Thermogenic flowering of the giant taro (*Alocasia macrorrhizos*, Araceae)

Anton Ivancic, Olivier Roupsard, José Quero Garcia, Vincent Lebot, Vesna Pochyla, and Tom Okpul

Abstract: The investigations of thermogenesis of *Alocasia macrorrhizos* (L.) G. Don inflorescences took place from December 2002 to February 2003, and from February 2004 to March 2004, in one of the wild populations on Espiritu Santo, Vanuatu (South Pacific). Temperatures were measured with six Copper-Constantan (type T) infra-millimetric thermocouples wired to a Campbell Scientific 10X data logger. The thermogenic period lasted 36–42 h, and heating was documented on the male part and the sterile appendix. The highest temperatures were recorded on the sterile appendix. They started to rise slightly before midnight and peaked between 0545 and 0600, when the inflorescence odour became the most intense. The average maximum temperature of 59 investigated inflorescences was 43.9 ± 0.6 °C. The absolute maximum was 47.4 °C. The maximum deviation from the ambient air temperature was 25.6 °C. The heating of the male part began 10–15 h before the inflorescence odour became the most intense and ended 2–3 h after the release of pollen. Its temperatures had two peaks: the first one appeared 15 min after the temperature peak of the sterile appendix, whereas the second one appeared at the time of the release of pollen. The dominating visitors of the flowering inflorescences were earwigs (*Labidura truncata* Kirby, Labiduridae, Dermaptera). Seed set was extremely rare.

Key words: giant taro, *Alocasia macrorrhizos*, thermogenesis, inflorescence development, pollination.

Résumé : L'activité thermogénétique des inflorescences de populations sauvages d'*Alocasia macrorrhizos* (L.) G. Don a été enregistrée à Espiritu Santo (Vanuatu, Pacifique Sud), entre décembre 2002 et février 2003, puis entre février 2004 et mars 2004. Les températures ont été mesurées à l'aide de six thermocouples cuivre-constantan (type T) de taille infra-millémétrique, reliés à une centrale d'acquisition automatique Campbell Scientific 10X. La période thermogénétique dure de 36 à 42 heures et ne fut détectée que sur la partie mâle et sur l'appendice stérile. On enregistre les plus hautes températures sur les appendices stériles. Ces températures commencent à monter lentement avant minuit, et atteignent un pic entre 05h45 et 06h00, lorsque l'odeur de l'inflorescence devient plus intense. La température maximale moyenne des 59 inflorescences mesurées était de 43,9 ± 0,6 °C. Le maximum absolu fut de 47,4 °C. L'écart maximal à la température ambiante fut de 25,6 °C. L'activité thermogénétique de la partie mâle démarrait 10 à 15 heures avant que l'inflorescence ne devienne très odorante, et s'arrêtait 2 à 3 heures après la libération du pollen. Deux pics furent enregistrés: le premier apparaissait 15 min après celui de l'appendice stérile, alors que le deuxième apparaissait au moment de la libération du pollen. Les insectes visiteurs les plus abondants étaient des perce-oreilles (*Labidura truncata* Kirby, Labiduridae, Dermaptera). La production de graines était extrêmement rare.

Mots clés : taro géant, *Alocasia macrorrhizos*, thermogenèse, inflorescence développement, pollinisation.

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Introduction

Thermogenesis has been documented in several genera of the Araceae family such as *Alocasia* (Yafuso 1993; Miyake and Yafuso 2003), *Amorphophallus* (Lamprecht et al. 2002), *Anubias* (Barabé and Gibernau 2000), *Arum* (Skubatz et al. 1990; Albre et al. 2003), *Cercestis* (Barabé and Gibernau 2000), *Colocasia* (Ivancic et al. 2004), *Dieffenbachia* (Barabé and Gibernau 2000), *Dracunculus* (Seymour and Schultze-Motel 1999), *Helicodiceros* (Seymour et al. 2003), *Homalomena* (Barabé and Gibernau 2000), *Philodendron* (Seymour 1999; Gibernau and Barabé 2000), *Sauromatum* (Skubatz et al. 1991), *Symplocarpus* (Seymour and Blaylock 1999), and *Xanthosoma* (Meeuse and Raskin 1988).

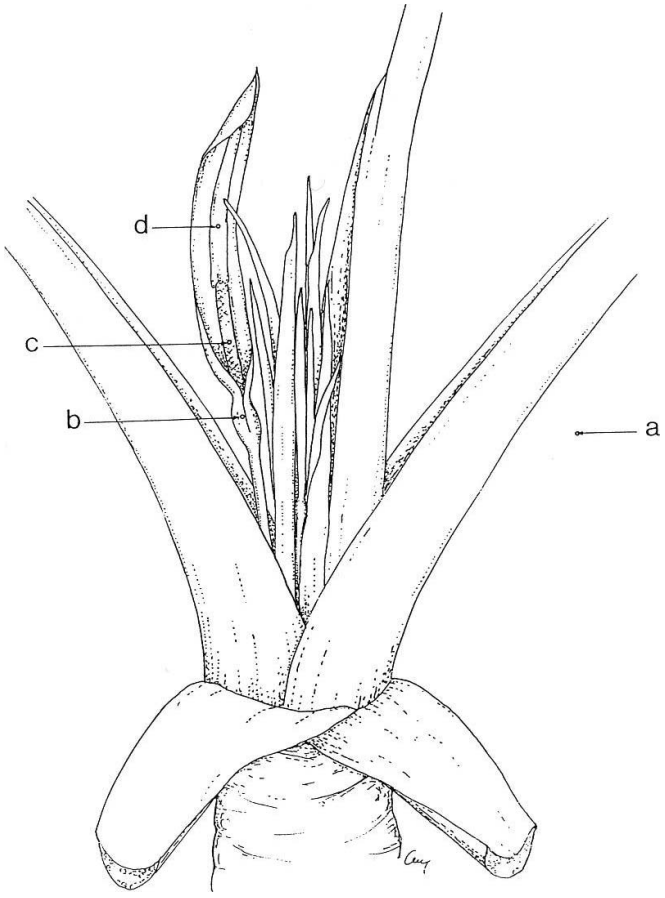
The genus *Alocasia* (Schott) G. Don comprises some 70 species (Hay 1990) and thermogenesis of some of its species has probably been known for a long time. The most detailed studies were conducted on *Alocasia odora* (Lodd.) Spach by Yafuso (1993) and Miyake and Yafuso (2003). They found that thermogenic activity occurrs in cycles and is synchronized with the receptivity of stigmas, release of odour, release of pollen, and visits by pollinating insects.

Thermogenesis of *Alocasia macrorrhizos* (L.) G. Don (the giant taro) has not yet been systematically analysed. Genotypes growing in an optimal environment can develop much larger inflorescences than *A. odora* and therefore their thermogenic potential is expected to be higher.

Alocasia macrorrhizos is a large, succulent perennial herb with a large, elongated stem. The stem, which is above ground, can be up to 1 m long and 20 cm in diameter (Purseglove 1979). The plants have several broadly sagittate leaves, bluntly triangular in outline, indistinctly leathery, with the secondary venation prominent. Inflorescences are relatively large and usually appear in clusters. The upper part of the spathe is pale yellow, membranous, oblong, and hood-forming, and it falls soon after anthesis (Hay 1990). The spadix is divided into female part (below), sterile region, male part, and sterile appendix (Figs. 1, 2). Like many other aroids, it is an allogamous and entomophylous species (Ivancic and Lebot 2000). The distribution in different geographical regions suggests that several insect species may be involved in its pollination. In southeast Queensland, Australia, according to Shaw and Cantrell (1983), four species of pollinating insects were most commonly encountered within open chambers of the giant taro inflorescences (two belonged to Hymenoptera: Apidae, and two to Coleoptera: Nitidulidae and Staphylinidae). Within open spathal chambers, they occasionally recorded several other species (belonging to Thysanoptera, Diptera, Coleoptera, and Hymenoptera).

Alocasia macrorrhizos occurs world wide and is grown as a crop in the South Pacific and in tropical parts of Australia, Asia, Africa, and South America. It is grown in only a few countries in the South Pacific (e.g., Western Samoa, Tonga, Wallis and Futuna, and some parts of Papua New Guinea and the Solomon Islands), and in most cases, it is a minor crop. In Vanuatu, it is considered a neglected crop and is grown extensively on only a few islands (e.g., Ambae island). Its yield potential is very high and there are no significant pest and disease problems (TANSAO 2002). The major problems with growing it as a crop include its very long vegetation period (generally longer than 2 years) and lodging.

Fig. 1. The positions of thermocouples: a, ambient air (under the shade of a fresh leaf, at the height of the base of the studied inflorescence); b, in the middle of the female part; c, in the middle of the male part; d, at one-third of the appendix length.

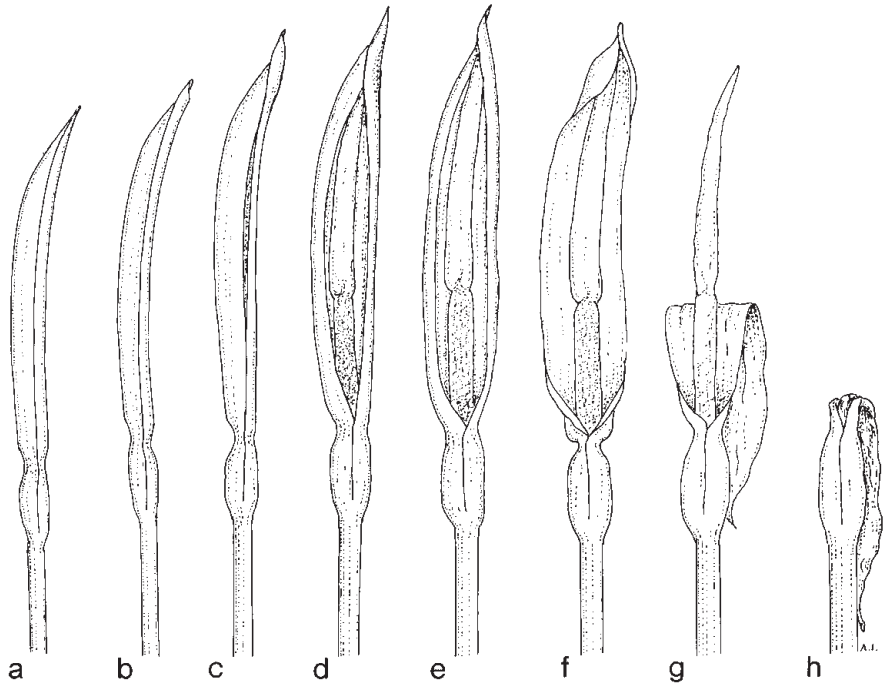


The genotypes of *A. macrorrhizos* are usually divided into two groups: wild and cultivated. Corms of the wild genotypes cannot be used as food because of an extremely high concentration of calcium oxalate crystals. Cultivated genotypes are distinguished mainly by leaf and corm characteristics. The most important are length, diameter, and smoothness of the corm exterior, and traits associated with the corm flesh such as colour, chemical composition, dry matter content, content of fibres, texture, and taste.

The centre of origin of *A. macrorrhizos* is probably Sri Lanka or India (Purseglove 1979; Plucknett 1984). From this area it has spread to most tropical and subtropical regions. The exact routes of its spread are still being discussed and are probably similar to those of *Colocasia esculenta* (L.) Schott, which have been described by Yen and Wheeler (1968).

In Vanuatu, *A. macrorrhizos* has been present since ancient times (Weightman 1989). The first genotypes probably originated from the Solomon Islands, to which they were probably brought from Papua New Guinea. In recent history,

Fig. 2. Development of a giant taro (*Alocasia macrorrhizos*) inflorescence and fruit head over a 17-d period (sketching took place at the beginning of 2003 in one of the wild populations at the Vanuatu Agricultural Research and Training Centre near Luganville, on the Island of Espiritu Santo, Vanuatu). (*a*) 7 d old (5 d before becoming fragrant and thermogenically active). (*b*) 9 d old. (*c*) 11 d old (24 h before becoming intensively fragrant and reaching the temperature peak). (*d*) 12 d old (at 0300, approximately 3 h before the appendix reached its maximum temperature). (*e*) 3 h later, when the appendix reached its maximum temperature. (*f*) 13 d old (when pollen was released). (*g*) 15 d old (2 d after the release of pollen). (*h*) 17 d old.



some of the genotypes (especially ornamentals) were introduced by French, British, and Polynesian settlers.

This study was associated with the Vanuatu aroid breeding program aimed at creating new cultivars characterised by earlier maturity. The program started in 1998 with the genetic recombination of superior local cultivars. The hybridization procedure is relatively simple (because of monoecy and protogyny). The inflorescence used as the female component has to be emasculated (the male part, together with the sterile appendix, has to be removed) before it starts attracting pollinating insects. With a small knife, the breeder has to cut the spathe and the spadix in the constricted region between male and female part of the inflorescence. The pollination is usually carried out immediately after emasculation. The lower part of the spathe is carefully removed and then pollen is distributed on stigmas. The pollinated inflorescence has to be protected from uncontrolled pollination (by pollinating insects) by cotton. The activity of pollinating insects is closely associated with odour release and thermogenic activity. The data about thermogenesis may be very useful for those who have to conduct exact crosses.

This article represents the first systematic study of the thermogenesis of *A. macrorrhizos* based on the analysis of a large number of plants (wild genotypes) growing in natural environmental conditions. The main objective was to analyze (*i*) the morphological variation of inflorescences; (*ii*) the patterns of heat production of the main parts of inflorescences (female part, male part, and sterile appendix) throughout the flowering cycle, and (*iii*) the impact of thermogenesis on the pollination system.

Materials and methods

Location of the experiment and climatic conditions

The investigation took place 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 investigated plant material was growing on a deep and fertile soil, covering a coral limestone plateau, 2.8 km from the seashore, at an altitude of 80 m. Slope, surface drainage, and stone content were close to zero. The soil profile originated from ancient volcanic ashes, layered over the coral bench. Clay and fine silts comprised more than 80% of the soil content. Soil water content (SWC; g H_20·g $soil^{-1}$) ranged from 35% at pF4.2 to 50% at pF2.5, so extractable water was less than 15%.

The climate of Espiritu Santo is tropical oceanic, averaging 2745 mm of rainfall per year (1989–2000). The average rainfall during the hot and rainy season (from December to April) is 335 mm per month, whereas during the drier season (from July to September), it is 117 mm per month. The average temperatures during the warmest period of the year are 25.3 °C in December, 25.6 °C in January, and 26.0 °C in February. The average lowest temperatures (in most instances, they occur between 0300 and 0500) are 20.5 °C in December, 20.4 °C in January, and 21.7 °C in February. The

average daily global radiation, maximum temperature, air humidity, maximum vapour pressure deficit, and daily potential evapotranspiration (Priestley-Taylor) are respectively 20.0 $MJ \cdot m^{-2} \cdot d^{-1}$, 30.3 °C, 89.8%, 10.8 hPa, and 5.4 mm during the rainy season, and 14.5 $MJ \cdot m^{-2} \cdot d^{-1}$, 27.6 °C, 86.1%, 8.1 hPa, and 3.5 mm during the dry season.

Climatic parameters were measured continuously at the height of 22 m on a tower located 360 m away from the location of the investigated population. They were monitored on a Campbell Scientific 10X data logger (Campbell Scientific Ltd., Shepshed, Loughborough, UK) every 30 s and averaged semihourly. Global radiation (Rg) was measured with a silicon cell pyranometer SKS1110 (Skye Instruments Ltd., Llandridod Wells, Powys, UK); air temperature and relative humidity with a MP100a (Campbell Scientific), and rainfall with an ARG100 (Campbell Scientific).

Plant material and investigation method

The investigation of thermogenesis started with a series of preliminary studies, which took place in 1999, 2000, and 2001 (at VARTC), aimed at the determination of the most suitable time and method for recording temperatures. It was found that the most appropriate period was at the beginning of the rainy season (from the beginning of November to the end of February, depending on year), during the warmest part of the year.

The main part of the investigation took place from 23 December 2002 to 4 February 2003, in one of the largest wild populations at VARTC. December 2002 was relatively very dry (51.7 mm of rainfall). January and February had more rainfall (190 and 237 mm, respectively). The investigated population consisted of 94 plants that were 2.5–5 years old. The aim of this investigation (in 2002–2003) was to analyse the variation of the main morphological parameters of inflorescences (listed in Table 1), the incidence of seed formation, and the variation associated with thermogenesis. Temperature was studied on 59 randomly chosen inflorescences (in the same population). On each individual inflorescence, temperatures were monitored over a period of 2.5–3.5 d (emphasis was on the final stage of the female phase, when inflorescences became odorous, and the male phase).

The investigation of thermogenesis was repeated in February and March 2004 (on two plants) and individual inflorescences were monitored over a period of 8–11 d. The main objective was to determine whether thermogenic activity consisted of more than two cycles (as is the case for *A. odora* described by Yafuso 1993 and Miyake and Yafuso 2003).

The following temperatures were recorded: the ambient air (under the shade of a fresh leaf, at the height of the base of the studied inflorescence) and inflorescence (spadix). The inflorescence temperatures were recorded within the female and male parts (in the middle of each of these parts, inside the outer zone of the spongy tissue) and the appendix (at one-third of its length, inside the outer zone of the spongy tissue; Fig. 1). The latter measuring point was determined in a preliminary study that indicated that normally developed appendices were, on average, the thickest at that point. The spadix temperatures represented a compromise between the temperature of the surface and that of the spongy tissue in the centre. On a smaller sample of plants (ca. 30 plants), temperatures were also recorded inside the petiole tissue of the youngest fully developed leaf (25 cm from the petiole base).

The decision to place the thermocouples (for measuring ambient air temperatures) under the shade of a fresh leaf was based on the results of a preliminary study that compared the recordings made by thermocouples protected by an aluminium sheet, shaded by leaves, or not shaded. The first two options gave almost identical results, and shading by leaves was considered to be a natural solution. (The giant taro leaves were extremely large, having average length of 80.3 ± 8.7 cm and an average width of 57.2 ± 6.9 cm.)

Temperatures were measured with six Copper-Constantan (type T) infra-millimetric thermocouples. The thermocouples were sheltered against direct radiation and wired on a Campbell Scientific 10X data logger, located less than 3 m away. Voltages (mV) were compared with the datalogger internal thermistance reference in differential mode. Temperatures were measured every 10 s and averaged every 15 min. For controlling the automatic temperature recordings, the electronic handheld thermometer Ebro TFN 1093 SK (sensor NiCr-Ni (thermocouple K), 175 mm × 0.9 mm; Ebro Electronic GmbH & Co. Ingolstadt, Germany), which has a resolution of 0.1 °C and an accuracy of ±0.4 °C (over the range of –10 to +80 °C), was used. This thermometer was used every third morning, between 0500 and 0930, when spadices were the most active.

The notes concerning the developmental stages were taken four times a day (the emphasis was put on early morning hours, from 0445 to 1030) on each of the investigated inflorescences. The notes included mainly the data associated with morphological and physiological changes (e.g., the changes of the colour of the spathe, time when it started to unfold, time when the inflorescence became odorous, time of the release of the first pollen, presence of pollinating insects, and time when the spadix started to wilt).

Results

Flowering biology

On Espiritu Santo, *A. macrorrhizos* does not flower continuously; however, flowering plants can be found year round. Our five years of observations indicate that flowering is the most frequent from the beginning of November to the end of February when days are warm and long. During this period, the majority of plants, growing in normal environmental conditions, developed 8–16 inflorescence clusters and then they rested for 6–12 months, depending on the genotype, plant age, and the environment. In less favourable conditions, the nonflowering period lasted much longer (1.5 years or more).

The anthesis of an individual inflorescence, in optimal weather conditions, lasted 2.5 d on average. Artificial pollination indicated that stigmas became fully receptive in the early morning hours, approximately 24–26 h before the inflorescence became maximally odorous (2 d before pollen was shed). The spathe started to open 18–24 h before the spadix would have become maximally odorous (Fig. 2*c*). It continued to unfold until pollen had been released. Later, when the male part and the sterile appendix became soft, the spathe bent downwards (Fig. 2*g*).

Table 1. Mean values and variation of the main quantitative traits of *Alocasia macrorrhizos* inflorescences measured on the day that they became odorous (n = 51).

Trait (cm)	Min.	Max.	Mean	SEM	CV (%)
Peduncle length	20.8	35.4	26.41	0.48	13.01
Peduncle width (longer axis)[a]	1.25	2.60	1.65	0.04	15.72
Spathe length	22.8	37.5	29.84	0.49	11.90
Spathe width	5.20	8.60	6.13	0.10	11.92
Inflorescence (spadix) length	22.0	37.1	28.94	0.47	11.56
Female part length	1.9	3.1	2.35	0.40	12.10
Female part diameter	1.12	2.10	1.62	0.03	11.49
Sterile band length	1.5	3.0	2.17	0.04	13.23
Constriction diameter	0.65	1.08	0.83	0.01	11.78
Male part length	5.8	9.5	7.20	0.10	9.94
Male part diameter	1.2	2.0	1.50	0.02	10.94
Appendix length	13.0	26.4	17.42	0.38	15.51
Appendix width (long axis)[b]	1.35	2.45	1.78	0.03	14.12
Appendix width (short axis)[b]	0.70	1.60	1.09	0.03	20.53

[a]Longer axis of the cross-section (in most cases it was elliptic) measured at one-half of the peduncle length.
[b]Cross-section of the appendix (the shape varied from elliptic to almost rectangular) measured one-third of the way up from the base of the appendix.

During the night before the release of pollen, the constricted part of the spathe became tight, thus closing the space between the male and the female region, whereas the part above flattened (previously it was funnel shaped) (Figs. 2*e*, 2*f*). In this way, chances of self-pollination were reduced to a minimum and the pollinating insects were given more space to move around the base of the male part of the spadix. The first pollen was released between 0545 and 0600, 1 d after the inflorescence had became the most intensively odorous (Fig. 2*f*). On rainy days, the release of pollen was delayed for approximately 30–45 min. In extreme situations, the delay exceeded more than 1 h, and in some instances pollen was not released at all.

Almost all pollinating inflorescences were visited by earwigs (*Labidura truncata* Kirby, Labiduridae, Dermaptera). These relatively large (usually more than 2 cm long) insects cannot fly and were most active in the early morning hours, when pollen, which they use as food, was being released. Insects belonging to the Drosophilidae (Diptera) family were rarely present. If they were present, they were chased to the upper part of the inflorescence (around the sterile appendix) by the earwigs. Most of the earwigs were moving around the base of the male portion. Flowering inflorescences without earwigs were rare. The average number of earwigs per (flowering) inflorescence was 2.45 ± 0.32 (P = 0.05). On large inflorescences, it was possible to see more than five earwigs. Owing to a relatively high density of plants (1.2–1.7 plants·m^{-2}), these nonflying insects, according to our observations, could in some instances actively participate in cross-pollination, although they had no significant influence on seed set. The floral chamber was too small to enable comfortable movement of these insects around pistillate flowers. In an extended study of 14 wild populations of *A. macorrhizos* at VARTC (the largest population was used for the thermogenic study), involving 513 plants, only two flowering individuals developed normal fruit heads (clusters of berries) with viable seeds. However, this does not mean that the pistillate flowers of only two inflorescences were pollinated (with compatible pollen). The main reason for the very low number of normal fruit heads was probably an insufficient number of fertilized pistillate flowers per inflorescence. We observed that fruit heads that reached maturity contained at least 20 berries with viable seeds. Fruit heads with only a few developing berries usually failed to reach maturity. A similar phenomenon was observed by Ivancic and Lebot (2000) in *Colocasia esculenta*.

Morphological variation of inflorescences

The plants of the studied population (at the beginning of 2003) were vigorous and healthy. They were growing in optimal conditions; the soil was fertile and the air humidity was relatively high because the surrounding trees sheltered the plants from the wind. Most of the plants (83 out of 94) were flowering. The average number of inflorescences in various stages of development and (or) fruit heads per plant was 9.9 ± 1.9 (ranging from 0 to 32), whereas the average number of inflorescences at anthesis was 1.1 ± 0.2 (ranging from 0 to 4).

The inflorescences were well developed and large (Table 1). The sterile appendix represented (on average) 60.2% of the total length of the spadix, whereas the male part represented 24.9%. The female part was relatively short (on average 8.1% of the total length of the spadix).

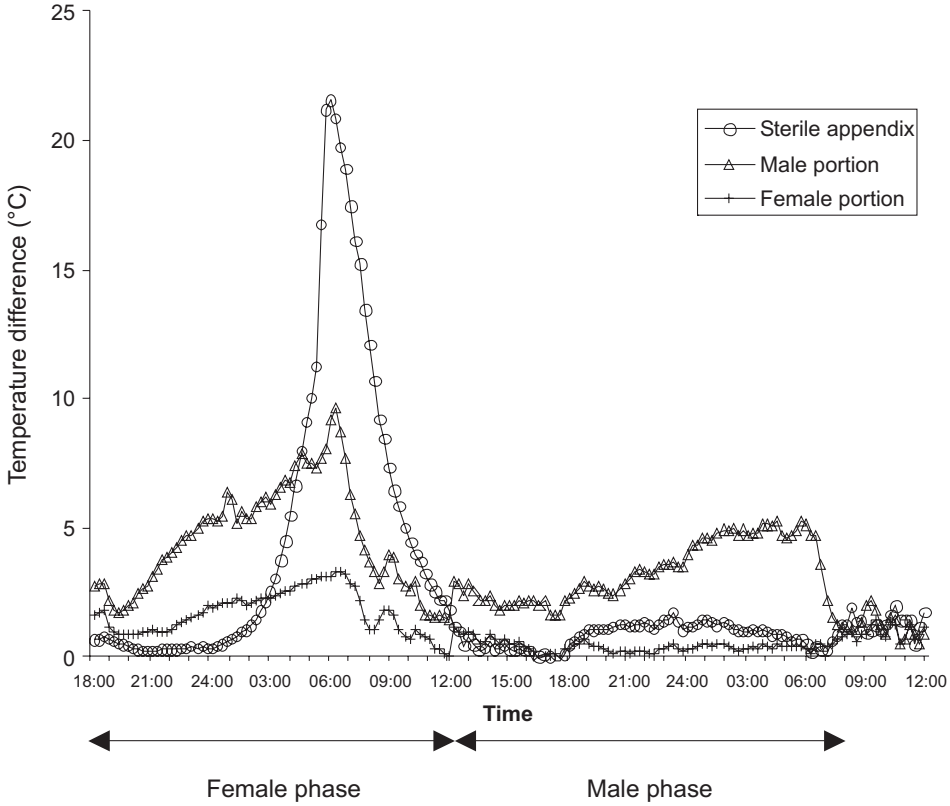
Thermogenic cycles

The thermogenic activity lasted approximately 36–42 h (Figs. 3, 4) and was divided into two cycles. The duration of the first cycle (the female phase) varied from 15 to 22 h. It started late in the afternoon (between 1500 and 2000), approximately 10–15 h before the inflorescence became maximally odorous, and ended on the following day, between 1100 and 1300. It was followed by the male phase, which lasted 19–22 h and ended approximately 2–3 h after the release of the first pollen (between 0800 and 0900).

The female phase

The most active was the sterile appendix. Its temperatures started to increase slightly before midnight. The increase

Fig. 3. Temperature differences between the three main parts of the spadix of the giant taro (*Alocasia macrorrhizos*) and the ambient air during the 42-h period starting at 1800 (approximately 12 h before the sterile appendix temperatures peaked) and ending at 1200 (approximately 6 h after the release of pollen). Temperatures represent averages measured on 59 inflorescences.



was very fast, reaching the peak within 6 h, between 0545 and 0600 (Figs. 3, 4). The average maximum value was 43.9 ± 0.6 °C (n = 59 inflorescences; the average ambient air temperature was 22.4 ± 0.5 °C). The absolute maximum was 47.4 °C, recorded at 0550 on 29 December 2002 (cloudy morning, ambient air temperature was 26.0 °C) on a sterile appendix that was 23.4 cm long. Temperatures above 47 °C were recorded two more times in January 2003 using the electronic handheld thermometer Ebro TFN 1093 SK. In 2004, the absolute maximum temperature of the sterile appendix was 44.7 °C, recorded on 23 February at 0630 when the ambient air temperature was 27.1 °C. The maximum deviation of the sterile appendix temperature from the ambient air temperature was 25.6 °C, recorded at 0545 on 9 January 2003.

The peak of the thermogenic heating of the sterile appendix was associated with the release of the most intensive odour. After reaching the peak, the temperature of the sterile appendix decreased sharply (Figs. 3, 4). In 4 h, it decreased approximately 10 °C. However, it remained above the ambient air temperature for another 19–22 h because of the thermogenic activity of the male part below.

The thermogenic activity of the male part started 4–7 h earlier than that of the sterile appendix (between 1500 and 2000). At first, the temperature increase was slow, but after midnight, it became faster (Figs. 3, 4). The temperature peak was reached a bit later than that of the sterile appendix, and it was obviously the result of the synchronous heating of the male part and the sterile appendix. The highest temperature attained was 33.1 °C (5.8 °C above the ambient air temperature) and was recorded at 0645 on 4 February 2004 (15 min after the temperature of the sterile appendix had reached its maximum of 44.7 °C).

The temperatures of the female part rarely deviated from those of the ambient air by more than 2.0 °C. The greatest deviation was recorded between 0600 and 0630, 15–20 min after the male part reached its temperature peak. When taking into consideration the temperature peak of the sterile appendix, the delay was 30–45 min (Figs. 3, 4). This suggests that the female part was not thermogenically active and that deviations from ambient air temperatures were caused by heating of the sterile appendix and (or) male part. Thus is further indicated by the course of the temperature deviations of the female part from the ambient air, which was found to be the very similar (if not identical) to the course the temperature deviations of the nonthermogenic petiole tissue (Fig. 5). The only exception was the period of approximately 40 h when the sterile appendix and (or) the male part were thermogenically active.

The male phase

During the male phase, only the male portion was thermogenically active. At the beginning, its temperatures increased slowly. The thermogenic activity intensified after midnight (Fig. 3). At 0300, the temperatures were very close to the peak. The peak was reached between 0545 and 0630, the time of the pollen release. The highest value, 29.9 °C

Fig. 4. Differences in temperatures between the main parts of the spadix of the giant taro (*Alocasia macrorrhizos*) and the ambient air during the 11-d period (data are averages for two plants). The peak of the sterile appendix temperature is considered time 0.

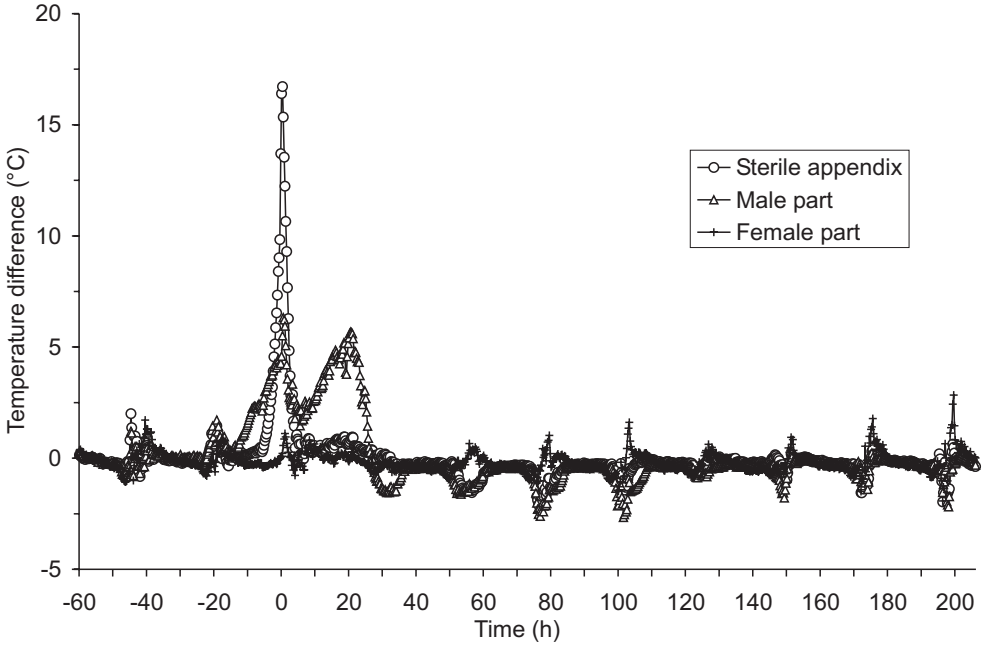
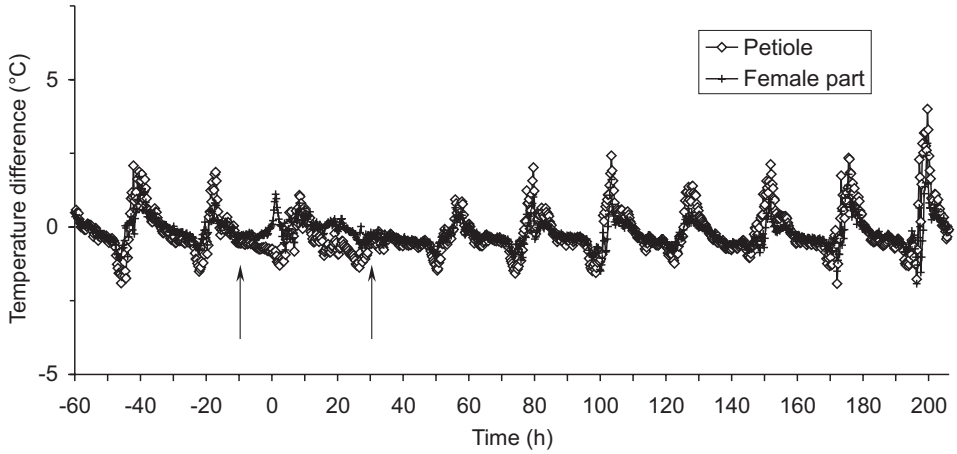


Fig. 5. Temperature deviations of the leaf petiole tissue and the female part of the spadix of the giant taro (*Alocasia macrorrhizos*) from the ambient air during the 11-d period (data are averages for two plants). The peak of the sterile appendix temperature is considered time 0. Arrows indicate the period when temperatures of the female part were influenced by thermogenesis of the sterile appendix and (or) the male part.



(6.3 °C above the ambient air temperature), however, was recorded at 0300 (on 9 March 2004).

After the release of pollen, temperature of the male part started to decrease. At 1030 its average deviation from the ambient air temperature was less than 1 °C.

Discussion

Flowering biology

Inflorescences of the studied plants were relatively large and well developed. However, the female part was relatively small and represented less than 10% of the total length of the spadix (Table 1). One of the consequences was a relatively small floral chamber and a limited number of pistillate flowers. Small floral chambers may indicate an adaptation to pollination by smaller insects (i.e., flies belonging to Drosophilidae family).

The pollinating insects were attracted by warm and odorous spadices from (pollinating) inflorescences that were a day older and in this way they were encouraged to transport pollen from older inflorescences to younger ones. Although the pollinating inflorescences were also warm, their temperatures were much lower, they lacked odour or the odour was too weak, and the open spathes did not provide reliable shelter. The main function of heating the pollinating inflorescences is probably to increase the activity of insects. The insects needed the external energy because pollen was released

early in the morning (in most instances before 06h00) when ambient temperatures were still cool.

Seed set was extremely rare. One reason could be an insufficient number of efficient pollinating insects adapted to pollinate the giant taros. Another reason could be the aggressive behaviour of the earwigs, which chased all other insects away. Rare seed set could also be caused by self-incompatibility and incompatibility among plants within clones (because of predominant vegetative propagation, the majority of the neighbouring plants probably belonged to the same clone). Several years of practical breeding experience led us to conclude that *A. macrorrhizos* is predominantly a self-incompatible species and that pollination within plants and clones rarely results in seed set.

Rare seed set and dominating vegetative propagation suggest that this species has probably not yet fully adapted to the specific environmental conditions of the Vanuatu archipelago. Because of vegetative propagation, the evolution process was probably very slow and consequently the plants probably have not changed much. Sexually multiplied pollinating insects under natural selection pressure were probably more dynamic. Earwigs may represent a deviation in this process of evolution. The earwigs explore the thermogenic activity of the giant taro inflorescences and feed on pollen, but they do provide any benefits to the plants.

The presence of earwigs and rare seed set suggest that hybridization for breeding purposes on Espiritu Santo may be carried out without protecting (isolating) the parental inflorescences from uncontrolled pollination. This may change if genetically different parental materials are grown together in a dense population. In such cases, protection of parental inflorescences would probably be required because pollen is relatively dry and light and may be spread (for short distances) by wind.

Thermogenesis and thermogenic potential

The analysis of the temperature course of *A. macrorrhizos* inflorescences over an 11-d period indicated that there were 11 peaks (Fig. 4). However, the analysis of the temperature course of the nonthermogenic leaf petiole tissue (Fig. 5) indicated that most of the peaks were not associated with thermogenesis. The period of thermogenic activity was relatively short. It lasted less than two full days and represented a more or less a continuous process that was not divided into two distinctly separate cycles (similar to *Colocasia esculenta*, see Ivancic et al. 2004), although the temperature course of the male part had two distinct peaks (Figs. 3, 4). There was little similarity with the thermogenesis of *A. odora* described by Okinawa by Yafuso (1993), which lasted more than two days and had more than two cycles.

Alocasia macrorrhizos appears to be the most thermogenically active during early morning, whereas *A. odora*, according to Yafuso (1993), produces heat around mid-day. The thermogenic activity of *A. macrorrhizos* appears to be comparable to that of the tetraphasic pattern described for *Arum italicum* by Albre et al. (2003). The male part and the sterile appendix of *Arum* inflorescences produce, respectively, three and one heat peaks. In fact, in Fig. 3, the thermogenic activtity looks clearly tetraphasic. However, the first peak (ca. 18–20 h before the sterile appendix reached its maximum temperature) could be caused by direct solar radiation. This is supported by the occurrence of a temperature peak in the nonthermogenic leaf petiole tissue at the same time (Fig. 5). At that stage (Fig. 2*c*), the spathe was more or less completely enfolding the spadix and was still green, similar to the petiole surface. The green pigmentation enabled more efficient absorption of the solar energy and faster warming when compared with those of the ambient air.

The highest temperatures were produced by the sterile appendix and were more than 20 °C above the ambient air temperature. These temperatures were much higher than those documented on *A. odora* by Yafuso (1993) and Miyake and Yafuso (2003). The main reasons for such high temperatures were (*i*) the genetic background of the species, (*ii*) the optimal environment (enabling vigorous growth, absence of pests and diseases), (*iii*) plant age (the studied plants were 2.5–5 years old, the age when flowering was the most intensive), and (*iv*) large inflorescences (the average length of the sterile appendix and the male portion of the spadix was 17.42 and 7.20 cm, respectively; Table 1). According to Purseglove (1979), the sterile appendix is (on average) 15 cm long. As suggested by Gibernau and Barabé (2002), larger inflorescences probably have higher thermogenic potential. Small and thin inflorescences generally generate lower temperatures and at the same time they cool faster. An example is the thermogenic heating of *Colocasia esculenta* (L.) Schott inflorescences described by Ivancic et al. (2004). Maximum deviations from ambient air temperatures never exceeded 7 °C. Among the reasons for such high deviations from the ambient air temperature could be the position (under the shade of a fresh leaf, at the height of the base of the studied inflorescence) of the thermocouples used to measure the ambient air temperature. However, the highest values were recorded before 0600 when all plants of the studied population were in complete shade because of nearby tall trees. This complete shading lasted until 0715. The differences between shaded and nonshaded positions became obvious after 0745, and by noon the differences could exceed 6 °C.

Another factor influencing the thermogenic expression was the synchronous heating of the male part and the sterile appendix during the female phase (when odour was released). The sterile appendix was larger and thus produced more heat. Similar synchronous heating of these two parts was also documented on two *Philodendron* species (Barabé et al. 2002); however, more heat was produced by the male part, which was larger. The spathe efficiently protects the spadix as it heats up, thereby reducing cooling. Larger inflorescences had a wider and softer spongy tissue, and thus heat from the male part could influence the temperature of the sterile appendix and vice versa.

The female part was not affected very much by the thermogenic activity of the male part and the sterile appendix. The reasons could be the constriction between the male and the female part (the diameter of the constriction was almost two times smaller than the diameter of the male portion), and the funnel shape of the open spathe above the constriction (which reduced the spread of heat downwards). The spadix temperatures were also influenced by the temperature of the air. Temperatures exceeding 45 °C were, in all cases, obtained during cloudy mornings, following warm,

cloudy nights (clear nights were generally 3–6 °C cooler). This was probably the main reason that the spadix temperature peaks were not associated with the maximum deviations from the ambient air temperatures.

The female part was not found to be thermogenically active even though there were obvious deviations from ambient air temperatures (Fig. 4) and from the temperatures of other parts of the spadix. The peaks of these deviations appeared each day between 1130 and 1330, starting one day after the release of pollen. To explain these deviations, the temperature course of the female part was compared with the temperature course of the petiole tissue. The peaks appeared at the same time (Fig. 5), suggesting that the temperature deviations were a result of the green surface, which absorbed solar energy faster than the ambient air.

Active cooling was not documented. However, the data presented in Fig. 4 indicate that there were some negative deviations of the temperatures of the male part (and to some extent of the sterile appendix) from those of the ambient air. The first negative deviation appeared two days after the release of pollen, between 0930 and 1100 (approximately 2.5–3 h before the ambient air temperature reached its maximum), reaching its "negative" peak (temperatures that were 2.5–3.5 °C lower than those of the ambient air) at approximately 1000. The most probable reason was the evaporation of water and other volatile substances from the decaying tissues. During cool nights, these dead tissues absorbed water that then started to evaporate when the air temperature reached 30–33 °C. The temperature differences disappeared when the tissues dried (between 1230 and 1330) and reappeared at the same time on following days. The male part was probably more hygroscopic because of remnant pollen grains that had not been released during the male phase.

The thermogenesis of *A. macrorrhizos* represents a complex process that depends on many intrinsic and extrinsic factors and their interactions. To obtain more complete information about thermogenic activity of this species, it would be very useful to analyse the relationship between the inflorescence size (especially the size of male part and the sterile appendix) and thermogenic heating. It may also be useful to compare the thermogenic activity of plants exposed to full sun with that of plants grown in permanent shade (the plants studied in this paper were exposed to sunlight for 4–8 $h \cdot d^{-1}$).

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