough to prevent stigmas from receiving deposits of pollen from the same inflorescence. However, the constriction sometimes became loosened, because the encircled position of the constricted area of the spadix was pushed upwards during the blooming sequence. A very similar mechanism of the closure of the space between the male and female parts has been described in *C. esculenta* (Ivancic et al. 2004) and was closely associated with the activities of the pollinators. Early in the morning, the pollinators entered the floral chamber of a warm inflorescence in the female phase. They had come from an inflorescence that was a day older, and they were dusted with pollen. As the volume of the floral chamber began to decrease, they moved to the upper part of the inflorescence, where they were trapped until the release of pollen the following morning.

The efficiency of the mechanism of self-incompatibility is considered to depend on specific genetic structure. Most of the *C. gigantea* genotypes grown on Espiritu Santo were at least partly self-compatible (unpublished data).

On Espiritu Santo island, *C. gigantea* is an introduced species. This species could be found only around the two major towns. It may have been introduced by European or Chinese settlers, probably in the late 19th century (Weightman 1989). The late introduction could be one reason for the relatively low number of pollinator insects visiting the flowers and the absence of species-specific pollinator insect species.

Thermogenesis

Analysis of the time course of heat production of *C. gigantea* inflorescences shows that there were two main peaks associated with thermogenesis (Fig. 5). The first one appeared during the female phase and the second during the male phase. Female and male phases were clearly divided. During the female phase, the temperature was generated by the male part and probably the lower part of the sterile region, whereas, during the male phase, only the male part was thermogenically active. In this way, the male part generated heat twice.

The temperature peak that appeared between 0745 and 0800, one day after the pollen release (Fig. 5), was probably not caused by thermogenic heating. The temperatures of the leaf petiole and the male part of the spadix did not differ much, but they were higher than those of the ambient air. The most probable reason for this deviation from the ambient air temperature was slower cooling of the thick spongy interior of the petiole and the male part. The petiole tissue was, on average, 4–6 cm thick, and thermocouples were inserted 2–3 cm deep inside. It is also obvious that, during late afternoon on the day after the pollen release, temperatures of the male part were above temperatures of the petiole tissue (Fig. 5). The reason could be the spathe (Fig. 1, stages g and h), which started to close after the release of pollen. In such an enclosed upper part of the spadix, there was an empty space between the spathe and the surface of the male part (on average 0.20–0.25 cm wide), which was probably very efficient in protection from fast cooling.

One of the specific characteristics of the *C. gigantea* thermogenesis could be heating within the sterile region during the female phase. Our study showed that the temperatures within the lower zone of the sterile region were higher than the temperatures in the tissues below and above it. However, considering the resolution and accuracy of the thermometer, the sample size and the sensitivity of the tissue, it was not possible to prove this. Differences were not significant (Table 5). To obtain proof, additional experiments are needed, such as analysis of the respiration of the floral chamber. Heating in the lower part of the spadix has also been described in *Sauromatum guttatum* Schott by Raskin et al. (1989). However, the inflorescences of these two species have several differences. The second heating zone of *S. guttatum* is the sterile appendix, and not the male part. The heat-producing appendix of *S. guttatum* is relatively far from the floral chamber—above the sterile zone and the male part. Since there are two zones separating it from the floral chamber, another heating zone is probably a necessity to maintain optimal temperatures. The heating male part of *C. gigantea* inflorescences is separated from the floral chamber only by one zone: the sterile region. However, its length may exceed 6 cm, and there is an extended constricted area, the temperature of which may be highly influenced by the outside environment.

The main function of the hot male part during the female phase is probably to attract insect pollinators into the floral chamber. Some of these insects probably come from one-day-older inflorescences and carry pollen on their bodies. As the temperature around the male part may exceed 42°C, the insects probably search for a more comfortable environment for their activities, and that is the floral chamber, where temperatures rarely exceed 35°C. A very similar situation was observed in *Alocasia macrorrhizos*, where temperatures exceeded 47°C (unpublished data). The escape from the hot spot, however, remains a hypothesis that needs to be supported by further studies. Useful data could be obtained by the study of the behaviour of the pollination insects artificially trapped around hot spots. If it is too hot for them, they will probably try to escape.

Our results suggest that thermogenic heating is closely associated with insect pollination. Its precise role, however, should be determined at the centre of origin of *C. gigantea*, in the presence of insects that specialise in pollinating this species. It would also be useful to find out if thermogenic heating of the sterile region appears in other *Colocasia* species.

References

Albre J, Quilichini A, Gibernau M (2003) Pollination ecology of *Arum italicum* (Araceae). Bot J Linn Soc 141:205–214

Barabé D, Gibernau M (2000) Étude comparative de la production de chaleur chez quelques Araceae. Adansonia 22:253–263

Barabé D, Lacroix D, Gibernau M (2003) Development of the flower and inflorescence of *Arum italicum* (Araceae). Can J Bot 81:622–632

Cai X-Z, Long C-L, Liu K-M (2006) *Colocasia yunnanensis* (Araceae), a new species from Yunnan, China. Ann Bot Fenn 43:139–142

Chouteau M, Barabé D, Gibernau M (2007) Thermogenesis in *Syngonium* (Araceae). Can J Bot 85:184–190

Gibernau M, Barabé D (2000) Thermogenesis in three *Philodendron* species (Araceae) of French Guiana. Can J Bot 78:685–689

Gibernau M, Barabé D (2002) Pollination ecology of *Philodendron squamiferum* (Araceae). Can J Bot 80:316–320

Gibernau M, Barabé D, Labat D, Cerdan P, Dejean L (2003) Reproductive biology of *Montrichardia arborescens* (Araceae) in French Guiana. J Trop Ecol 19:103–107

Gibernau M, Barabé D, Moisson M, Trombe A (2005) Physical constraints on temperature difference in some thermogenic aroid inflorescences. Ann Bot 96:117–125

Ivancic A, Lebot V (1999) Botany and genetics of New Caledonian wild taro, *Colocasia esculenta*. Pac Sci 53:273–285

Ivancic A, Lebot V (2000) The genetics and breeding of taro. Series Rèperes. CIRAD, Montpellier

Ivancic A, Lebot V, Roupsard O, Quero Garcia J, Okpul T (2004) Thermogenic flowering of taro (*Colocasia esculenta*, Araceae). Can J Bot 82:1557–1565

Ivancic A, Roupsard O, Quero Garcia J, Lebot V, Pochyla V, Okpul T (2005) Thermogenic flowering of the giant taro (*Alocasia macrorrhizos*, Araceae). Can J Bot 83:647–655

Kramadibrata K, Hambali GG (1983) Peranan beberapa serangga pengunjung perbungaan pada penyerbukan *Colocasia esculenta* var. *esculenta* dan *C. gigantea* (The roles of some insects in pollination of *Colocasia esculenta* var. *esculenta* and *C. gigantea*). Berita Biol 2:143–146

de Lamarck J-B (1778) Flore française. Tome 3; L'Imprimerie Royale, Paris, p 538

Lamprecht I, Schmolz E, Blanco L, Romero CM (2002) Flower ovens: thermal investigations on heat producing plants. Thermochim Acta 391:107–118

Leick E (1915) Die Erwärmungstypen der Araceen und ihre blütenbiologische Deutung. Berichte der Deutschen Botanischen Gesellschaft 33:518–536

Maia ACD, Schlindwein C (2006) *Caladium bicolor* (Araceae) and *Cyclocephala celata* (Coleoptera, Dynastinae): a well-established pollination system in the northern Atlantic rainforest of Pernambuco, Brazil. Plant Biol (Stuttg) 8:529–534

Matthews PJ (2004) Taro. In: Krech S III, McNeill JR, Merchant C (eds) Encyclopedia of world environmental history, vol 3. Routledge, New York London, pp 1185–1186

Meeuse BJD, Raskin I (1988) Sexual reproduction in the arum family, with emphasis on thermogenicity. Sex Plant Reprod 1:3–15

Miyake T, Yafuso M (2003) Floral scents affect reproductive success in fly-pollinated *Alocasia odora* (Araceae). Am J Bot 90:370–376

Nagy KA, Odell DK, Seymour RS (1972) Temperature regulation by the inflorescence of *Philodendron*. Science 178:1195–1197

Naiola BP, Danimihardja S, Imamuddin H (1984) Flowering behavior in *Colocasia gigantea* Hook. f. In: Shideler FS, Rincon H (eds) Proceedings of the sixth symposium of the international society for tropical root crops, 21–26 February 1983. International Potato Center (CIP), Lima, Peru, p 131

Raskin I, Turner IM, Melander WR (1989) Regulation of heat production in the inflorescences of an *Arum* lily by endogenous salicylic acid. Proc Natl Acad Sci U S A 86:2214–2218

Schmucker T (1925) Beiträge zur Biologie und Physiologie von *Arum maculatum*. Flora 118/119:460–475

Seymour R (1999) Pattern of respiration by intact inflorescences of the thermogenic arum lily *Philodendron selloum*. J Exp Bot 50:845–852

Seymour RS, Blaylock AJ (1999) Switching off the heater: influence of ambient temperature on thermoregulation by eastern skunk cabbage *Symplocarpus foetidus*. J Exp Bot 50:1525–1532

Seymour RS, Schultze-Motel P (1999) Respiration, temperature regulation and energetics of thermogenic inflorescences of the dragon lily *Dracunculus vulgaris* (Araceae). Proc R Soc Lond B Biol Sci 266/1432:1975–1983

Seymour RS, Gibernau M, Ito K (2003) Thermogenesis and respiration of the dead horse arum *Helicodiceros muscivorus*, a pseudo-thermoregulatory aroid associated with fly pollination. Funct Ecol 17:886–894

Skubatz H, Nelson TA, Meeuse BJD, Dong AM, Bendich AJ (1990) Infrared thermography of *Arum* lily inflorescences. Planta 182:432–436

Skubatz H, Nelson TA, Meeuse BJD, Bendich AJ (1991) Heat production in the voodoo lily (*Sauromatum guttatum*) as monitored by infrared thermography. Plant Physiol 95:1084–1088

Takenaka K, Yin J-T, Wen S-Y, Toda MJ (2006) Pollination mutualism between a new species of the genus *Colocasiomyia* de Meijere (Diptera: Drosophilidae) and *Steudnera colocasiifolia* (Araceae) in Yunnan, China. Entomol Sci 9:79–91

Weightman B (1989) Agriculture in Vanuatu—a historical review. The British Friends of Vanuatu. Grosvenor, Portsmouth

Yafuso M (1993) Thermogenesis of *Alocasia odora* (Araceae) and the role of *Colocasiomyia* Flies (Diptera: Drosophilidae) as cross-pollinators. Popul Ecol 22/3:601–606