Thermogenesis in the Aroids

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ABSTRACT

Thermogenesis, as it occurs in the plant inflorescence has been observed and studied for over two centuries. At least seven thermogenic families of plants are known including Annonaceae, Araceae, Arecaceae, Aristolochiaceae, Cycadaceae, Cyclanthaceae, and Nymphaeaceae. The sequence of thermogenic events is very precise and highly synchronized in each species. The physiology is not well understood, but the recent identification of salicylic acid as the triggering hormone for thermogenesis has opened the door for further research, especially in the areas of plant signal transduction pathways and systemically acquired resistances. Thermogenesis has proven to be an advantageous process to plants for maximizing pollination and limiting hybridization. Beetle pollinators also benefit from the phenomenon.

INTRODUCTION

Aroids have been admired and cultivated for their beauty, variety, and unique form for years. Now, scientists are studying them for another fascinating quality: their amazing capacity to produce heat. Lamarck (1778) was the first to describe thermogenesis when he gave an account of the ability of *Arum italicum* Miller to raise the temperature of its inflorescence, although it wasn't until 1987 that the compound responsible for triggering this phenomenon was isolated and identified as salicylic acid (Raskin et al., 1987). Researchers worked for many years testing theories about the purposes of thermogenesis and acquiring the data that led to our present understanding of the physiology of the process. The following is a brief overview of the history behind our knowledge of thermogenesis, how it occurs in various aroids, and the future areas of research that are unfolding in light of this knowledge.

THE PROCESS OF THERMOGENESIS

Thermogenesis, the metabolic process of generating heat, has been observed in the inflorescences of several diverse families of plants. These include the Annonaceae, Araceae, Arecaceae, Aristolochiaceae, Cycadaceae, Cyclanthaceae, and Nymphaeaceae (Raskin et al., 1987). Three of these families are closely related monocots: the cosmopolitan Araceae; the pantropical Arecaceae; and the strictly neotropical Cyclanthaceae (Hutchinson, 1969; Cronquist, 1988; Gottsberger, 1990). However, thermogenesis has been most widely studied in the Araceae, where it is found to occur in many genera (Meeuse, 1975; Robacker et al., 1988; Raskin, 1992).

The characteristic inflorescence of the Araceae, the spathe and spadix, is either bisexual, or unisexual with male and female flowers segregated into distinct zones. The specific floral arrangement of each spadix allows pollination processes to operate on a level higher than that of the individual flower because the whole inflorescence, therefore, can act in thermogenic synchrony (Beach, 1986). Early researchers studying thermogenesis in aroids noted that the sequence and location of warmth are very precise, both in duration and degree of heating. In addition, the various sequences are consistent, and distinct to each species (Kraus, 1896; Leick, 1915; Schmucker, 1925).

Leick (1915) concluded that there are four general patterns of thermogenesis demonstrated by the genera *Monstera, Philodendron, Colocasia,* and *Arum.* He considered the genus *Monstera* to have the most primitive system of thermogenesis because he found that this genus follows a fairly simple pattern of moderate heat production. The inflorescence in the Monsteroideae is unisexual, i.e. all the flowers are similar and have both male and female parts. The spadix heats up on three consecutive days, but the amount of heat produced is never more than a few degrees nor is it generated for more than a few hours in the afternoon and early evening. On the first day the middle and base of the spadix are the warmest. On the second day the maximum amount of heat is at the apex, however, this is barely warmer than the rest of the spadix. During the peak warmth this day, the anthers open. The third day brings one last warm period that is much cooler than the previous ones. The spadix is always cool during the night and in no way does the spathe enclose the spadix.

Another example of thermogenesis that is simple in sequence, but extreme in length and degree of heating, is found in the genus *Symplocarpus.* In this genus the whole spadix, having hermaphroditic flowers, heats up all at once. The spadix may generate heat steadily for as long as two weeks and produce enough heat to raise the temperature of the spadix 35°C above the surrounding air temperature (ambient). During this time the flowers mature, attract pollinators, and are fertilized. All of this takes place in the winter in temperate climates, sometimes with snow on the ground (Meeuse, 1975).

Leick's second pattern of thermogenesis was thoroughly studied by Nagy *et al.* (1972) and described by Gottsberger & Silberbauer-Gottsberger (1991) for *Philodendron selloum* K. Koch. This species' inflorescence is arranged with the fertile male flowers at the distal end (toward the apex) of the spadix, then a region of sterile male flowers (staminodia) situated between the fertile male flowers and the female flowers, and the fertile female flowers forming near the base of the spadix. Anthesis (the maturation of the inflorescence) begins in the early evening as the spathe opens to reveal staminodia as warm as 45°C. The staminodia produce and release odors that are effectively dispersed (through volatization) and serve to attract, specifically, *Erioscelis emarginata* Mannerheim, a scarab beetle. Beetles enter the floral chamber (the larger "kettle" surrounding the receptive female flowers) formed by the enveloping spathe. They mate, eat pollen and staminodia, and lick sticky exudate from the stigma, then rest. Twenty-four hours later the spathe opens slightly, leaving only a narrow opening through which the beetles can squeeze out. The spadix begins to cool toward evening and the beetles leave. At that time the male flowers are ripe and extrude copious amounts of pollen that adheres to the bodies of the escaping beetles. In the evening hours they fly away, but soon they are attracted to other *P. selloum* inflorescenses just entering the anthesis phase. This time when the beetles enter the floral chamber, they are laden with the pollen of the inflorescence visited the night before and proceed to pollinate the fertile female flowers of the new inflorescence.

A more intricate process of thermogenesis was observed in the genus *Colocasia.* The periods of heat production may be as many as five, and the amount of heat produced may raise the temperature of the spadix many degrees above ambient. The exact sequence and intensity are apparently contingent on the temperature of the surrounding environment of the plant. The genus produces a bisexual spadix with an infertile 'appendix' forming at the apex, male flowers in the middle, and female flowers near the base. The first warming period involves mainly the sterile, appendicular region which gets very warm, and the female, basal region which heats only moderately. The anthers mature during a cooler second or third warming period. Maximum heat is always produced in the mid-afternoon. Cooler temperatures in the environment lessen the amount of heat produced, while higher temperatures elevate it. Cooler temperatures also increase the total number of warming periods, thus possibly maximizing the amount of time the plant is attractive to pollinators that may be less active due to the cooler weather (Hoppe, 1879; Leick, 1915).

The most complex process of thermogenesis is typified by the genus *Arum,* the inflorescences of which are well-known as arum lilies. The spadices in this genus are divided into four distinct zones. From the apical end to the base these are: an appendix; then a cluster of bristly staminodia; below them the male flowers, followed by another ring of bristly staminodia; and the female flowers at the base. On the day of anthesis, the appendix heats up and disperses odors drawing a multitude of insects. The precise odor in many aroids following this general pattern of thermogenesis is specific to each species, and frequently attracts a particular species or family of insect, usually a beetle, fly, gnat, bee, or wasp. The odors produced by an inflorescence may change in the course of flowering, initially they awaken an urge to feed in the potential pollinators, and later arouse the desire to mate (Robacker et al., 1988; Diamond, 1989). Landing on the spadix and crawling inside the floral chamber, insects find all surfaces covered with slippery oil. While this alone may prevent them from exiting the inflorescence, the bristly staminodes form a bar-like barrier to further discourage escape. The heating of the appendix (and thus the period of attraction) is not long, but it is usually intense, producing temperatures well above ambient, and it occurs in the late morning or early afternoon when many insects are out foraging. Soon the spadix cools and the spathe tightens around the spadix preventing the insects' escape. In the evening the female flowers enter a period of thermogenesis which moderately warms the floral chamber and encourages the insects to remain active. All night they remain in the floral chamber feeding, and becoming covered with the sticky fluid produced by the stigmas. By the next day, the bristles have wilted somewhat, the surfaces are not so slippery, the male flowers have matured, and the inflorescence is cool. The insects leave, but first must crawl through the male flowers where they acquire a coating of pollen that they will carry to the next inflorescence.

Other researchers have given detailed accounts of the capacity for thermogenesis in additional species. Van der Pijl (1937) described the heating sequences in species of *Amorphophallus,* and El-Din (1968) studied *Schizocasia portei* Schott (now synonymous with *Alocasia portei* Becc. ex Engl.). Meeuse & Buggeln (1969) tested the effects of several environmental factors on *Sauromatum guttatum* Schott; and the process of thermogenesis in *Symplocarpus foetidus* (L.) Nutt. was described by Camazine & Niklas (1984) and Knutson (1972a, 1972b, 1974). Meeuse (1975) investigated a wide range of aroid genera. Leick (1915) suggested that the well-defined, "step-wise" pattern in which thermogenesis proceeds is evidence for the close taxonomic relationship between thermogenic species.

Hoping to find out what precipitates thermogenesis, early researchers studied the effects of light and dark on the inception of the process (Schmucker, 1925; van der Pijl, 1937; Matile, 1958; Meeuse & Buggeln, 1969) and its hormonal control (Buggeln & Meeuse, 1971). Many experiments were conducted on aroid inflorescences regulating the wavelengths of light and the length of time plants were exposed to light and dark. These experiments determined that it is the male flower primordia that are stimulated by a certain sequence of light and dark, particular to each species, that activates the heating of the inflorescence (van Herk, 1937a, 1937b, 1937c; Meeuse & Buggeln, 1969). Van Herk (1937b) suggested that the male flower primordia, thus stimulated, produce an unknown (at that time) hormone, that he named "calorigen," that triggers the heating process.

PHYSIOLOGY OF THERMOGENESIS

In the last few decades, scientists have worked hard to decipher the chemical identity of the elusive hormone, "calorigen," and much progress has been made in understanding the physiology of thermogenesis. The fact that production of heat in the inflorescence is a respiratory event was acknowledged even in the nineteenth century as reported by Kraus (1896). Nagy et al. (1972) showed that metabolic respiration in some aroids, measured by rate of oxygen consumption, approaches the same rate as that of hovering hummingbirds and sphinx moths. The object, of course, of this high rate of respiration in plants is to produce heat, rather than to produce ATP (as animals do) that provides the energy for rapid muscle movement (Meeuse, 1966). To accomplish this tremendous increase in metabolism the mitochondria in the inflorescence switch to an electron transport pathway (a part of the respiration process) known as the "cyanide resistant pathway" (Meeuse, 1975). This respiratory pathway is found exclusively in plant mitochondria although it is similar to the cyanide resistant pathway known in animals (Raskin et al., 1989). Bendall (1958) measured cytochromes (critical components of the electron transport system) during stages of spadix development in *Arum maculatum* L., and ap Rees et al. (1976) determined pathways of carbohydrate oxidation in the same species. Bendall (1958) determined that mature aroid spadices contain elevated amounts of cytochrome B_7. However, all of the cytochromes and the complete oxidation reactions involved have not been fully determined yet. There is also an increase in the number of mitochondria per cell in the inflorescence, just prior to the onset of thermogenesis (Aked, 1989). Raskin et al. (1990) measured the levels of salicylic acid found in various reproductive structures of thermogenic taxa and various tissues of non-thermogenic taxa.

After decades of research Raskin et al. (1987, 1989) published the results of studies that determined that salicylic acid is the triggering substance ("calorigen") for thermogenesis. Salicylic acid is also responsible for initiating the production of odoriferous chemicals and unfolding the spathe (Robacker et al., 1988).

Thermogenesis is fueled by quantities of starch and lipids (oils) in the spadix tissues of all thermogenic plants (van der Pijl, 1937; Walker *et al.,* 1983; Tang *et al.,* 1987; Robacker *et al.,* 1988; Aked, 1989; Gottsberger, 1990). Walker *et al.* (1983) found that during heat production in *Philodendron selloum* K. Koch respiration was fueled with lipids, solely, using mitochondrial β-oxidation (normally occurring in animal tissues) rather than glyoxysomal β-oxidation (the usual method for plant tissues). It is evident that the lipid fuels are stored close to the site of thermogenesis and not transported from other plant tissues. One exception to this is *Symplocarpus foetidus* (L.) Nutt., the eastern skunk cabbage. This plant uses tremendous quantities of starch, stored in its large roots, to maintain higher than ambient temperatures for long periods, sometimes melting several inches of snow (Small, 1959; Knutson, 1972a, 1972b, 1974).

ECOLOGICAL ASPECTS

Originally, it was suggested that the heat of thermogenesis helped to volatize, and thus disperse, the odor-producing chemicals that attract pollinators. The odors produced by many thermogenic aroids are exceedingly repugnant to humans, being those associated with dung and rotting flesh. These odors combined with the fleshy colors of the inflorescences are, however, highly attractive to carrion and dung beetles, and of course some of the odors produced are sweet or spicy (Kraus, 1896; van der Pijl, 1937; van Herk, 1937a, 1937b; Matile, 1958; Smith & Meeuse, 1966; Meeuse, 1966, 1975; Moodie, 1975; Robacker et al., 1988; Diamond, 1989; Weiss, 1989). Many of these odoriferous chemicals have been isolated and analyzed, some of which are skatole, putrescine, ammonia (Diamond, 1989), amines, indole (Camazine & Niklas, 1984), and cadaverine (Smith & Meeuse, 1966). Three chemical compounds (diethylamine,1,6-hexanediamine, and 1,2-propanediamine) isolated with gas chromatography by Smith & Meeuse (1966), had not been reported from any higher plants previously. All of these chemicals and compounds are effectively dispersed by heat, because they are quite volatile (Moodie, 1975). In spite of this, researchers doubted that the attraction of pollinators was the sole purpose of thermogenesis because the production of heat is so energy-expensive to the plant, and most of these species can reproduce vegetatively anyway. However, as more studies were done it became apparent that the exact chemical composition, thus the intensity, quality, and essence of the attractive odors, change minute by minute and from place to place between male, female, and sterile parts of the inflorescence. These changes are synchronized, perfectly and specifically, to effect optimal pollination for each species. Furthermore, El-Din (1968), working with *Schizocasia portei* Schott, isolated only one odor-producing compound and suggested that because it is unusual to find only one substance present, it may signify a high pollinator specificity. Such specificity implies a process with a result that is physiologically profitable to the plant species in spite of the cost.

The indirect advantage of having such a precise process of thermogenesis may be the production of genetically variable seed achieved with the increase in cross pollination brought about by the process (Robacker *et al.*, 1988). Plants that grow from this seed will have a greater ability to adapt to changing environmental conditions and thus survive when a species lacking genetic variability may perish.

The precision of pollinator attraction and flowering sequence may also serve to preserve the integrity of a species. Sometimes, the timing of the sequence of anthesis effectively prohibits hybridization because each species attracts only pollinators that have visited other individuals of the same species, therefore carrying only the same species' pollen. This is especially important in circumstances when hybridization is not only possible but quite likely (due to two or more closely related taxa in immediate proximity of one another) without some means of limitation (Robacker *et al.*, 1988; Weiss, 1989; Gottsberger, 1989, 1990). Self-fertilization, which limits the genetic variability of a species, is usually prevented by the process of protogyny, meaning reproduction in which the sequencing of processes is arranged so that the female flowers mature first and are fertilized before the male flowers mature, and all thermogenetic aroids are protogynous (van der Pijl, 1937). When hybridization and/or self-fertilization are prevented, then pollination by another individual of the same species is important. The highly attractive thermogenic inflorescence enables species-specific pollinators to find another mature inflorescence of the same species especially where individuals of a species may be found far apart, as in much of the tropical rainforest or on dry savannas inhabited by such species as *Philodendron selloum* (Gottsberger, 1986).

Thermogenesis is beneficial to the insect pollinator, too. The warmth of thermogenesis and shelter of the floral structure supply an attractive place for insects to rest, copulate, and remain safe from predators, as well as providing nutritious food for them (Moodie, 1975; Robacker et al., 1988; Gottsberger, 1990).

At least one aroid, *Symplocarpus foetidus,* maintains a regulated, sustained thermogenesis allowing the plant to grow and flower at the coldest time of the year when there is little competition for either the plant or its pollinators. This plant is able to sustain a constant temperature in the inflorescence regardless of fluctuations in the ambient air temperature (Moodie, 1976; Robacker *et al.*, 1988; Camazine & Niklas, 1984; Weiss, 1989).

FUTURE CONSIDERATIONS

Everything that has been discovered about the process of thermogenesis, including the determination of the role of salicylic acid, still does not answer all the questions that researchers have concerning this phenomenon. Instead, new questions have been raised (Raskin *et al.*, 1989; Raskin, 1992). It is known that cyanide resistant respiration accompanied by heat production occurs in ripening fruit (Aked, 1989), particularly mangoes, and in plants adapting to frost. However, it is not known if salicylic acid is present or if thermogenesis is occurring in these instances (Kumar *et al.*, 1990). Salicylic acid has been shown to stimulate both flowering in duckweed (Ben-Tal & Cleland, 1982), and the biosynthesis of ethylene, a hormone that promotes fruit ripening (Weiss, 1989). It has been found that salicylic acid induces a systematic acquired resistance to fungal and viral infections in cucumbers (Metraux *et al.*, 1990), and a similar response by tobacco to viral infection was observed by Malamy *et al.* (1990) and Yalpani *et al.* (1993). These findings, coupled with the role of thermogenesis in the pollination of flowers, suggest that salicylic acid may play an important part in the signal transduction pathways of plants (Raskin, 1992; Yalpani *et al.*, 1993). If salicylic acid's function as a plant hormone includes the capability of not only triggering cyanide resistant respiration, but also, switching metabolism back to ordinary respiration, then it may prove to be a critical, as well as versatile, regulatory factor in both thermogenic and nonthermogenic plants (Weiss, 1989; Raskin *et al.*, 1989; Malamy *et al.*, 1990).

CONCLUSIONS

Researchers have not yet reached a complete understanding of the ecological role and physiological mechanism of thermogenesis. The phenomenon proves to be a complex process found in several, diverse taxa. More taxa capable of thermogenesis will probably be discovered, especially in the tropical rainforests of the world. The precision and synchronicity with which thermogenesis proceeds gives evidence to a highly evolved system of pollination. Further research on thermogenic plants will reveal new information about the regulation of plant metabolism and response, as well as clarify the phylogenetic relationships and processes of evolution that have taken place, particularly in floral development. Clearly the thermogenic aroids have contributed tremendously to the wealth of scientific knowledge.

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Anthurium veitchii Masters growing at Joseph Fondeur's Tropical Paradise Nursery in Davie, Florida. Note fused upper leaf. Photo by Jim Donovan.